EFFECT OF FOREST MANAGEMENT ON THE DIVERSITY AND COMPOSITION OF UNDERSTORY VEGETATION, BUTTERFLY (LEPIDOPTERA) AND CARABID BEETLE (COLEOPTERA: CARABIDAE) ASSEMBLAGES IN JACK PINE (*PINUS BANKSIANA*) FORESTS IN SOUTHEASTERN MANITOBA

By

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

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Department of Entomology
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ABSTRACT

The health of biological communities may be affected by forest management practices. The influence of reforestation strategies on understory vegetation, butterfly and carabid beetle assemblages was examined. Sampling was conducted in planted and naturally regenerating forests of 15, 25, 35 and 50 years of age. In addition, carabid beetle data were compared to those gathered in the same sites in 1991 – 1994 to assess how well temporal changes were predicted by the previous experimental design. Assemblage composition of plant and carabid beetle assemblages showed age-related trends and this related to canopy density. These communities also responded to effects of forest management; assemblages of 15-year-old planted sites tended to be distinct from natural sites. The use of butterflies as indicators in this study was hampered by small sample sizes. The original chronosequence study design predicted the current study results, validating the use of chronosequence studies when examining carabid assemblages in forests.

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1. INTRODUCTION

Disturbance is an integral part of healthy boreal forest ecosystem functioning (Barnes et al. 1998). Historically, stand clearing fire was a common occurrence in the boreal forest region, especially in jack pine forests (Heinselman 1973). Constituent flora and fauna of such forests are well adapted to this disturbance which promotes significant habitat heterogeneity over the landscape (Esseen et al. 1997). The degree to which forest management emulates the key features of natural disturbance and regeneration will potentially determine the long-term health of the biotic community (Haila et al. 1994). However, important structural components found in natural forests are often lost or altered in managed forests (Esseen et al. 1997). For example, the amount of dead woody debris in harvested and planted stands is reduced compared to natural forests. Structural changes, in turn, may affect the biological community (Esseen et al. 1997).

Recently, the forest industry has determined that forest health must be a priority, and monitoring of this is being instituted (e.g. Canadian Council of Forest Ministers 2000). A healthy managed forest may be considered to be one where a completely integrated community of flora and fauna exists within the physical environment (Monnig and Byler 1992). This state requires the presence of a natural range of species and genetic richness (Noss 1993). Because of our inadequate knowledge about how ecosystems work, we must use naturalness as a proxy for forest health (Spence et al. 1999); diversity and quality of the constituent biotic community in a managed forest should match that of a natural stand of a similar age or severity of disturbance.

The complexity inherent in an ecosystem precludes a complete evaluation of its state. Therefore, indicators must be selected to provide information about ecosystem

quality that cannot be measured directly (Landres et al. 1988). Measurable characteristics must be chosen that will reliably reflect the health or quality of a defined area and convey information about ecological trends (Ferris and Humphrey 1999).

Various biota have been employed as ecological indicators (Ferris and Humphrey 1999). Insects and other arthropod groups seem to be ideal biological indicators because of their ubiquitous distribution, abundance and importance in various ecological functions (Rosenberg et al. 1986). Insects often respond in a predictable manner to alterations in their environment (Rosenberg et al. 1986) and this characteristic response to perturbation suggests their utility as ecological indicators. The response of understory plant communities can also provide valuable information regarding forest conditions as they have a close relationship to both soil and microclimate conditions, as well as providing habitat or food for local fauna (Ferris and Humphrey 1999)

The objective of this study was to evaluate the influence of reforestation strategies on the local biological community in forests of different successional stages. Two insect groups, butterflies and carabid beetles, were selected as indicator groups to evaluate the effects of these influences. In addition, the understory plant community was examined for response to regeneration strategy.

This thesis is organized in paper style. The response of understory vegetation, butterflies and carabid beetles to forest alterations associated with regeneration type and with forest age are examined in separate chapters.

2. Literature Review

Boreal Forest

The boreal zone is extensive and occupies approximately 30% of the Canadian mainland (Danks and Footit 1989). It is bounded by grasslands and deciduous parkland to the south and sub-arctic taiga to the north (Danks and Footit 1989; Scott 1995). The boreal forest zone is characterized by continuous closed forests, composed primarily of conifers (Rowe 1972). Throughout the boreal zone the constituent vegetation is remarkably uniform, and pines are commonly associated with drier sites (Wein and MacLean 1983; Danks and Footit 1989). Jack pine (*Pinus banksiana* Lamb.) populates these drier sites in the central and eastern boreal region of Canada (Wein and MacLean 1983).

Boreal conifer forests, especially pine stands, are characterized by large, crown fires (Johnson 1992). This occurs for a number of reasons including high flammability of conifers, large fuel loads, and weather conditions conducive to ignition (Van Wagner 1983; Johnson 1992). Fire, in turn, plays an essential role in the ecology of pine forests, and jack pine is particularly well suited to regenerating after fire (Cayford and McRae 1983). Jack pine cones are serotinous, and typically do not open until exposed to high temperatures, thus fire stimulates seed dispersal (Cayford and McRae 1983). In addition to reducing competition, severe fire exposes mineral soil which creates an ideal seedbed for germination of the newly dispersed jack pine seeds (Cayford and McRae 1983; Chrosciewicz 1990). In the regions near Manitoba, intervals between fire in jack pine forests are estimated to be 50–100 years before European settlement, therefore, fire

would have played a key role in the ecology of jack pine communities (Heinselman 1973).

Effects of Forest Management

Forest management practices include harvesting, stand management and reforestation techniques, all of which may alter the structure and composition of the forest ecosystem at the stand level (Hansen et al. 1991; Smith et al. 1997), and influence spatial patterns and stand processes (Esseen et al. 1997). These effects have the potential to have an influence on local biota.

A patchy and diverse forest structure is characteristic of natural post-fire regeneration in the boreal zone (Nilsson et al. 2001). Structurally, both vertical and horizontal spatial patterns may be altered by reforestation, which tends to decrease the heterogeneity of a stand (Hansen et al. 1991). A reduction in understory development due to a lack of shrubs or tree saplings may be evident in managed stands (Esseen et al. 1997), reducing vertical diversity. Changes in vertical structure may affect the biological community, as this element has been related to diversity in some insect groups (Murdoch et al. 1972). Changes in horizontal diversity, such as the reduction of patchiness, may also affect biological diversity (Esseen et al. 1997). Certain invertebrate species depend upon forest gaps for protection from wind and provision of a warm microclimate (Nilsson et al. 2001). Presumably, certain plant species also require glades to meet their light requirements.

Understory plant diversity may be altered by stand management and reforestation techniques. Higher vascular plant diversity may be found in young post-harvest forest

stands than in their post-fire counterparts (Reich et al. 2001). However, qualitative differences in early successional ground level flora may also exist; burned stands tend to be occupied by unique, colonizing species (Abrams and Dickmann 1982). In addition, some understory species are favoured by management and may increase in abundance after harvest, at times out-competing other plant species (Esseen et al. 1997). Floral diversity may consequently influence the faunal community due to both structural and trophic effects (Vane-Wright 1978; Bell et al. 2001).

Dead wood in the form of fallen logs or standing dead wood in a forest stand is markedly affected by harvest techniques. Harvested sites tend to have significantly less coarse woody debris than their naturally regenerating counterparts. Pedlar et al. (2002) found that newly clearcut sites had less than one third of the amount of coarse woody debris of a newly burned stand. The amount of woody debris that remains will be affected by different harvesting strategies, with methods that leave slash in situ contributing more to the organic legacy of the site (Keenan and Kimmons 1993). The quality of woody debris also differs between managed and natural forests. Woody debris in harvested sites tends to be smaller in diameter, whereas burned sites support a variety of sizes of debris (Similä et al. 2002).

The presence of dead wood may influence the long-term health of the ecosystem (Esseen et al. 1997). Fallen woody debris provides an essential substrate for the germination of various plants including later successional tree seedlings, such as white spruce (Lee and Sturgess 2001; Stewart et al. 2001). For animals it provides nesting sites, food sources, oviposition media and sites for protection from predators and environmental fluctuations (Goulet 1974; Samuelsson et al. 1994). It also provides a

long-term source of organic material and nutrients in the boreal ecosystem, and eventually becomes a vital soil component (Siitonen 2001). The magnitude of the importance of coarse woody debris in a boreal forest stand is well illustrated by a Finnish study, where at least 4,000 to 5,000 species are dependant on dead wood habitat (Siitonen 2001). A reduction in this ecosystem component is thought to have negatively affected more species than any other consequence of forest management (Esseen et al. 1997).

Alteration in litter quality is another consequence of reforestation strategies. Commercially undesirable boreal tree species, such as hardwoods, have often been eliminated from managed softwood stands (Esseen et al. 1997; Koivula et al. 1999). This management practice may affect litter quality. The litter layer provides a favourable habitat for ground dwelling fauna by reducing temperature fluctuations, maintaining moisture levels and providing refuge from predation (Uetz 1975; Koivula et al. 1999). With increasing litter complexity and depth, a greater selection of niche space is available and more species may inhabit this layer (Uetz 1975; Koivula et al. 1999). In coniferous forests, areas with plentiful deciduous litter are good source habitats for certain ground dwelling insects (Haila et al. 1994). Deciduous litter also differs chemically and nutritionally from conifer litter (Barnes et al. 1998), therefore the maintenance of a natural proportion of leaf litter, especially in the predominantly coniferous boreal forest region, is likely of some trophic importance.

Evaluating the Effects of Forest Management

Clearly, assessing the various potential ecological impacts of management strategies on forested ecosystems is a complicated issue. Tools must be selected to allow

the evaluation of the effects of these activities. Changes in environmental variables caused by management strategies can lead to changes in the composition of biological communities (Spellerberg 1993), and these changes in the biotic community or its physical environment can be measured. Various environmental indices, including diversity measures and compositional analysis are well documented (Magurran 1988; Spellerberg 1993; Legendre and Legendre 1998).

There are three aspects of ecosystem diversity that can provide an indication of the overall health of the system under study: compositional, structural and functional (Schulze and Mooney 1994; Ferris and Humphrey 1999). Compositional diversity refers to the biological diversity of the system and considers the variety and identity of constituent taxa (Noss 1990). Structural diversity refers to the physical architecture or pattern of the area under study (Ferris and Humphrey 1999). Ecosystem processes such as nutrient cycling, decomposition, nitrogen fixation and microhabitat turnover are examples of functional diversity (Franklin 1988; Ferris and Humphrey 1999).

Although all three components of ecosystem diversity are essential for ecosystem functionality, it is not practical to measure all of the aspects of any single diversity component, nor is it reasonable to measure aspects of all three. An indicator or a group of indicators must be chosen to serve as a surrogate measure of overall ecosystem diversity (Lindenmayer et al. 2000). Regardless of the choice of indicator type, certain criteria must be met. An indicator must be ecologically significant, reliable and reasonable to measure in terms of cost and time (Ferris and Humphrey 1999). Practically, the indicator should be one that can be related to forest management practices (Ferris and Humphrey 1999) so that resulting recommendations can be implemented easily. Indicators must be

carefully chosen for the specific ecosystem in question, as the selection of an unsuitable indicator may give erroneous results leading to inappropriate management initiatives. These resultant management strategies could in turn irreparably alter the ecosystem under study (Lindenmayer et al. 2000).

Typically, measurement of biodiversity in the forest setting has focused on either compositional or structural diversity, as they are more straightforward to assess than functional diversity (Ferris and Humphrey 1999). The status of functional processes is often inferred from other diversity measures (Ferris and Humphrey 1999).

Structure-based indicators at the stand level include vertical stand structure, number of retained old trees, volume and quality of downed logs, amount and quality of standing dead wood and stand complexity (Ferris-Kaan et al. 1998; Ferris and Humphrey 1999; Lindenmayer et al. 2000; Nilsson et al. 2001). Careful surveys of a variety of structural elements may elicit considerable information about the diversity of specialized niches available for colonization. Further, the measurements of key habitat structures, such as downed logs and standing dead wood, may provide insight into potential habitat available for rare species; studies in the Swedish boreal forest indicate that a high percentage of threatened species depend upon these elements for survival (Berg et al. 1994).

Compositional diversity is commonly measured by selecting a taxon or group that is thought to reflect the impact of disturbance on the forest type being evaluated (Holloway and Stork 1991). Compositional indicators used in forests include floristic, fungal, invertebrate and vertebrate taxa (Ferris and Humphrey 1999). The advantage to using these indicators is that they can integrate the cumulative effect of a number of

different ecosystem structures and functions, and may reflect the state of the ecosystem over time (Rosenberg et al. 1986). For example, herbivorous insects such as butterflies integrate such components as light conditions, moisture, and growth cycles of specific plants. Therefore, changes in butterfly assemblages or abundance may indicate a change in one or more of these elements (Brown 1997).

Choosing a Compositional Indicator Group

In general, the compositional group chosen for analysis needs to have a wide distribution but specific temporal or spatial habitat requirements (Holloway and Stork 1991). It must also reflect some ecosystem component (Holloway and Stork 1991). Biological sensitivity to disturbance is essential and it must show a measurable and predictable response to the ecosystem perturbation under study (Holloway and Stork 1991).

Either taxonomic or functional groups, or a combination of the two, may be used as indicators. Taxonomic indicator groups may be chosen for analysis at the species, genus or family level (McGeoch 1998). Functional groups, including guilds, communities and trophic groups, may also be employed as indicators (McGeoch 1998). In the forest environment, diversity at the species level seems to be most commonly used to investigate ecosystem effects (e.g.Niemelä et al. 1993; Beaudry et al. 1997; Lewis 2001; Koivula and Niemelä 2002; Koivula et al. 2002; Similä et al. 2003). The collection of species level data is advocated (Danks 1996) because different species within a higher taxonomic level may show diverse responses to ecosystem change (Jonsson and Jonsell 1999). This information may be lost when a study uses higher taxonomic groups.

Compositional indicators

Understory vegetation

Fire ecology

Understory plant species in forest types that are prone to fire have characteristic strategies that allow them to persist in these habitats; these strategies include avoidance of damage and early post-fire colonization (Barnes et al. 1998). Regenerative organs of some species, for example shrubs such as *Arctostaphylos uva-ursi* and *Vaccinium* spp., may be buried beneath the soil surface, allowing them to escape damage if the fire does not burn the forest floor deeply (Rowe 1983; Schimmel and Granström 1996; Barnes et al. 1998). Other species are able to colonize a newly burned area rapidly. Species such as *Ceratodon purpureus* and *Epilobium angustifolium* disperse via wind borne seeds, and others, such as *Prunus pensylvanica* and *Symphoricarpos* spp., by producing hard-coated seeds that remain dormant in the soil until conditions are suitable (Rowe 1983; Barnes et al. 1998).

Mechanisms of post-fire regeneration in the understory depend upon the depth of the fire damage and the depth of the regenerative structures (Schimmel and Granström 1996). After more superficial fires, regeneration from vegetative structures is most prevalent, whereas after fires burning the forest floor more deeply, establishment from seed is more common (Ahlgren 1960; Schimmel and Granström 1996). After especially deep fires, where most of the organic layer is removed, the soil seed bank is severely diminished and colonization by wind-dispersing species prevails (Schimmel and Granström 1996).

Response to forest succession and management

Many factors influence the response of the understory vegetation community to fire, including, pre-fire conditions, fire season, seed supply, fire intensity, nutrient availability, surface geology, microclimate and competition (Ahlgren 1960; Chipman and Johnson 2002). After an initial increase in species richness and diversity after fire, a reduction in understory diversity is generally evident as the canopy closes and basal density increases (Pitkänen S. 2001; Chipman and Johnson 2002; Hunt et al. 2003; Purdon et al. 2004). Species evenness tends to decrease with forest age, as the abundance of non-dominant species declines (de Grandpré et al. 1993). In addition, the composition of the understory community changes with succession; some species disappear as soon as the canopy closes, while others appear (de Grandpré et al. 1993).

Several studies compare the relative effects of harvest and fire on the boreal forest understory although none examine the influence of regeneration type. Differences in species richness between disturbance types are found in some components of understory vegetation in forests regenerating naturally after differing disturbance. Higher vascular plant species richness is found in burned than in harvested jack pine forests for the first five years after disturbance (Abrams and Dickmann 1982). Although species diversity is similar immediately after disturbance, it decreases more rapidly in the first six years after harvest than it does after fire (Abrams and Dickmann 1982). In jack pine forests ranging in age from 25 to 40 years, higher vascular plant species richness and diversity are found in harvested than burned stands (Reich et al. 2001). It is not clear whether these differences in findings are due to differences in forest age or are contradictory results. In later stages of succession, no differences in vascular plant diversity are found between

disturbance types (Reich et al. 2001), therefore, management induced differences in the understory may be mitigated by time.

Other types of understory vegetation, such as shrubs and moss, appear less sensitive to differing disturbance type. The shrub layer either shows either no difference between disturbance types, or shows less response to disturbance type than the ground layer vascular plants (Johnston and Elliott 1996). In addition, no difference in moss diversity is found between disturbance types (Reich et al. 2001).

Understory community composition is influenced by disturbance type, especially in the initial few years of re-establishment. Typically, post-fire pioneer species colonize a newly burned site (Abrams and Dickmann 1982; Nguyen-Xuan et al. 2000). Burned sites may have especially distinctive communities in the initial years after disturbance. One study identifies 40 understory plant species, many of them rare, which are exclusive to newly burned sites, whereas only two species are exclusive to harvested sites (Abrams and Dickmann 1982). These compositional differences are primarily a result of a reduction in annual and biennial species in harvested forests (Abrams and Dickmann 1982). Although, much depends on fire severity, as damage to the seed bank or to vegetative buds may affect the species available to colonize the newly burned site, and post-fire nutrient availability may influence plant distribution (Ahlgren 1960; Schimmel and Granström 1996). In comparison, sites disturbed by harvest typically have more residual plant species, as some species are only partly destroyed by site preparation (Nguyen-Xuan et al. 2000; Pykälä 2004).

The post-harvest community though also depends on the severity of site preparation. Removal of organic material decreases the re-sprouting of residual species, and favours colonization by seed and spore producing species (Haeussler et al. 2002).

Butterflies

Biology

The primary factors influencing butterfly distribution are the availability of an adequate and appropriate food source for the larvae, as well as a source of nectar or other liquid for the adults (Ehrlich 1984). Butterfly species are almost exclusively phytophagous and most of their feeding occurs during the immature stage of development (Dempster 1983). Butterflies are well-recognized for displaying some degree of host-specificity. From a physiological point of view, the reliance on a certain type of plant for nutrition requires a metabolic adjustment by the insect to deal with the nutritional imbalance inherent in that specific plant (Ehrlich and Raven 1964). Angiosperms generally contain one or more secondary compounds (Harborne 1982), that deter most animals but facilitate nutrient uptake in host specific insects (Ehrlich and Raven 1964). Physiological adjustment to food plant chemistry makes it difficult for the insect to use other plant resources efficiently and therefore restricts its food sources (Ehrlich and Raven 1964). Individual species vary in the level of host-specificity that they exhibit as larvae; some species feed exclusively on one plant species, while others may feed on a small group of taxonomically and chemically related plant species (Lorkovic 1968 in Gilbert and Singer 1975; Howe 1975; Vane-Wright 1978). Yet other butterfly species

feed even more generally, using a number of unrelated plants as suitable food sources (Klassen et al. 1989 for examples).

While adult butterflies may not show the same degree of fidelity to host plants as larvae do, they do tend to exhibit some preferences (New 1997). Adult butterflies require liquid food and many species are exclusively nectar feeders. Some nectar feeding species do show a preference for certain kinds of flowers (Howe 1975). While it may be argued that adult butterflies are too mobile to be reliable indicators of habitat quality, flight activity of females tends to be focused primarily on food procurement and locating host plants for oviposition (Petersen 1954; Ehrlich 1984). Therefore the presence of female butterflies is likely to indicate the presence of larval host plants. Although the plant species providing nutrition to adult butterflies may differ from those exploited during the larval stage, these plants may occur in the same habitat (Ehrlich 1984).

If butterflies have specific host requirements, then a diverse butterfly assemblage in an ecosystem would be expected to be indicative of diverse flora. Some tropical forest biodiversity studies have reported a positive correlation between butterfly and plant species diversity at a range of spatial scales (Thomas and Mallorie 1985; Osborn et al. 1999). Others conclude that plant diversity does not influence butterfly diversity directly, but rather that the diversity of the two co-vary, likely responding to similar environmental factors (Hawkins and Porter 2003). Because several butterfly species may exploit the same larval food source, butterfly diversity may not perfectly correspond to the diversity of plants in a habitat (Vane-Wright 1978); nevertheless, assemblage diversity is likely to give a relative indication of the floral diversity of a stand.

Habitat selection by adult butterflies may also be influenced by the degree of canopy cover (Warren 1985). Different butterfly species in forested areas exhibit preferences for different levels of shade (Pollard 1977); the bulk of species are more common in the least shaded stands or those with open glades (Warren 1985). A few species, such as the Satyrinae, favour more heavily shaded, closed forests (Warren 1985; Rudolph and Ely 2000).

In forested areas, many butterfly species are typically found in open glades. Papilionidae and Pieridae especially tend to favour open habitats, where their thermal and nectar requirements are met (Rudolph and Ely 2000). These species may also require gaps for mate location (Warren 1985). The quality of the gaps may be influenced not only by floristic quality but also by the availability of low vegetation, which serves to provide shelter in windy conditions (Pollard and Yates 1993). Although species showing an affinity for gaps or more open canopy conditions do tend to be more mobile generalist species (Hamer et al. 2003), their presence does provide important information regarding the degree of canopy closure, the degree of forest patchiness and the quality of the gaps present. Therefore, gap dependant species are important to consider in boreal forest health studies (Nilsson et al. 2001).

Species preferring more heavily shaded areas tend to be those with a more restricted distribution (Spitzer et al. 1997; Vu and Yuan 2003; Hamer et al. 2003). Species with restricted distribution generally have very precise habitat requirements and are inclined to be sedentary; therefore, they are affected most heavily by habitat disturbance or alteration in environmental quality (Kitahara and Fujii 1994; Warren et al.

2001). The presence or absence of these species will provide important information regarding the structural quality of managed forest ecosystems.

Sampling

Sampling techniques for butterflies include bait trapping and transect data collection (e.g. Kremen 1994; Elliott 1997). Two methods of transect sampling are identified, visual identification of species sighted on transect walks and hand collection (e.g. Pollard 1977; Elliott 1997). There are certain limitations to each of these techniques. Bait trapping biases the collection toward Nymphalidae (Kremen 1994). Field identification of butterflies to species is unreliable when species are similar (Pollard et al. 1975), and this is a concern in southeastern Manitoba where species of similar appearance such as some *Speyeria* sp., *Phyciodes* sp. and Hesperidae are found. Hand netting, while eliminating the drawbacks of the former strategies, is hindered in dense forest habitats. In addition, some butterflies are strong fliers, and so are difficult to catch by this method (Pollard and Yates 1993).

Response to forest succession and management

The butterfly community is not typically employed as an indicator of forest successional processes, however changes in the assemblage with forest age are recognized. An initial increase in both species richness and species diversity is found as forests age, followed by a decline in these diversity values as forests continue to age and the canopy closes (Elliott 1997). A turnover in species dominance is evident as the forest

ages, depending on the openness of the forest; shade preferring species such as *Enodia anthedon* (A.H. Clark) dominate in older, closed canopy forests (Elliott 1997).

The use of butterfly indicators to evaluate the health of managed forests is not well-documented in the boreal forest region. The sole boreal forest study that I have found that employed butterflies as indicators of habitat evaluated the effect of regeneration type (planted and natural regeneration) on butterfly diversity in jack pine forests (Elliott 1997). Elliott (1997) found a significant difference in species diversity in only the first of two study years; this difference was due to greater butterfly diversity in young, naturally regenerating jack pine stands than in plantations of a similar age. Species richness was influenced by stand age in the first year of study, with the number of species peaking in 15-year-old plantations and 25-year-old naturally regenerating stands. Of the environmental variables considered in this study, only mean light intensity explained the butterfly species present at a stand level. Beta diversity was found to differ significantly, with one of the similarity measures used, in the second study year. In this year, greater similarity was noted between planted stands, thus beta diversity was greater among natural stands. When the butterfly communities were examined more specifically, qualitative differences were noted. In forests up to 15-years after disturbance, the assemblage in naturally regenerating stands tended to be comprised primarily of host plant specialists. In contrast, the butterfly community in plantations was dominated by feeding generalists.

Butterflies have been used more frequently to investigate the effect of forest management in tropical environments (e.g. Willott et al. 2000; Stork et al. 2003). Logging in tropical forests tends to be selective (Lewis 2001). Selected trees are

removed, increasing the number of canopy gaps, in addition to causing local disturbance in understory vegetation (Wood and Gillman 1998). While the use of butterfly indicators in tropical forests does not directly support their use in boreal forest studies, these results can give some indication of the relative efficacy of the use of this invertebrate group in northern regions.

Results from these tropical forest studies have been mixed. The most variable results have been those for species richness and diversity measures. In different studies, species richness has been found to increase (Wood and Gillman 1998; Willott et al. 2000), decrease (Hill et al. 1995) or remain unchanged (Wood and Gillman 1998; Lewis 2001; Ghazoul 2002; Hamer et al. 2003) in selectively logged stands compared with unlogged stands. Similarly, in various studies, species diversity has been found to increase (Willott et al. 2000), decrease (Hill et al. 1995; Ghazoul 2002) or remain similar (Hamer et al. 2003) with logging disturbance. Finally, species evenness has been found to decrease (Hill et al. 1995) or remain unchanged (Willott et al. 2000) in logged stands.

A more consistent finding in tropical forest studies is a qualitative change in butterfly species assemblages with selective logging (Hill et al. 1995; Wood and Gillman 1998; Ghazoul 2002; Hamer et al. 2003). Characteristic species of undisturbed, climax tropical forest tended to be species with restricted habitat range (Hill et al. 1995; Hamer et al. 1997). Open habitat species, with more generalized distributions, had greater representation in more disturbed sites (Raguso and Llorente-Bousquets 1990; Willott et al. 2000; Hamer et al. 2003). Unlogged stands tended to have butterfly assemblages with greater taxonomic distinctiveness than their logged counterparts (Hill et al. 1995).

Carabid beetles

Biology

Carabid species are well-documented to have preferred ranges of microclimate. The most important parameters are light, temperature and humidity (Thiele 1977). These parameters are interrelated as denser canopy increases light absorption, moderates ground temperature and increases relative humidity (Oke 1987). The influence these interrelated parameters have on carabid diversity measures is well-documented. Canopy closure, as well as increased tree height and density, have all been found to correspond to decreased carabid diversity (Ings and Hartley 1999; Jukes et al. 2001; Koivula and Niemelä 2002; Koivula et al. 2002). Stands supporting a greater variety of environmental conditions tend to have a higher level of carabid species richness (Jukes et al. 2001).

Carabids demonstrate different magnitudes of optimal ranges for both temperature and moisture, with some species exhibiting quite narrow tolerance ranges (Thiele 1977). Carabid assemblages in forested environments are comprised of habitat generalists, forest generalists, and forest specialists (Niemelä et al. 1992a). The proportion of carabid species of each distribution type is expected to provide an indication of the degree of canopy closure or heterogeneity of a stand. For instance, homogeneous shade has been found to be unfavourable to forest specialist species (Jukes et al. 2001).

Carabids display sensitivity to forest floor structure, in particular to the presence and amount of deciduous leaf litter (Koivula et al. 1999). Structurally complex litter, such as deciduous litter, may influence ground biota by buffering temperature and moisture fluctuations, as well as offering protection from predation (Uetz 1979; Bultman and Uetz 1984; Koivula et al. 1999). Further, the structural complexity of deciduous litter, in

comparison to coniferous litter, may increase the number of available niches for both carabids and their prey items in a forest stand, as well as increase the ease of invertebrate movement within the litter layer (Koivula et al. 1999; Pearce et al. 2003). Carabid assemblage composition differs between deciduous and coniferous forests within a region (Pearce et al. 2003), and the addition of deciduous litter to a stand alters the carabid community by increasing the proportional abundance of some species (Koivula et al. 1999).

Relative abundance of certain carabid species is related to coarse woody debris of certain decay stages in particular habitats. For example, *Agonum gratiosum* (Mannerheim) is positively associated with the volume of newly fallen debris in mature deciduous stands, while in a clearcut habitat *Agonum retractum* LeConte is associated with volumes of intermediately decayed wood and *Pterostichus adstrictus* Eschscholtz, *Pterostichus pensylvanicus* LeConte and *Synuchus impunctatus* (Say) are associated with moderately decayed wood (Pearce et al. 2003). Dependence of certain species on coarse woody debris may be due in part to reproductive requirements, as *P. adstrictus* is known to require downed wood for oviposition (Goulet 1974). This finding seems to suggest that an estimate of the presence of a biologically adequate amount and quality of decaying wood could be made through the presence or absence of certain species in an assemblage. Realistically, it is more likely that the absence of certain carabid species, known to be dependant on coarse woody debris or snags, could indicate a forest stand lacking of dead wood.

It has also been documented that carabid assemblages vary with the understory plant community and its structure in forest ecosystems (Niemelä and Spence 1994;

Antvogel and Bonn 2001; Jukes et al. 2001). This is not likely to be a direct relationship for the most part as carabids are predominately predators. However, some granivores such as *Amara* and *Harpalus* species (Toft and Bilde 2002) may respond directly to vegetation to some degree. In practice, *Amara* and *Harpalus* species were found to be more prevalent in newly cut boreal mixed-woods and clearings (Šustek 1981; Spence et al. 1997), therefore they may be indicative of understory quality in newly disturbed stands. Overall, the relationship between carabids and vegetation likely illustrates a similar response to heterogeneity in microclimatic conditions (Antvogel and Bonn 2001). Regardless, a relatively diverse carabid fauna is likely to be associated with a relatively diverse flora.

Soil properties such as moisture, pH and compaction have been shown to affect carabid distribution (Paje and Mossakowski 1984; Baguette 1993; Antvogel and Bonn 2001). Carabid species demonstrate different optima with respect to soil moisture conditions, and different species show different ranges of tolerance to moisture variation (Thiele 1977). In laboratory experiments, most species from hygric sites demonstrated a preference for more moist conditions while those from more xeric sites either choose dry conditions or tolerate a range of conditions (Thiele 1977). As predicted from the laboratory experiments, soil moisture has been found to have an influence on carabid assemblages in natural environments; carabids demonstrate a strong response to moisture gradients even over the scale of a few meters (Antvogel and Bonn 2001). Chemical properties of soil, such as pH, also affect carabid distribution (Antvogel and Bonn 2001). In a laboratory setting, five of seven tested species demonstrated significant preference for pH that was similar to that of the soil on which they were collected (Paje and

Mossakowski 1984). Finally, a significant negative correlation between soil compactness and carabid species richness has been documented (Magura et al. 2003). Soil compactness may influence diversity by inhibiting oviposition and hibernation within the soil (Magura et al. 2003). Undoubtedly, the effects of these soil parameters are interrelated and do not influence carabid assemblages independently.

The influence of forest structure, especially as it relates to microclimate, not only affects the carabid community, but also affects their food source (Koivula and Niemelä 2002). Adult carabid species can be separated into three groups with respect to diet: phytophages, polyphagous predators and oligophagous predators (Thiele 1977). Oligophagous predators include the Cychrini, which feed on molluscs, and microarthropod specialists such as *Notiophilus,* which feed on collembola, mites and other microfauna (Hengeveld 1980a; Hengeveld 1980b; Toft and Bilde 2002). Adult carabids tend to supplement their habitual food items and even become scavengers when required (Toft and Bilde 2002), however larvae tend to be more exclusively carnivorous than adults and therefore are more restricted in their food range (Lövei and Sutherland 1996). In practice, carabid abundance has been found to be related to the abundance of prey items. *Calosoma sycophanta* (Linné) larvae are more abundant when gypsy moth populations are high than when there are few moths (Weseloh 1985). However, prey abundance has not been found to affect carabid diversity (Guillemain et al. 1997). Because of their broad feeding habits, carabids may not provide detailed information regarding the state of the food web; however, the number of individuals caught may respond to the abundance of species of lower trophic levels.

Specific evaluation of the carabid assemblage may provide an estimate of habitat quality. The presence of feeding specialists, for example Cychrini, may provide a measure of information regarding the recovery of the forest; they would not be expected to be able to thrive in a stand until the mollusc community, presumably relatively slow to colonize, has been re-established. The primary limitation to drawing conclusions based upon carabid feeding behaviour is that specialized feeding tends to be by preference and not obligation; carabids remain generally a polyphagous group (Toft and Bilde 2002).

It would be impossible to separate the influence of each of these parameters of forest structure on carabid assemblages. Regardless, it is evident that various components of forest structure affect the composition of local carabid assemblages. Using natural, healthy boreal forest stands as a standard, it should be possible to measure the relative cumulative ecosystem impacts of different forest management strategies.

Sampling

Methods for collecting carabid beetles include pitfall trapping, hand collection, heat extraction and litter washing (Greenslade 1964; Niemelä et al. 1988; Spence and Niemelä 1994; Butterfield 1997). Pitfall trapping is the commonest method for collecting carabid beetles in forest studies (e.g. Holliday 1992; Niemelä et al. 1993; Jukes et al. 2001; Pearce et al. 2003), however this technique has several drawbacks. Trap catch depends on both the population density and the activity level of the constituent community (Greenslade 1964). The activity level of the carabid community in turn may be influenced by weather, physical impedance of ground vegetation, and by the inherent behaviour of the species (Greenslade 1964). In addition, pitfall trapping is biased toward

the collection of larger bodied carabids (Spence and Niemelä 1994). However, pitfall trapping is preferred as it is convenient and cost effective, and is often the only available option (Greenslade 1964). Despite the limitations associated with this strategy, the use of continuous pitfall trapping is considered a relatively reliable method of sampling the carabid assemblage (Baars 1979).

Response to forest succession and management

In the boreal forest region, carabids have been used primarily to study the effects of stand clearing disturbance, with the focus on the influences of the subsequent succession on carabid assemblages. Carabid assemblages have been used to study the effect of fire, as well as to monitor the recovery of the faunal community. In newly burned sites, distinct carabid assemblages are found compared to those in unburned sites; the assemblages in burned stands tend to recover over the course of ten years (Richardson and Holliday 1982; Holliday 1992). Likewise, carabid assemblages and diversity measures have been used to study the effect of clearcut harvesting and subsequent succession in the boreal forest (Niemelä et al. 1993; Niemelä et al. 1994; Koivula et al. 2002). These post-harvest studies commonly show higher diversity in younger stands where the assemblage is composed of both open habitat and forest generalist species (Niemelä et al. 1993; Niemelä et al. 1994; Koivula et al. 2002). With increasing canopy closure, species diversity is generally found to decrease and the carabid assemblage changes with the recovery of forest specialists and reduction of open habitat species (Niemelä et al. 1993; Koivula and Niemelä 2002; Koivula et al. 2002).

Carabids have also been employed, albeit less often, to study the effects of various management strategies on boreal forest health. Comparing plantations with natural regeneration in jack pine stands in Manitoba, Lafrenière (1994) found that local diversity was similar among treatment types, although it was affected by the interaction of treatment type and stand age with one of two diversity indices in one of two study years. A trend of reduced beta diversity in plantations was also noted, but was significant in only one study year and with only one of the two tests used. The carabid assemblage in this study was found to change with stand age; as expected, open habitat species decreased with stand age concomitant with an increase in mature forest species. Differences in both carabid assemblages and environmental parameters were related to stand age rather than treatment type. Compositional differences between regeneration types appeared to have been primarily due to the presence of pyrophilous species in young, naturally regenerating stands.

Several studies in the boreal region have employed carabid assemblages to investigate the effects of forest management practices such as thinning (Koivula 2002), elimination of aspen (Koivula et al. 1999), prescribed burning (Beaudry et al. 1997) and control of competing vegetation (Duchesne et al. 1999). Carabid assemblages are sensitive to forest thinning; decreased tree density in mature stands favours forest generalists (Koivula 2002). Carabids are also responsive to the differing ecosystem effects of clearcut versus clearcut followed by prescribed burning; burning increases diversity and favours the occurrence of certain species (Beaudry et al. 1997). Carabid communities respond to deciduous litter addition in coniferous stands, with the catch of some species increasing and that of others decreasing; species richness remains similar

between treatment and control sites (Koivula et al. 1999). Finally, although carabid diversity remains unaffected by understory competition control methods, ten of 30 carabid species responded to the method of competition control used (Duchesne et al. 1999).

Methods of Community Analysis

Once the appropriate compositional indicator has been selected, measurement tools must be selected which may help to illustrate any effects of management. These tools may be generally categorized as diversity measures and composition measures.

Diversity measures

Alpha diversity

These diversity indices essentially express the range of species inherent in a local, defined area. They include such measures as species richness (number of species), species diversity (alpha diversity) and species evenness (Magurran 1988; Spellerberg 1993). This category of techniques tends to be frequently used in forest management studies (e.g.Wood and Gillman 1998; Buddle et al. 2000; Magura et al. 2000).

Two commonly used alpha diversity measures are the log series alpha and Shannon Wiener indices (Magurran 1988). The log series alpha index describes the log series distribution commonly associated with many habitats (Fisher et al. 1943), including forests where a few species dominate the community (Magurran 1988). This index is calculated from the number of species and the number of individuals in a sample (Fisher et al. 1943). It shows a high level of discriminant ability (Kempton and Taylor

1974) and a low level of sensitivity to sample size (Magurran 1988), and as such would be expected to be a superior diversity measure in forest management studies. In addition, the log series alpha index is less influenced by the most abundant species than other measures (Taylor et al. 1976).

The Shannon Wiener index is calculated from the proportional abundance of each species of the community. It has only moderate discriminant ability and is moderately sensitive to sample size (Magurran 1988). Regardless of its limitations, this index is commonly used in the analysis of understory vegetation (e.g. de Grandpré and Bergeron 1997; Bråkenhielm and Liu 1998; Newmaster and Bell 2002).

Beta diversity

In addition to local diversity, landscape level diversity (beta diversity) estimates may be calculated. Beta diversity can be determined by comparing the similarity of two or more replicate sites (Magurran 1988). Although beta diversity is not commonly measured in forest management studies, it is of considerable importance, as a reduction in beta diversity would signal a loss of species of species over a region.

Both Jaccards' index and Kendalls' τ can be used to measure the degree of similarity between pairs of sites. Jaccards' index is a widely used similarity measure, based on the presence or absence of species (Magurran 1988). This index is simple to calculate, however it does not consider species abundance. Because species are of equal value in the equation whether they are abundant or rare, two dissimilar sites may appear to be very similar (Magurran 1988). Another approach to measuring similarity between sites is the use of correlation coefficients (Krebs 1989). The use of Kendalls' τ is one

such method, providing a quantitative, pair-wise measure (Kendall 1962), considering the relative abundance of community members. In a review of similarity indices, Kendalls' τ was determined to provide consistent results, and was deemed the best similarity index available (Huhta 1979). Kendalls' τ is used in different ways, for example, species not occurring in both replicates (e.g. Elliott 1997) or species represented by a single individual in one replicate and absent from the other (e.g. Huhta 1979), may be eliminated from the analysis. However, rare species are an ecologically relevant part of the assemblage; therefore inclusion of species represented in at least one of the replicates should be considered.

Community composition analysis

Biological communities are inherently complex. They are composed of a number of different species of differing levels of occurrence, and the community as a whole may respond to a number of different environmental parameters (Gauch 1982). Unlike univariate analysis, multivariate techniques take into account the entire community, providing a model of its underlying structure (Gauch 1982). Ordination is one of these techniques; it functions by representing a multidimensional set of data in lower dimensional space, such that patterns in the data can be seen more clearly (Pielou 1984). Ordination diagrams depict the biological community in two dimensional space, where species or samples that are more similar are closer to together and those that differ are further apart; these objects are represented along axes according to an ordered relationship (Gauch 1982). The axes of these ordination biplots are selected to characterize the greatest amount of variance in the data set (Legendre and Legendre

1998). Parametric ordination techniques are based on eigenanalysis of the data matrix; therefore each ordination axis has an eigenvalue. Eigenvalues associated with ordination axes describe the amount of variance within the data set that can be explained by that axis (Gauch 1982).

There are two main categories of ordination techniques, unconstrained and constrained. Unconstrained ordination includes methods such as Principle Components Analysis (PCA) and Correspondence analysis (CA) which generate ordinations from a single data set, illustrating similarities and differences between species and sites based upon a set of species data (Legendre and Legendre 1998). Constrained, or canonical, techniques, including Redundancy Analysis (RDA) and Canonical Correspondence Analysis (CCA), are those which compare two data matrices, typically one containing species and the other containing environmental data (Legendre and Legendre 1998). The representation of species and sites in these forms of ordination are constrained by environmental variables, therefore from the results we can infer the relative importance of each of the environmental variables in influencing the community composition (ter Braak 1986). Environmental variables are depicted as vectors in the ordination diagram, the direction, length and placement of which depict the influence of these parameters on the species data set (ter Braak 1986; ter Braak and Šmilauer 1998).

The selection of specific ordination techniques depends upon the underlying structure of the species data, both Principal Components Analysis and Redundancy Analysis are based on a linear model of species distribution, while Correspondence Analysis and Canonical Correspondence Analysis are based on a unimodal model

(Jongman et al. 1995). Many species data sets are not strictly unimodal or linear, and may be depicted by either technique (N. Kenkel, personal communication).

Chronosequence Studies

Chronosequence studies are often used to evaluate ecological succession in forests and other environments (Pickett 1989). Sites are selected to represent a sequence of developmental stages, these sites having a common climate, substrate, relief and flora (Powers and van Cleve 1991). Thus space is substituted for time and results can be obtained in a relatively short period of time. This method is most successful when used in ecosystems that exhibit a very strong successional dynamic (Pickett 1989) such as forests. Drawbacks to this method include variability occurring as a result of changes in forest management methods, and a minimization of the importance of site history in successional dynamics (Powers and van Cleve 1991; Bakker et al. 1996). Despite these problems, in chronosequence sites revisited 12 to 14 years later, the basic patterns of successional change in floral communities were predicted by the initial results in sites that had not been subsequently disturbed (Debussche et al. 1996; Foster and Tilman 2000). I could not locate any studies evaluating the effectiveness of using chronosequence studies with invertebrates, therefore this is an important aspect to examine.

3.1 Effect of forest management on forest structure and understory vegetation diversity and composition in jack pine forests (*Pinus banksiana*) in southeastern Manitoba

Abstract

The health of biological communities may be affected by forest management practices including reforestation. The response of forest structure characteristics and understory vegetation to stand level differences associated with forest age and regeneration type was examined. Sampling was conducted in planted and naturally regenerating jack pine forests of 15, 25, 35, and 50 years of age. For each of the understory components spring ground vegetation, summer ground vegetation, shrubs and moss, per cent cover, species richness, alpha diversity and species evenness was examined for the influence of forest age and regeneration type. Beta diversity between replicates was compared. Assemblage composition was evaluated with ordination analysis. A number of environmental characteristics including canopy closure, light attenuation, overstory structure, ground cover and coarse woody debris were sampled in the same sites and the influence of the age and regeneration examined. The main findings were the following:

- The height and diameter of jack pine trees increased with forest age. Concomitantly, the degree of canopy closure increased. In these forests the canopy effectively closed between 15 and 25 years and this appears to have influenced the understory assemblages; species composition of spring and summer ground vegetation, moss and shrubs was distinct in the 15-year-old sites. These sites were dominated by plant species typical of open habitats.

- The number of jack pine stems decreased with forest age in the naturally regenerating sites. The initially dense patches of jack pine stems undergo substantial self-thinning between 15 and 25 years.
- Ground cover character changed with forest age. Per cent cover of grass litter decreased and per cent cover of conifer litter increased with age as grasses becomes less prominent and conifers became more established. The per cent cover of bare ground decreased with forest age as the understory recovered. The number of coarse woody debris pieces was highest in 15-year-old naturally regenerating forests and decreased with age. Planted sites had significantly less coarse woody debris.
- Per cent cover of spring ground vegetation increased with forest age; a similar trend was evident in summer ground vegetation. Per cent cover of both spring and summer ground vegetation was greater in naturally regenerating forests. Cover of spring vegetation in mid-aged sites appeared to be inversely related to shrub cover which showed a trend to higher cover in mid-aged planted forests. Species richness of spring vegetation in natural forests exceeded that of planted forests, these differences persisted in the 50-year-old sites.
- The moss assemblage showed distinct age-related changes. Moss species richness increased with forest age. Species diversity and evenness were significantly affected by age and showed similar trends; diversity values decreased with age until 35 years after which they increased.

INTRODUCTION

The physical architecture or pattern of forests often influences the biological communities that inhabit them. Important structural patterns and components include stand complexity, both vertical and horizontal; volume and quality of downed logs; amount and quality of standing dead wood; and litter complexity (Uetz 1979; Ferris-Kaan et al. 1998; Ferris and Humphrey 1999; Lindenmayer et al. 2000; Nilsson et al. 2001). Surveying these components can elicit considerable information about the overall physical conditions of the stand, as well as the number and the diversity of specialized niches available for colonization.

Biological indicators also tell about community structure in forests and have included floristic, fungal, invertebrate and vertebrate taxa (Ferris and Humphrey 1999). The advantage of using these biological indicators is that they may integrate the cumulative effect of a number of different ecosystem attributes and processes (Rosenberg et al. 1986). Plants in particular have merit as indicators as they have a close relationship to both soil and microclimate conditions, as well as providing habitat or food for local fauna (Ferris and Humphrey 1999). In addition, the ecological requirements and characteristics of many boreal understory species are well known (e.g. Scoggan 1957; Looman and Best 1979). Used in combination with structural features, understory composition may provide considerable information regarding the influence of forest management and the availability of resources for local fauna.

The specific objectives of this study are as follows:

- To determine whether structural characteristics of forests differ between naturally regenerating and planted forests, and if so at what forest age

- To determine whether alpha diversity of the understory vegetation differs between planted and naturally regenerated jack pine stands of a similar age.
- To determine whether alpha diversity of the understory vegetation is influenced by forest age.
- To determine whether beta diversity of the understory vegetation differs between planted and naturally regenerated stands.
- To compare the understory vegetation community occurring in planted jack pine stands to those occurring in naturally regenerated stands of a similar age.

MATERIALS AND METHODS

General Study Area

This study was conducted in the Sandilands Provincial Forest, a forest reserve located in southeastern Manitoba. The Forest is located in the western portion of the Rainy River section of the Great Lakes – St. Lawrence Forest Region (Rowe 1972). The Rainy River section is subject to the relatively cold, dry climate of the prairies, thus pines dominate (Rowe 1972; Scott 1995). Jack pine (*Pinus banksiana* Lamb.) especially thrives in disturbed areas (Scott 1995). The Manitoba Lowlands section of the Boreal Forest Region borders this area directly to the west (Rowe 1972).

The surface geology of the region is recent and glacial deposits which are primarily sandy in nature (Mueller-Dombois 1964). Physiographically, the Sandilands Provincial Forest is comprised of upland areas, underlain by remnant beach ridges, interspersed among extensive, poorly drained lowland areas (Mueller-Dombois 1964). The well-drained upland areas are dominated by trembling aspen (*Populus tremuloides*

Michx.) and white spruce (*Picea glauca* (Moench) Voss), with nearly pure stands of jack pine (*Pinus banksiana* Lamb.) occurring on especially well-drained, sandy areas (Mueller-Dombois 1964). In contrast, lowland sites are dominated by black spruce (*Picea mariana* (Mill.) Britton, Sterns & Poggenb.) and tamarack (*Larix laricina* (Du Roi) K. Koch) (Mueller-Dombois 1964).

The soils in the upland areas of this region are primarily of the Sandilands and Woodridge Series (Smith and Ehrlich 1964). Soils of both these series develop on fine to coarse sandy till, show minimal podzolization, and are extremely well drained (Anderson 1960). These soils are inherently of low fertility and have low moisture-retention capacity (Smith and Ehrlich 1964).

Climate is sub-humid continental, characterized by long, cold winters and short, warm summers (Kenkel et al. 1997). Climatic information for the region is generalized from data collected by the Environment Canada recording station located in Steinbach, Manitoba (Environment Canada 2005). Mean annual temperature is approximately 2.7°C. The daily average temperature in July is 19° C, and in January is -17°C. Average annual precipitation in the area is approximately 540 mm per year, with approximately 80% of this occurring as rainfall. Published estimates of the growing season in this region range from 160–200 days (Anderson 1960).

Experimental Design

Sixteen sites were established, eight in naturally regenerating forests and eight in planted forests. Two replicates representing each of four different forest ages in each regeneration type were used; the approximate ages of these forests were 15, 25, 35 and 50

years. All of the natural forests were determined to be regenerating after fire (Lafrenière 1994). The disturbance type of the planted sites could not be determined definitively; however, fire maps of the region do not indicate that these sites were affected by fire prior to planting, with the exception of the two 50-year-old forests. Of the two 50-year-old planted forests, one may have been affected by fire the year before planting, and the other was affected by a fire, of undetermined severity, approximately nine years before. Information regarding site preparation at these sites was not available.

Site Description

The sites were originally selected by Rheal Lafrenière in 1991, with the assistance of fire maps and plantation records provided by the Manitoba Department of Natural Resources (now Manitoba Conservation). At the time of initial selection, the forests were approximately 5, 15, 25 and 40 years of age; this was confirmed by increment borer samples taken from these sites (Lafrenière 1994). At the time of initial selection, the five-year-old forests were dominated by trees between two and five years of age, the 15-year-old forests consisted of 10- to 15-year-old trees, the 25-year old forests were made up of 20- to 30-year-old trees and the 40-year-old forests were composed of 30- to 50-year-old trees (Lafrenière 1994). Lafrenière (1994) used these sites to examine arthropod diversity in 1991-1992. Subsequently, Elliott (1997) compared arthropod diversity using the same sites in the 1993-1994-time period. During the original period of study, only one replicate of a 15-year-old naturally regenerated site could be located. With the aid of the 1998 Manitoba Conservation Forest Inventory database, a second replicate representing what is

now a 25-year-old forest was located; the age of this forest was confirmed by increment borer samples.

The sites used for the original studies were located and re-established, along with the newly selected site. The study sites were 100 X 100 m, and were located in forest stands that were a minimum of two hectares in size. Sites were located at least 20 m away from any major discontinuity such as a roadway or trail. All sites were dominated by jack pine, with a minimum tree composition of 75% jack pine stems. All sites were all located on well-drained upland regions. Specific site locations can be found in Table 3.1.1 and Figure 3.1.1

Sites were given code names corresponding to regeneration type (B = Natural or PL = Planted), year of origin (e.g. 89 = 1989), and replicate (A or B). For example, B87A is the first replicate of is a site that was regenerating naturally after an ecosystem-altering fire in 1987. Similarly, PL52B is the second replicate of a site that that was planted in 1952. Replicate designators are used as a convenient method of naming sites only, these letters do not imply a blocked design.

A full description of the initial appearance of the sites can be found in Lafrenière (1994) and Elliott (1997). To characterize the sites at the time of the current study, photographs of representative areas of each site were taken and these were used to generate the general site descriptions that are presented in the results.

Field Methods

Canopy closure

A Lemmon Company Model C spherical densiometer was used to measure canopy closure. Measurements were taken at 16 locations, in a four by four grid pattern centered at the middle of each site, with 20 m intervals between sample locations (Figure 3.1.2). Measurement techniques and calculations followed standard techniques (Englund et al. 2000). The 16 measurements were averaged to calculate a mean canopy closure value for each site.

Light attenuation

A Gossen photometer was used to measure light attenuation through the canopy, and through the shrub layer. Light attenuation measurements were taken between 10:00 AM and 4:00 PM, in cloud free conditions, between the end of June and the middle of August. Light measurements in LUX units were taken at the same 16 locations used for densiometer measurements. They were taken at 2 m and 20 cm above the forest floor and standardized using control readings taken at the same heights in open areas before and after site measurements. The 16 values were averaged for each measurement height and presented as a single average value for each site.

Ground cover

Ground cover was sampled using a stratified random design with five, 1 X 1 m quadrats selected per quarter of each plot. Percent cover of shrubs, herbaceous

vegetation, moss, lichen, coarse woody debris, fine woody debris, conifer litter, deciduous-type litter, grass litter, bare ground, and rock was recorded for each quadrat.

Understory vegetation

Four components of understory vegetation were sampled; spring ground vegetation, summer ground vegetation, moss and shrubs. Ground vegetation consisted of all vascular plants less than 30 cm in height (Lafrenière 1994). The shrub layer consisted of all plants greater than 30 cm but less than 2 m in height (Lafrenière 1994).

Ground vegetation was sampled over two periods, late spring (31 May – 3 June 2004) and late summer (21 July – 31 July 2003) (Lafrenière 1994; Elliott 1997). In each sampling period, 20, 1 X 1 m quadrats were sampled per site in a stratified random sampling design where five samples were selected from each quarter of the site (de Grandpré et al. 1993). Ground vegetation was identified in the field, and percent cover of each species represented in the quadrat was recorded. When a species could not be identified in the field, a sample was collected and preserved for later identification in the laboratory. Sampling occurred within a maximum 10 d period to ensure consistency of ground vegetation between sites. Forest floor moss was sampled in an identical fashion, between 21 July and 31 July 2003.

The shrub layer vegetation was sampled in a similar manner but five, 2 X 2 m were selected per quarter of the site. Shrub layer sampling took place between 14 June and 17 June 2004.

For each understory component sampled, each plant in the quadrat was identified to species, or to the lowest taxonomic level possible. Field identification was

accomplished with the assistance of regional field guides (Vance et al. 1993; Johnson et al. 1995; Baldwin and Sims 1997). Collected samples were identified by Elizabeth Punter, Department of Botany, with the assistance of herbarium specimens. Unless otherwise specified, only those plants identified to species or morphospecies were used for statistical analysis. Species authorities are provided in the related appendices.

Overstory

Overstory sampling was conducted to determine tree species distribution, stand density and average tree height. The overstory consisted of all woody species greater than 2 m in height (Lafrenière 1994). Sampling was conducted in two randomly selected, 10 X 10 m quadrats per quarter of each site. The species of each tree within each quadrat was determined. The diameter at breast height (dbh) of each of these trees was measured using standard calipers.

Five representative examples of the dominant tree species per quadrat were selected for height measurement. Tree height was measured with a Suunto PM5/360 clinometer using the measurement techniques and calculations outlined in the instruction manual (Suunto 1998).

Coarse woody debris

A line-transect sampling method was used to sample downed, coarse woody debris. In each site, four, 100 m long north-south transects were randomly selected, two from each half of the site. The transect line was marked in 1 m increments. The number of coarse woody debris pieces occurring in every other 1 m length of each transect was

recorded. A coarse woody debris piece was counted if its centerline crossed the transect line, if it exceeded 7.5 cm in diameter at the point where it crossed the transect line, and was not self-supporting (British Columbia Ministry of Sustainable Resource Management 2004). The decay stage of each documented piece was also recorded using the criteria described in Table 3.1.2 (British Columbia Ministry of Sustainable Resource Management 2004).

The diameter at breast height (dbh) of each standing, dead tree (snag) in each of two, randomly selected, 10 X 10 m quadrats per quarter was measured for each site. As all snags were of a similar degree of decomposition, no assessment of decay stage was made. All snags consisted of hard, intact wood with largely intact bark.

Statistical Analysis

Each of the following four components of the understory vegetation were analyzed separately: spring ground vegetation, summer ground vegetation, shrubs and moss. For each of these components, the following analyses were performed. The total cover of all of the vegetation in each component was used as a general, abundance indicator. The total number of species (species richness), and the Shannon-Wiener (H') index were used to assess alpha diversity of each of these understory components within each. The Shannon-Wiener index was calculated from the following equation:

$$H' = \sum_{i=1}^{S} pi \log_e pi$$

Where s is the total number of species found in the site and p_i is the mean percent cover of the i^{th} species divided by the total percent cover of all species found in

the site (Krebs 1989). The percent cover values used to calculate p_i were taken from the average of all of the quadrats sampled per site.

Species evenness for each site was determined by using the Shannon-Wiener measure of evenness (E_H) (Southwood 2000). It was calculated with the equation:

$$E_H = \frac{H'}{\log_e S}$$

Where S is the total number of species.

Jaccard's index (C_J) and Kendall's τ correlation coefficient were used to measure beta diversity of each of the replicate pairs. Jaccard's index was calculated with the following equation:

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

Where j is the number of species present in both replicates A and B, a is the number of species present only in replicate A and b is the number of species found only in replicate B (Southwood 2000).

Kendall's τ correlation coefficient (Kendall 1962) was calculated using SYSTAT (SYSTAT 2002). This correlation was calculated based on the abundance of all species present in either or both of the two replicates.

The effect of regeneration type, forest age, and the interaction of the two, on the each of the above vegetation parameters was conducted using analysis of variance. Beta diversity measures were compared using a paired t-test.

The effect of regeneration type, forest age and the interaction of the two was evaluated for the environmental variables relating to canopy closure, light attenuation, overstory and snag characteristics using analysis of variance. Multivariate analysis of variance was performed on the ground cover types using the general linear model. Because of the large number of cover types, ground cover was split into two categories and each was examined in a separate multivariate analysis of variance. Per cent cover of each of the living plant components shrub, herb, moss and lichen were analysed together, as were per cent cover of each of the non-plant components coarse woody debris, fine woody debris, grass litter, conifer litter, deciduous litter and bare ground. Because the presence of rock was primarily a local finding, it was not included in the analysis. Contingency table analysis using log linear modelling was used to compare the quality of coarse woody debris between regeneration types and forest ages.

Data was tested for normality prior to analysis by graphing residuals from a general linear model estimate against the estimated values, and assessing the distribution pattern in the scattergram. When heterogeneity of residuals was noted, data were appropriately transformed and analysed in that form. For all analysis, an alpha value of 0.05 was considered significant. SYSTAT 10.2 was used for all of the preceding analyses (SYSTAT 2002).

Principal Components Analysis (PCA) and Redundancy Analysis (RDA) were selected for multivariate analysis as these two techniques provided the best representation

of the raw data. Two Redundancy Analyses were performed for each data set. First, the data was constrained by the experimental design variables forest age (Ages 15, 25, 35 and 50) and regeneration type (Natural and Planted), which were all coded as nominal variables. Second, the same data was constrained by the measured environmental variables. For both analyses Monte Carlo simulation was used (499 permutations); in the second model only the environmental variables found to be significant ($p \leq 0.05$) were included in the model as they were considered to have the strongest influence on the assemblage. Environmental variables that might be expected to autocorrelate with the biological community, or variables that would not be expected to directly influence the community, were not included as environmental variables in the model.

These techniques were performed on each of the vegetation groups using the default settings of CANOCO 4.5 (ter Braak and Šmilauer 1998) with the exception of the previously noted and of the following:

- Species data was log transformed using the $\log_e + 1$ transformation provided in the program. This method was employed to reduce the influence of very abundant species.
- Weighted average scores were used to plot the ordination diagrams. This has the effect of orienting the sites in species space rather than environment.

In all Principal Components Analysis and Redundancy Analysis ordination diagrams, the first and second ordination axes are portrayed.

RESULTS

General Site Appearance

The 15-year-old sites of both regeneration types had generally open canopies. Morphologically, the naturally regenerating sites consisted of dense aggregations of jack pine, interspersed with wide open glades (Figure 3.1.3). In comparison, the planted sites were uniformly treed (Figure 3.1.4). Of the two naturally regenerating sites, one contained more areas of bare ground, and the soil and ground vegetation layer in this site appeared to be reduced as compared to its replicate. Fallen dead-wood was evident in the naturally regenerating sites, while less was apparent in the planted sites. Of the two planted sites, one had more woody debris.

The 25-year-old sites of both regeneration types had a higher degree of canopy closure than the 15-year-old sites. The naturally regenerating forests of this age were less densely treed than their 15-year-old counterparts. Of the two naturally regenerating sites, one had an aggregated pattern of tree distribution, while the other was more uniformly vegetated. The two planted sites retained the uniformly vegetated appearance of a planted forest. Of the two, one had a more developed shrub layer.

The 35-year-old sites had a similar degree of canopy closure to the 25-year-old sites. As well, morphologically they were generally of a similar appearance to the 25-year-old sites. Of the two naturally regenerating sites, one had a more aggregated distribution of trees while the other had a more uniform distribution. Of the two planted sites, one replicate had a considerably developed shrub layer and a reduced overstory layer.

The 50-year-old sites had a more elevated canopy than the 35-year-old sites. The tree distribution among all of these sites was generally similar; however one of the naturally regenerating sites was characterized by gaps created by the death of mature trees; in these gaps ferns were thriving.

Environment

Site summaries of all environment variables can be found in Appendix 1.

Canopy closure

The degree of canopy closure was significantly influenced by forest age but not by regeneration method or by the interaction of age and regeneration type (Table 3.1.3). With the exception of the 15-year-old forests, where canopy closure in naturally regenerating sites tended to exceed that of their planted counterparts, canopy closure was similar in both regeneration types (Figure 3.1.5). The degree of canopy cover increased between 15- and 25-years forests and changed little after 25 years. The degree of canopy variability, as indicated by the coefficient of variability of the densiometer readings, was determined as an indicator of relative canopy heterogeneity within each site. This measure was not significantly influenced by any of the three factors (Table 3.1.3); however, the canopies of the youngest, naturally regenerating sites tended to be more variable than those of the youngest planted sites (Figure 3.1.6). There was no clear overall trend in canopy variability occurring with either regeneration type or forest age.

Light attenuation

Light attenuation to 20 cm and to two metres was not significantly affected by regeneration type, forest age or by the interaction of the two (Table 3.1.3). Light attenuation to 20 cm and to two metres was generally similar between the two regeneration types, although light attenuation to two metres was less in 15-year-old planted sites (Figures 3.1.7 and 3.1.8). Light attenuation increased with forest age in a similar pattern to canopy closure. Attenuation between two metres and 20 cm was close to being significantly influenced by regeneration type but not by forest age or the interaction of the two (Table 3.1.3). More light was lost between the two metre and 20 cm levels in planted sites than in naturally regenerating ones, especially in the 15-and 35-year-old forests (Figure 3.1.9).

Ground cover

Within the plant cover component of the ground cover, there was no significant effect of regeneration type (Wilks' Lambda = 0.313; df = 4,5; $p > 0.05$), forest age (Wilks' Lambda = 0.179; df = 12,13; $p > 0.05$) or the interaction of the two (Wilks' Lambda = 0.352; df = 12,13; $p > 0.05$) with multivariate analysis of variance. With univariate analysis of variance, there was no significant influence of regeneration type, forest age or the interaction of the two on $\log_e$ transformed per cent shrub cover (Table 3.1.4). Shrub cover tended to be higher in planted sites up until the 50-year age group and this was most noticable in the 35-year-old planted sites (Figure 3.1.10). An increase in shrub cover occurred with forest age, however peaked in the 35-year-old sites in the planted sites. There was a significant effect of regeneration type on per cent cover of

herbaceous plants (Table 3.1.4). This was a result of the greater proportion of herb cover in naturally regenerating forests especially in 35- and 50-year-old sites (Figure 3.1.11). Neither forest age nor the interaction of regeneration type and age influenced per cent herb cover. There were no significant differences in per cent cover of moss ($\log_e$ transformed) or lichen (Table 3.1.4), however some trends were noted. Moss cover in 15-year-old planted sites tended to exceed that in naturally regenerating sites of the same age, but the reverse was found in the 25-year old sites (Figure 3.1.12). Moss cover tended to increase with forest age in a generally similar pattern in both regeneration types. Lichen cover in planted sites tended to exceed that in naturally regenerating sites at most forest stages, with the exception of 35-year-old forests (Figure 3.1.13). Lichen cover was lowest in the 50-year-old forests. Overall, with the exception of lichen, there was a general trend to increasing cover of understory vegetation with increasing forest age.

Neither regeneration type (Wilks' Lambda = 0.480; df = 6,3; $p > 0.05$), forest age (Wilks' Lambda = 0.035; df = 18,8; $p > 0.05$) nor the interaction of the two (Wilks' Lambda = 0.135; df = 18,8; $p > 0.05$) had significant influence on the distribution of the non-plant ground cover component as a whole. When each of these components was evaluated with univariate analysis of variance, there was a significant effect of forest age, but not of regeneration type or the interaction of the two, on per cent coarse woody debris cover (Table 3.1.4). A higher per cent cover of coarse woody debris was found in 15-year-old sites, especially in those regenerating naturally after fire (Figure 3.1.14). Coarse woody debris cover was least evident in the mid-aged sites, and subsequently increased with forest age. There was no significant influence of any of the three factors on per cent cover of fine woody debris (Table 3.1.4). The per cent ground cover of fine woody debris

was highest in 15-year-old naturally regenerating forests (Figure 3.1.15). It tended to be highest in youngest and oldest forests, the pattern differing slightly between sites of different regeneration types. There was a significant influence of forest age on grass litter cover, however, neither regeneration type nor the interaction of forest age and regeneration type was significant (Table 3.1.4). The cover of grass litter decreased with forest age (Figure 3.1.16). This trend was especially evident in the planted sites where this litter type initially tended to be more abundant than in the naturally regenerating sites. There was a significant effect of age, but not of regeneration type or the interaction of the two factors, on conifer litter cover (Table 3.1.4). The per cent cover of conifer litter tended to increase with forest age, this increase was especially evident between 15-and 25-year-old sites (Figure 3.1.17); conifer litter in naturally regenerating 15-year-old sites tended to exceed that of planted sites. There were no significant differences in deciduous litter cover ($\log_e$ x +1 transformed). Per cent cover of deciduous litter did not follow a clear regeneration or age related pattern, but, with the exception of the 15-year-old sites, generally followed the same pattern as shrub cover (Figure 3.1.18). In the 15-year-old sites there tended to be a higher cover of deciduous litter in naturally regenerating forests. There was a significant influence of forest age on bare ground ($\log_e$ x +1 transformed) (Table 3.1.4); regeneration type and the interaction of age and regeneration had no effect. The occurrence of bare ground was essentially limited to the youngest sites, especially those regenerating naturally after fire (Figure 3.1.19).

Overstory vegetation

A full summary of the tree species sampled in each site can be found in Appendix 2. The number of stems per hectare was not significantly affected by regeneration type or forest age, however approached significance when the interaction term was considered (Table 3.1.3). The number of stems per hectare was very high in the 15-year-old naturally regenerating sites (Figure 3.1.20). A high stem density was also noted in the 35-year-old planted sites, however, this was strongly influenced by PL64B, which had a high density of *Corylus cornuta*, much of which fit the definition of a tree. Because this measure included multi-stemmed species, such as *C. cornuta*, the number of jack pine stems per ha was analysed separately. The number of jack pine stems per ha was significantly affected by forest age, regeneration type and by the interaction of the two. The number of jack pine stems was higher in the naturally regenerating sites and this was especially evident in the younger sites (Figure 3.1.21).

The overall average tree diameter was not significantly different in sites of differing regeneration types or ages (Table 3.1.3). Average tree diameter in planted sites tended to exceed those of the naturally regenerating sites of the same age until 50 years (Figure 3.1.22). Tree diameter showed a general trend of increase with forest age. Because this measure included the average diameter of all the specimens defined by the 2 m height criteria, a number of species more traditionally defined as shrubs were included in this measurement. Therefore, the average tree diameter in sites that had a number of shrubs fitting the tree criteria tended to be lower. When the average diameter of jack pine stem was evaluated, there was a significant effect of forest age. Regeneration type approached significance but the interaction of the two factors was not significant (Table

3.1.3). Jack pine diameter in planted sites tended to exceed that of naturally regenerating sites, however, in the 50-year-old sites, jack pine diameter was more similar between regeneration types (Figure 3.1.23). Jack pine diameter increased with forest age and this increase was especially apparent between 15-year-old forests and the remainder of the sites.

The average jack pine tree height was significantly influenced by forest age but not by regeneration type or the interaction of regeneration type and age (Table 3.1.3). The average height of trees in naturally regenerating forests tended to exceed those of planted forests slightly in sites less than 50 years of age (Figure 3.1.24). Tree height in 50-year-old forests was similar in both regeneration types. Tree height increased steadily with forest age in both regeneration types.

Coarse woody debris

On analysis of variance of the number of pieces of coarse woody debris, regeneration type, age and the interaction of the two were highly significant (Table 3.1.3). There was a significant interaction between decay class and forest age (χ^2 = 163.18, df = 12, $p < 0.005$), but not between decay class and regeneration type ($\chi^2 = 7.51$, df = 4, $p > 0.05$). The greatest amount of woody debris was found in sites naturally regenerating after fire, especially in 15- and 50-year-old sites (Figure 3.1.25). In both regeneration types, the amount of woody debris was greatest in the youngest sites, least in the mid-aged sites and intermediate in the oldest sites. In the youngest, sites debris was in the early stages of decay (class 4 and 5), while in the older sites a variety of decay stages were present (Figures 3.1.26 a and b).

Snags

The number of snags per hectare was not significantly influenced by regeneration type, forest age or the interaction of the two (Table 3.1.3). Snags tended to be more prevalent in naturally regenerating sites, especially in mid-aged stands (Figure 3.1.27). In comparison, there were no snags found within the sample quadrats in the 25-year-old planted forests. However, the number of snags per hectare per regeneration type was similar in 50-year-old sites. Average snag diameter was significantly affected by forest age but not by regeneration type, or the interaction of the two (Table 3.1.3). Snag diameter was similar between the two regeneration types in the youngest and the oldest forests; however the diameter of the snags in 35-year-old naturally regenerating forests tended to exceed those of planted forests (Figure 3.1.28). Average snag diameter tended to increase with forest age.

Spring Ground Vegetation

The species of spring ground vegetation accounting for the highest per cent cover over all sites are presented in Table 3.1.5 and complete results of the spring ground vegetation sampling are listed in Appendix 3. The 15-year-old sites were dominated *Arctostaphylos uva-ursi*, *Vaccinium angustifolium* and grasses. The 25-year-old sites were characterized by *V. angustifolium*, *A. uva-ursi,* and *Fragaria virginiana,* as well as *Anemone quinquefolia* and *Maianthemum canadense*. The 35-year-old sites had a similar plant community to the 25-year-old sites, although the grass, *Oryzopsis asperifolia* was more common in the older sites. The 50-year-old sites were characterized by a greater

cover of *Pyrola virens*, in addition to *A. quinquefolia*, *V. angustifolium*, *M. canadense* and *A. uva-ursi*.

Both regeneration type and forest age had a significant effect on the per cent cover of the spring ground vegetation, but the interaction of the two factors did not (Table 3.1.6). Per cent cover was greater in naturally regenerating sites, especially in the 25- and 35-year-old sites (Figure 3.1.29). This was due in part to the influence of *A. uva-ursi*, *V. angustifolium* which were prevalent in these sites (Table 3.1.5). Despite the differences in representation between regeneration types, the per cent cover of these species was not significantly influenced by regeneration type (*A. uva-ursi* ($\log_e$ x + 1): $F_{1,8} = 0.423$, $p > 0.05$; *V. angustifolium* ($\log_e$) $F_{1,8} = 1.374$, $p > 0.05$), or by the interaction of regeneration type and forest age (*A. uva-ursi* ($\log_e$ x + 1): $F_{1,8} = 2.350$, $p > 0.05$; *V. angustifolium* ($\log_e$) $F_{1,8} = 1.742$, $p > 0.05$). Per cent cover of spring ground vegetation generally increased with forest age in both regeneration types, however followed a different pattern of increase. The greatest increase in ground cover in naturally regenerating sites occurred between 15- and 25-year-old sites, while, the increase in ground cover in planted sites occurred later, between 35 and 50 years.

Species richness was significantly influenced by regeneration type but not by forest age or the interaction of the two factors (Table 3.1.6). Species richness tended to be greater in naturally regenerating forests at all stages, however, this was especially evident in the 50-year-old forests (Figure 3.1.30). In general, species richness tended to increase with forest age however there was a reduction in species richness in planted sites between 35 and 50 years.

Species diversity, as indicated by the Shannon-Wiener Index, was not significantly affected by regeneration type, forest age or the interaction of the two (Table 3.1.6). Species diversity was similar between regeneration types in 25- and 35-year-old forests but tended to be higher in the 50-year-old natural sites than in the planted sites of the same age (Figure 3.1.31). In general there was a trend to increasing diversity with forest age, although the 50-year-old planted sites were less diverse than mid-aged planted forests.

The species evenness of spring ground vegetation was not significantly influenced by forest age, regeneration type or the interaction of the two (Table 3.1.6). Species evenness followed different patterns in each regeneration type (Figure 3.1.32). In general, species evenness tended to increase with forest age.

Beta diversity was unaffected by regeneration type when either the Kendall's τ coefficient ($df = 3$, $t = -0.178$, $p > 0.05$) or Jaccard's index ($df = 3$, $t = 1.867$, $p > 0.05$) were employed. Similar trends were evident for both measures (Figures 3.1.33 and 3.3.34). Beta diversity was lowest in mid-aged sites – replicates were the most similar in 25-year-old natural and 35-year-old planted sites. Beta diversity was highest in 50-year-old sites in both regeneration types.

Principal Components Analysis of spring species produced an ordination where 50% of the variation in species data was explained on the first two axes, 31.7% on the first and 18.3% on the second (Figure 3.1.35). Sites were generally distributed along axis one according to successional stage. Species characteristic of, or more dominant in, open habitats or clearings, such as *A. uva-ursi*, *P. virginiana*, *Antennaria neglecta* and *Viola adunca* strongly influenced the negative end of axis one, while species more

characteristic of closed forests, such as *A. quinquefolia* and *M. canadense*, influenced the opposite end of the axis. The 15-year-old sites, with the exception of B87A, were the most distinctive age related group in this ordination and were situated at the negative end of axis one. These sites tended to have higher representation of the species more typical of open habitats or clearings. Site B46A had a strong influence on the positive end of axis one. This site had a distinct ground vegetation community, with an absence of many of the open habitat species, a greater abundance of species common to closed canopy conditions and some unique species such as *Pteridium aquilinum*, *Equisetum scirpoides*, *Trientalis borealis* and *Petasites palmatus*.

The Redundancy Analysis of spring species constrained by regeneration type and forest age as environmental variables produced an ordination where 31% of the variation was explained along the first two axes; 18.2% on axis one and 12.8% on axis two (Figure 3.1.36). Although all environmental variables are included in the triplot, only Age 15 and Age 50 were significant. Age 15 influenced axis one more strongly, while Age 50 had a greater influence on axis two. Axis one corresponded to an age gradient where the 15-year-old sites separated from older sites. Species such as *P. virens*, *M. canadense*, *Cornus Canadensis*, *E. scirpoides* and *T. borealis*, were associated with Age 50. Although not significant, Age 25 was strongly associated with the opposite end of axis two. Associated with this variable were species such as *V. angustifolium*, *Symphoricarpos albus*, *Oryzopsis pungens* and the legume species.

The Redundancy Analysis of spring vegetation species constrained by the measured environmental variables produced an ordination where 33.3% of the variation was explained with the first two ordination axes, 22.6% along axis one, and 11.6% along

axis two (Figure 3.1.37). The environment variables light infiltration to 20 cm and tree height were significant. Light infiltration had a strong influence on axis one. Fifteen-year-old sites were situated at one end of axis one, while older sites such as B46A and PL65A were situated at the opposite extreme. Young sites with greater light attenuation, such as B87A, and older sites with reduced light attenuation for their age, such as B52B and B64A, were located more centrally along axis one. Along axis two, the sites older than 15-years were distributed on the basis of tree height. These older sites were generally grouped in a similar manner to the preceding Redundancy Analysis.

Summer Ground Vegetation

The most prevalent summer ground vegetation species are summarized in Table 3.1.7, a complete census of summer ground vegetation is found in Appendix 4. *Andropogon gerardii* and other grasses dominated the 15-year-old sites, along with *A. uva-ursi, V. angustifolium,* and *Salix* spp. Grasses, *V. angustifolium* and *A. uva-ursi*, in addition to *M. canadense* were common in 25- and 35-year-old sites. The 50-year-old sites had less grass cover and a greater abundance of *P. virens*, but otherwise had similar dominant species to the mid-aged sites.

Regeneration type significantly influenced the per cent cover of the summer vegetation, however, neither forest age nor the interaction of regeneration type and age had an affect (Table 3.1.6). The higher per cent cover in naturally regenerating sites was influenced by a number of species that were more abundant in naturally regenerating sites than in planted sites (Table 3.1.7). Per cent cover of summer ground vegetation species

tended to increase with forest age in naturally regenerating sites but tended to decrease with forest age in planted sites (Figure 3.1.38).

Neither regeneration type, forest age nor the interaction of the two had a significant influence on the species richness of summer ground vegetation (Table 3.1.6). Species richness tended to increase with stand age in naturally regenerating sites, but fluctuated in planted sites (Figure 3.1.39).

Similarly, the Shannon-Wiener diversity index was unaffected by forest age, regeneration type or the interaction of the two (Table 3.1.6). Species diversity tended to increase with forest age in both regeneration types, with the exception of the 50-year-old planted sites which showed similar diversity values to 25-year-old sites (Figure 3.1.40).

Species evenness of summer vegetation was not significantly affected by regeneration type, forest age or the interaction of the two (Table 3.1.6). Species evenness of naturally regenerating sites tended to exceed that of planted sites in 15- and 50-year-old forests (Figure 3.1.41). Species evenness tended to increase with forest age; as with spring vegetation, species evenness tended to decrease in 50-year-old planted sites.

Regeneration type had no significant influence on beta diversity with either of the two indices (Kendall's: $df = 3$, $t = 1.127$, $p > 0.05$, Jaccard's: $df = 3$, $t = 0.570$, $p > 0.05$). Beta diversity patterns were similar for both measures (Figures 3.1.42 and 3.1.43). Diversity of planted replicates exceeded that of naturally regenerating replicates until the 50-year stage. The beta diversity of the 25-year-old planted replicates was particularly high, otherwise the between replicate diversity tended to be lowest in the 25- and 35-year-old sites.

The Principal Components Analysis of the summer vegetation species produced an ordination where 44.6% of the variation in species data was explained on the first two ordination axes, 25.8% on the first and 18.8% on the second (Figure 3.1.44). There was a general separation of sites according to age along the first axis and the youngest sites tended to be the most distinct. Site B46A was the most distinct older site and had a strong influence on the opposite end of axis one. There was a distinct clustering of the youngest sites in this ordination diagram and these sites were associated with the presence of *Andropogon gerardi*. Species typical of closed forest, such as *A. quinquefolia* and *M. canadense* had a strong influence on the opposite end of axis one. Separation of sites along axis two was primarily due to the influence of B46A, a site tending to be floristically unique.

Redundancy Analysis of summer species constrained by forest age and regeneration type produced an ordination where 23% of the variation was accounted for on axis one and 10.8% on axis two (33.8% in total). Only Age 15 and Age 50 were significant environmental variables in this ordination (Figure 3.1.45). The presence of *A. gerardii* had a strong influence on the orientation of the Age 15 centroid. Other species associated with Age 15 were those associated with open sites such as *A. uva-ursi*, jack pine seedlings and *Anemone patens*. Similar plant species to those associated with 50-year-old sites in the preceding section were associated with Age 50 in this ordination.

Figure 3.1.46 depicts the ordination diagram for the same species data constrained by the significant environmental variables. In this ordination 36.2% of the species variation was explained along axes one and two; these axes accounted for 23.5% and 12.7% respectively. Both light infiltration to 20 cm and tree height were strongly

associated with axis one, which generally represented an age gradient; the youngest, most open sites were situated at one end of the axis and the older forests with taller trees and more closed canopies were positioned toward the opposite end. Species particularly associated with closed canopy conditions and with trees of greater height were *M. canadense* and *A. quinquefolia*. Many species located at the positive end of axis one, such as *Aralia nudicaulis*, *C. canadensis*, *Rubus pubescens*, *Galium triflorum* and *Epilobium angustifolium*, were either unique to B46A or far more common in this site, so rather than these species being associated with older forests, they are associated with one site in particular.

Shrubs

The most abundant shrub species are summarized in Table 3.1.8; a complete list of shrub vegetation sampled can be found in Appendix 5. The 15-year-old sites were dominated by species such as *Amelanchier alnifolia*, *Prunus pensylvanicus* and *Prunus. virginiana*. *Spiraea alba* was also found in these sites, however was more prevalent in the planted sites. Shrub cover was more extensive in the 25- and 35-year-old forests than in the 15-year-old sites. Particularly common in these forests were *P. virginiana*, *A. alnifolia* and *S. albus* however this pattern was strongly influenced by two sites: PL64B and PL76B, which had extensive development of the shrub layer. In the 50-year-old sites *Rosa acicularis* was the most abundant species, *P. virginiana* and *A. alnifolia* were also common.

Log_e transformed per cent cover of shrubs was unaffected by regeneration type, forest age or the interaction of the two (Table 3.1.6). Per cent shrub cover tended to

increase with forest age in both regeneration types; however, peak cover appeared to occur earlier in planted sites (Figure 3.1.47). Shrub cover in planted sites tended to exceed that of naturally regenerating sites, especially in the mid-aged sites.

Species richness of the shrub layer was not affected by regeneration type, age or the interaction of the two (Table 3.1.6). Species richness was generally comparable in both regeneration types. However, it tended to increase slightly with forest age in naturally regenerating sites but varied with age in planted sites (Figure 3.1.48).

Species diversity was similarly unaffected by the two factors or their interaction (Table 3.1.6). The Shannon-Wiener index values varied with forest age for both regeneration types, however tended to be the highest in the 50-year-old stands in both treatment types (Figure 3.1.49).

Species evenness of the shrub layer was significantly affected by forest age but not by regeneration type or the interaction of forest age and regeneration type (Table 3.1.6). Species evenness was similar in the two regeneration types although the 35-year-old planted sites appeared to have greater species evenness than naturally regenerating sites (Figure 3.1.50). Species evenness tended to increase with forest age, although 35-year-old naturally regenerating sites did not follow this trend.

Beta diversity of the shrub layer was unaffected by regeneration type with either measure (Kendall's: $df = 3$, $t = 0.142$, $p > 0.05$, Jaccard's: $df = 3$, $t = 0.402$, $p > 0.05$). It followed the same general trends in both methods (Figures 3.1.51 and 3.1.52). Beta diversity of 15- and 50-year-old naturally regenerating replicates tended to exceed their planted counterparts. Beta diversity in naturally regenerating forests changed over time,

initially decreasing in mid-aged stands, then increasing in 50-year-old forests. Beta diversity in planted forest did not follow a clear trend.

The Principal Components Analysis of the shrub species produced an ordination in which 57.7% of the species variation was explained on the first two ordination axes; 40.9% on axis one and 16.8% on axis two (Figure 3.1.53). Axis one generally represented a successional gradient where youngest sites were located at the negative end of the axis and the remainder of the sites were located further along this axis. Shrub species such as *S. alba*, *Prunus pumila*, and *Apocynum androsaemifolium* were associated with the negative end of axis one, while species such as *A. alnifolia, R. acicularis* and *V. angustifolium* were associated with the opposite end of the axis. This ordination was strongly influenced by three sites with high shrub cover: PL64B, B46A and PL76B.

The Redundancy Analysis of the shrub species constrained by forest age and regeneration type produced an ordination where 30% of the species variation was explained along the first two axes, 21.4% on axis one and 8.6% on axis two (Figure 3.1.54). Of the variables, only Age 15 proved to be significant. Age 15 had a strong influence on the distribution along axis one and the 15-year-old sites were closely associated with the positive end of this axis. The rest of the sites were generally distinct from the youngest sites.

The Redundancy Analysis of the same data constrained by the significant environmental variables produced an ordination where 27% of the species variation was explained along axis one and 21.4% along axis two (48.4% in total). The only significant variable was light attenuation to 20 cm (Figure 3.1.55). As in the previous ordination, 15-year-old sites tended to be distinct from the rest of the sites and were associated with axis

one. Because this model was constructed with one environmental variable, axis two is unconstrained, accounting for the large amount of variation explained along this axis.

Moss

A summary of the most prevalent moss species is presented in Table 3.1.9; a complete list of moss species can be found in Appendix 6. *Pluerozium schreberi* was by far the most abundant species overall, followed by *Dicranum polysetum* and *Ceratodon purpureus*. The most common species in the 15-year-old sites was *C. purpureus*; *P. schreberi* dominated the moss community in the older sites.

Log_e transformed per cent cover of moss was not significantly affected by regeneration type, nor by the interaction of the regeneration type and age; however, it was close to being significantly influenced by forest age (Table 3.1.6). A trend to increasing moss cover with stand age was evident (Figure 3.1.56).

Moss species richness was significantly affected by forest age but not by regeneration type or the interaction of age and regeneration type (Table 3.1.6). The 50-year-old sites tended to have higher species richness than the mid-aged and younger forests (Figure 3.1.57).

Similarly, there was a significant effect of forest age but not of regeneration type or the interaction of age and regeneration type on the Shannon-Wiener diversity index results. There was a decrease in moss diversity in planted forests until a low at 35 years (Figure 3.1.58). By comparison, there tended to be less overall age-related change in the species diversity in naturally regenerating sites.

Forest age had a significant influence on species evenness, however, regeneration type and the interaction of age and regeneration type did not (Table 3.1.6). Species evenness followed similar trends in both regeneration types (Figure 3.1.59). Species evenness tended to decrease with forest age until 35 years after which it increased. However, species evenness values in some sites were based on few species, as little as two; therefore this measure must be interpreted with some caution.

As with the other understory vegetation components, regeneration type had no influence on the beta diversity of the moss layer when either measure was considered (Kendall's: $df = 3$, $t = 0.286$, $p > 0.05$, Jaccard's: $df = 3$, $t = -0.019$, $p > 0.05$). However, these results are based on few species therefore these results should be interpreted with caution. Planted and naturally regenerating sites followed different trends in beta diversity, however, the highest level of similarity was generally found in mid-aged stands of both regeneration types in both measurement methods – in 25-year-old naturally regenerating forests and 35-year-old planted forests (Figures 3.1.60 and 3.1.61). These two methods of analysis elicited generally similar trends for planted sites, but differed in their treatment of naturally regenerating sites. With the Jaccard's index, 15- and 25-year-old naturally regenerating replicates were of a similar degree of similarity, however with the Kendall's τ, the 25-year-old replicates were more similar than the 15-year-old replicates.

The Principal Components Analysis of moss species produced an ordination that explained 77.4% of the species variation, the bulk of it, 65.2%, along axis one (Figure 3.1.62). The distribution of sites along axis one was dictated by three species, *C. purpureus* and *Hypnum revolutum*, which were much more prevalent in 15-year-old sites,

and *P. schreberi,* which tended to dominate sites older than 15 years. These three species tended to dictate the ordination by virtue of their distinctive distribution (Table 3.1.9) therefore the distribution of the rest of the moss species is largely artefact.

The influence of these three species of moss is well illustrated in Figure 3.1.63. In this Redundancy Analysis of species data constrained by the experimental design, the ordination explains a total of 61.9% of the species variation, with 58.7% of that variation being explained along axis one. In this diagram, only Age 15 is significant and it was strongly associated with *C. purpureus* and *H. revolutum.* The remainder of sites are strongly associated with *P. schreberi* and are not particularly distributed along axis one.

Of the measured environmental variables, canopy closure and light penetration to 2 m were significant (Figure 3.1.64). In this ordination, 60% of the variation was explained on the first two axes, 52.7% of it on axis one. Canopy closure was strongly associated with axis one and with the presence and dominance of *P. schreberi.* Distribution of sites along axis two was a function of the differences in sites older than 15 years. This distribution was strongly influenced by sites PL52A and PL78A which had distinctive moss assemblages.

DISCUSSION

Overstory and Light Conditions

Both the diameter and the height of jack pine trees increased with forest age and this would be expected to relate to changes in canopy closure and light attenuation. Accordingly, the degree of canopy closure increased with forest age and this was concomitant with a trend to a decrease in light penetration to 20 cm and 2 m. The greatest

change in conditions occurred between the 15- and the 25-year-old forests; little further change in either canopy closure or light attenuation was seen in older forests. This suggests that relatively complete canopy closure, i.e. the point at which the canopies of adjacent trees meet, occurred between 15 and 25 years in these forests. This would be expected as young jack pine are fast-growing and may reach a height of 6 m by 18 years of age in southeastern Manitoba (Kenkel et al. 1997).

The high number of tree stems per hectare in 15-year-old forests naturally regenerating after fire was expected. Jack pine seeds usually favour exposed mineral soil created by fire (Chrosciewicz 1974; Chrosciewicz 1990) and they germinate immediately after the disturbance (Kenkel et al. 1997). Patches of young jack pine are often very dense initially (Chrosciewicz 1971) and self thinning often does not occur until the forests are 20 – 30 years of age (Kenkel et al. 1997). Stem density was substantially reduced in the mid-aged naturally regenerating sites suggesting that in these forests, substantial self thinning occurs between 15 and 25 years and it continues until 35 years. In comparison, jack pine stem density remained similar in planted forest through all forest stages.

Although regeneration type had no significant influence on canopy conditions, light attenuation in the understory of planted forests tended to exceeded that of naturally regenerating forests, especially in the 15- and 35-year-old sites. The amount of light attenuation occurring between 2 m and 20 cm can be expected to generally relate to the degree of development of the shrub layer, therefore, this finding suggests that the shrub layer in planted forests is more developed. Greater light attenuation in the shrub layer would be expected to modify the ground level microclimate, buffering temperature and

moisture variability, in addition to decreasing the amount of light available for the growth of ground level vegetation (Oke 1987).

One site, B87A, had a high degree of canopy closure (53%) compared to the remainder of the 15-year-old forests. This site had relatively extensive areas of jack pine regeneration compared to its replicate, and in addition, trembling aspen had colonized the northern edge of this site providing more extensive tree cover. The trees of this site were taller (mean height 5.5 m), and this, in addition to greater canopy closure caused this site to appear to be more mature than the rest of the sites of this age group. These differences would be expected to influence understory vegetation and site fauna, contributing to differences in the assemblages between it and other forests of the same age within this study. It is difficult to say whether the differences between these two naturally regenerating sites represents a usual degree of site to site variability, however, there is no reason to believe that this would not be the case, as the structure and composition of young naturally regenerating sites would be expected to depend upon such factors as the composition of the forest prior fire and the severity of fire.

Ground Cover

Forest age influenced some aspects of ground cover including litter cover, bare ground and woody debris characteristics. The character of the litter layer changed with forest age. As litter production depends on the productivity of components of the plant community (Facelli and Pickett 1991), the character of the litter layer would be expected to change with forest succession. Grass litter decreased in per cent cover with forest age as grasses became a less dominant part of the understory vegetation. In contrast, the cover

of coniferous litter tended to increase, concomitant with the development of the coniferous overstory. This finding contrasts those of Ehnes (1998) who finds conifer litter cover to decrease with forest age in jack pine-dominated forests in eastern Manitoba. Litter accumulation depends upon both production and decomposition rates (Facelli and Pickett 1991), and the latter is affected by environment conditions including soil moisture (Brady and Weil 1999). Soils in the Sandilands region tend to be well drained and dry (Anderson 1960; Smith and Ehrlich 1964), therefore, litter decomposition rates in this area may be less than those of Ehne's study region. Litter structure may in turn influence plant community structure (Facelli and Pickett 1991) and insect assemblages (Koivula et al. 1999).

Per cent bare ground was significantly higher in the 15-year-old forests. In the boreal region, fire burns away organic material and exposes areas of mineral soil (Chrosciewicz 1990). Harvesting disturbs the forest floor as well, although does not tend to expose bare ground to the extent that fires does (Chrosciewicz 1990). After the initial bare ground phase, the understory plant community begins to recover (Rowe and Scotter 1973) and the amount of exposed ground would be expected to continue to decrease as the understory develops. This trend was evident in these sites, as per cent cover of the understory vegetation increased, the amount of bare ground decreased. This measure was strongly influenced by one site, B87B, which had many relatively large areas of bare ground.

Woody debris was most abundant in 15-year-old forests of both regeneration types. In boreal conifer forests, the volume of coarse woody debris in newly disturbed sites exceeds that of mature forests (Pedlar et al. 2002) and this trend appears to continue

into the 15-year-old sites of this study. After a decline in mid-aged forests a subsequent increase in the amount of woody was apparent in 50-year-old forests. A trend to increasing amounts of coarse woody debris as the forest reaches maturity is a trend common to many forests types (e.g. Spies et al. 1988; Sturtevant et al. 1997; Clark et al. 1998; Hély et al. 2000). Although increases in coarse woody debris accumulation occur in much older forests in other regions, jack pine forest reach maturity early, typically at 80-100 years (Kenkel et al. 1997), and as early as 70-90 years in southeastern Manitoba (T. Swanson, personal communication). Therefore, these trends would be expected to occur earlier in these sites.

In all 15-year-old sites, coarse woody debris was primarily in the early stages of decay, whereas in older forests woody debris of a variety of decay stages was present. As decay stage is one of the primary factors dictating the species inhabiting this substrate (Siitonen 2001), it would be expected that the presence of woody debris of different decay stages would contribute to floral and faunal diversity in these older sites.

Ground cover components such as plant cover and woody debris characteristics were also influenced by regeneration type. There was generally an inverse relationship between the proportion of herb and shrub vegetation, and different morphotype dominance patterns were seen in the different regeneration types. Herbaceous cover in naturally regenerating forests exceeded that of planted forests. Although there was not a significant influence of regeneration type on shrub cover, it tended to be higher in planted sites. A greater representation of shrubs in managed as compared to natural stands is a pattern common to other boreal conifer forests (Carleton and MacLellan 1994). The inverse relationship between shrubs and herbs was especially apparent in the 35-year-old

forests where the naturally regenerating sites supported far more herb cover than the planted sites, and the planted sites tended to have greater shrub cover. The relationship between herb and shrub cover in the young and mid-aged sites would be expected to occur as a result of competition for light; sites with high shrub cover had a greater degree of light attenuation through the shrub layer. For example, *A. uva-ursi* accounted for a large proportion of the herb layer in 25- and 35-year-old naturally regenerating sites, but formed a much smaller percentage of the herbaceous ground cover in the planted sites of the same age. *Arctostaphylos uva-ursi* typically grows in more exposed areas (Scoggan 1957), therefore it would be expected to have higher light requirements and thus would not thrive in these shrubby sites.

The amount of downed, coarse woody debris in 15-year-old naturally regenerating forests exceeded that of planted sites. A similar pattern is found in burned and harvested forests 13 years after disturbance in eastern Manitoba (Ehnes 1998), and in newly disturbed stands in northwestern Ontario (Pedlar et al. 2002). The degree of difference between regeneration types in this study exceeded that of the other studies, however, this may relate to differences in sampling regime (Ehnes 1998) and forest age (Pedlar et al. 2002). There was high snag volume in the newly burned sites examined by Pedlar et al. (2002), but snags were relatively rare in the 15-year-old forests of this study (Figure 3.1.27). Therefore, in the 15-year-old naturally regenerating sites of this study, downed, coarse woody would be comprised of both trees that were initially downed by fire as well as more recently fallen snags. This would account for the large amount of coarse woody debris in these sites relative to the newly disturbed sites examined by Pedlar et al (2002).

Although differences in woody debris between regeneration types did not persist in the mid-aged sites, a trend to greater abundance of woody debris was also apparent in the 50-year-old natural sites. This relates to the self thinning process of natural jack pine forests; tree mortality is very high in 20 – 35 year old stands (Kenkel et al. 1997). This phenomenon is illustrated by the snag density results; density in mid-aged naturally regenerating sites tended to exceed that of planted sites of the same age (Figure 3.1.27). The lesser amount of coarse woody debris in planted sites is of concern. In addition to providing an important substrate for some plants species (e.g. Lee and Sturgess 2001; Stewart et al. 2001), downed woody debris is important for some faunal communities (Goulet 1974; Samuelsson et al. 1994). Therefore in these managed forests, the community of saproxylic species may be altered, and the ecosystem services they provide may be affected. In addition, saproxylic species that have very specific habitat requirements may be lost from these managed forests entirely if their habitat is lost (Esseen et al. 1997). It should be noted the of the planted sites, one had approximately two and a half times the amount of woody debris of the other, suggesting that the coarse woody debris component in planted sites may be quite variable. This would depend to some extent on harvest methods, as harvesting methods leaving slash on the site would be expected to leave greater amounts of woody debris.

Understory Vegetation

Influence of forest age

Forest age influenced the understory vegetation in a number of ways. Per cent cover of spring ground vegetation increased with canopy closure in naturally regenerating

sites, however, did not increase substantially in planted sites until 50 years. A similar increase in cover of summer vegetation was seen in naturally regenerating sites older than 25-years. In planted sites, a reduction in cover with forest age was evident. An increased cover of ground vegetation would be expected with forest age given the development pattern of the herb community in these forests. Rather than species turnover, there is a trend to additive growth of the assemblage. As the forests age, more species join the assemblage, while few are lost, therefore the total cover of this community would be expected to expand over time, a pattern clearly seen in the naturally regenerating sites. The different pattern in the planted forests relates to development in the shrub layer and this will be discussed later in this section.

Species richness and diversity of both spring and summer vegetation increased with forest age, however the trend was only significant for species richness of spring vegetation. With the exception of 50-year-old plantations, species evenness also tended to increase with age. With increasing forest age, species more characteristic of mature forests began to occur in the assemblage, in addition to the established understory species tolerant of higher light conditions. This can be seen in both spring and summer ground vegetation communities. Fifteen-year-old sites tended to be dominated by species thriving in the post-disturbance conditions such as *A. uva-ursi*, *V. angustifolium* and grasses (Rowe and Scotter 1973; Rowe 1983). These species often persisted in abundance in older sites, along with species requiring more shade or soil moisture, such as *M. canadense*, *A. quinquefolia*, and *P. virens* (Looman and Best 1979). This is an interesting pattern in that many early successional species such as *A. uva-ursi* are documented to be shade-intolerant (Rowe 1983) yet clearly thrive in the closed canopy conditions of these

sites. Similar species patterns are evident in other boreal conifer forests, for example, *V. angustifolium* dominates the assemblage in newly burned sites as well as in forests 50 years post-fire in northern Quebec (Fortin et al. 1999). Likewise, *V. angustifolium* persists as a dominant part of the understory assemblage at the same time as species such as *M. canadense* increase in abundance with forest age in eastern Manitoba (Ehnes 1998).

The diversity trends in my study contrast with those described by other authors. Species richness of understory vegetation has often been found to increase in the initial years after disturbance (Chipman and Johnson 2002; Purdon et al. 2004), and this often continues until canopy closure (Hunt et al. 2003). However, after canopy closure, species richness and diversity tends to stay the same or decrease (Lindholm and Vasander 1987; Chipman and Johnson 2002; Hunt et al. 2003), while species evenness decreases as the abundance of non-dominant species decreases (de Grandpré et al. 1993). The contrasting results may have occurred for a number of reasons. Soils in the upland regions of the Sandilands Provincial Forest are particularly well drained, and this would be expected to limit the species that can colonize or thrive in the newly disturbed sites. Two species common in the 15-year-old sites, *V. angustifolium* and *A. uva-ursi*, thrive with overstory removal and may rapidly colonize disturbed sites (Rowe and Scotter 1973; Rowe 1983; Arnup et al. 1995; Fortin et al. 1999). Both species can reproduce asexually through rhizomes and tend to root in both the organic and mineral soil layer (Rowe 1983; Arnup et al. 1995). Reproduction of plants with such a rooting strategy is often stimulated by overstory removal, and by the removal of the litter layer, as long as disruption to the mineral layer is limited, thus both of these species can readily colonize newly disturbed areas (Arnup et al. 1995). *Andropogon gerardii* is well adapted to re-colonization of an

area after disturbance; it also regenerates from underground rhizomes (USDA Forest Service 1988). Re-growth of this species may be vigorous and it is stimulated by the removal of material shading the ground (USDA Forest Service 1988). Therefore, these three opportunistic species may monopolize resources and space, thereby suppressing or excluding other species; this pattern of species dominance has been found in newly disturbed jack pine sites in Michigan (Abrams and Dickmann 1982). In 1992, five years post-disturbance, these three species were also the most dominant (Lafrenière 1994), therefore it appears that many species were not able to establish in these sites until after canopy closure. As the canopy closes, growth conditions would be expected to change and these early colonizing species may not be able to compete as effectively for resources, allowing other species to establish. For example, *A. gerardii* was rarely found in older sites. The dry soil conditions of this region may allow some early successional species, such as *A. uva-ursi* and *V. angustifolium* to endure, as these species persisted in abundance in the mid-aged sites. These two species, especially *A. uva-ursi*, were much less abundant in 50-year-old sites perhaps relating to the high species richness and diversity found in the naturally regenerating sites of that age.

The time of year of sampling may also play a role in the discrepancies between this study and others, as species richness, especially in planted sites, tended to be higher in summer than the spring. In addition sampling regimes differed somewhat, some studies included shrubs, mosses or lichens with herbaceous ground cover (Hunt et al. 2003), or did not define the community specifically (Lindholm and Vasander 1987; Chipman and Johnson 2002), therefore differences within different components of the understory layer may have been missed. Finally, in this study some grasses, especially in the summer

sampling period, could not be identified to species, as they were not flowering, and therefore could not be used in the analysis. It is possible that if these were included, the findings might be somewhat different.

Community analysis also revealed some age-related trends in the understory herb community. The 15-year-old sites, with the exception of B87A, were the most distinctive age related group in the unconstrained ordinations (Figures 3.1.35 and 3.1.44). These sites tended to have a higher representation of species more typical of open habitats or clearings such as *A. gerardi*, *A. uva-ursi*, *A. neglecta* and *V. adunca* (Scoggan 1957; Looman and Best 1979). Site B46A had a strong influence on the distribution of sites in the ordinations. This site had a distinct ground vegetation community, with an absence of many of the open habitat species, a greater abundance of species common to moist, closed canopy conditions such as *A. quinquefolia* and *M. canadense* (Looman and Best 1979) and many unique species such as, *C. cornuta*, *T. borealis* and *P. aquilinum*. Rather than representing a true successional gradient, the unconstrained ordinations generally separated the more distinctive 15-year-old sites from the older sites. Site B87A tended to separate from the rest of the sites in the 15-year-age group due to a paucity of species, such as *A. uva-ursi* and *V. angustifolium* which tended to be the dominant species in the remainder of the 15-year-old sites. In addition, B87A had a greater abundance of some species, such as *F. virginiana* and *A. quinquefolia*, more common to the older sites of this study.

Constrained ordination analyses were also similar for both spring and summer ground vegetation (Figures 3.1.36, 3.1.37, 3.1.45 and 3.1.46). In these ordinations young sites were the most distinctive age-related group, again with the exception of B87A.

These sites were associated with relatively open canopy conditions where higher levels of light reached the forest floor. The sites older than 15 years, where the canopy was essentially closed, separated on the basis of tree height. This generally related to a successional gradient; in the closed canopy forests, those with taller trees supported plant species favouring higher moisture conditions, such as *P. virens*, *M. canadense*, *A. quinquefolia* and *Fragaria virginiana* (Looman and Best 1979) and these sites separated from those with shorter trees and with plants common to open or sandy woodlands such as *Oryzopsis pungens*, *Lathyrus ochroleucus* and *Symphoricarpos albus* (Looman and Best 1979).

The moss assemblage was strongly influenced by forest age. *Pleurozium schreberi* tended to increase in per cent cover with forest age, a trend common to this species (Ehnes 1998; Fortin et al. 1999; Hunt et al. 2003). This trend was primarily responsible for the increase in per cent cover of the moss assemblage with forest age. The increase in abundance of this species, as well as the loss or reduction of species such as *C. purpureus* and *H. revolutum* that were characteristic of 15-year-old sites, influenced the reduction in both species diversity and evenness in mid-aged sites. Diversity trends changed in the 50-year-old forests as more species became established. Forests provide an ideal environment for mosses and as a result, in a mature forest a number of species, some of low abundance, can persist (Newmaster and Bell 2002). Thus relatively high species diversity and evenness may be evident in these forests. However, the increase in species richness with forest age found in this study contrasts the findings of Reich et al. (2001) who note a trend to decreasing moss species richness between 30 and 80 year old jack pine forests. Although the results of the current study were strongly influenced by

one site, PL52A, which was particularly speciose, this does not explain the contrasting findings. It appears that in these forests there is a general trend to increasing species richness with forest age in all components of the understory, so perhaps this is a regional phenomenon.

The strong influence of *P. schreberi* is evident in the ordination diagrams (Figures 3.1.62, 3.1.63 and 3.1.64). The distribution of sites along axis one was strongly associated with the presence and abundance of this species, separating the 15-year-old sites which had a low abundance of this species, from sites older than 15 years.

The shrub assemblage also followed some age-related trends. The shrub community in 15-year-old forests differed from that of older forests (Figures 3.1.53, 3.1.54 and 3.1.55). Fifteen-year-old sites were characterized by species such as *P. pumila* and *S. alba*, both species more common to prairies or clearings (Scoggan 1957; Looman and Best 1979). However, sites with high shrub cover, such as PL64B, PL76B and B46A had a strong influence on the ordination diagrams, and this affected the distribution of the sites older than 15 years.

Although beta diversity was not significantly influenced by regeneration type, this measure showed similar trends over all of the vegetation types. Regardless of the diversity measure used, beta diversity between replicates was greatest in the 50-year-old stands. As the initial understory plant assemblage is known to depend a great deal on site specific factors such as the severity of disturbance and on pre-disturbance conditions (Ahlgren 1960; Schimmel and Granström 1996; Nguyen-Xuan et al. 2000; Pykälä 2004), beta diversity of the understory assemblages would be expected to be highest in young

forest and gradually decrease as forests age. Therefore, the trend in these forests is an interesting phenomenon.

Influence of regeneration type

Regeneration type had a strong influence on some aspects of the understory vegetation community including the richness of spring ground vegetation, total cover of spring and summer ground vegetation and community composition. Although not significant, there was also a trend to higher shrub cover in planted sites, especially in the 25- and 35-year-old forests. It would be difficult to attribute these differences specifically to regeneration method though, as disturbance type would have a strong influence on the understory community as well. Disturbance type (fire or harvest) is found to influence species richness, diversity, and species composition especially soon after the event (Abrams and Dickmann 1982; Johnston and Elliott 1996; Crites 1999; Nguyen-Xuan et al. 2000; Reich et al. 2001).

Total cover of spring vegetation was significantly greater in the naturally regenerating sites. The less extensive cover of herbaceous plants in 25- and 35-year-old planted sites likely related to the high cover of shrubs in these sites. Shrub species that were relatively abundant in these sites included species such as *A. alnifolia* and *C. cornuta* which often grew to over two metres and formed a sub-canopy in some areas, especially in PL64B. Both these species proliferate after logging, once the overstory is removed (Carleton and MacLellan 1994). Increased sprouting of *Amelanchier* species after disc trenching is documented (Arnup et al. 1995). Although vegetative reproduction of *C. cornuta* is generally deterred by site preparation, it does demonstrate aggressive

growth, often out-competing other species for moisture and light (Arnup et al. 1995). Therefore, harvesting and planting, when not followed with effective competition control strategies may alter the understory structure of a forest.

A greater number of spring plant species were present in naturally regenerating forests. These findings are comparable to those of Abrams and Dickmann (1982) who found higher vascular plant species richness in burned than harvested jack pine forests in the initial years after disturbance. Few studies describe the effects of disturbance type after the initial few years of forest re-establishment although changes persisted in many 25-40 year old jack pine stands; older forests showed either greater diversity post harvest than post fire or there was no difference between disturbance types (Reich et al. 2001). It is possible that initial differences in the plant community due to disturbance type have persisted to the current sites, particularly the 15-year-old sites. This may have occurred if the strong influence of dominant species in the planted sites inhibited colonization of new species. It is also conceivable that the high shrub cover in planted sites affected the species richness in those sites, as fewer ground species may be able to compete for resources in these shrubby sites. In addition, the greater canopy variability in the 15-year-old naturally regenerating sites may have influenced species richness in these sites by providing a variety of microclimatic conditions.

Differences in spring assemblage composition related to regeneration type were only evident in the 15-year-old sites. This primarily occurred because of differing abundances of the dominant species in sites of differing regeneration types, as most plant species influencing the ordination were common to both regeneration types. There was a higher abundance of *A. uva-ursi* and *V. angustifolium* in the planted sites and the greater

abundance of *R. acicularis* in the naturally regenerating ones. Ehnes (1998) also found per cent cover of *A. uva-ursi* and *V. angustifolium* in harvested areas exceeded that of burned sites at a similar point after disturbance. In these same sites, *R. acicularis* was initially more abundant in harvested than burned stands, however, this pattern reversed with forest age (Ehnes 1998).

Total cover of summer vegetation in naturally regenerating stands exceeded that of planted stands; this occurred in forests older than 15 years. This differed from the pattern found in the spring vegetation in that the summer ground vegetation cover in natural stands exceeded that of planted stands in the 50-year-old stands as well as the mid-aged sites. It is expected that the lower cover of summer vegetation in the 25- and 35-year-old planted stands was related to the high shrub cover in these same sites, as previously described. The trend to high summer vegetation cover in the 50-year-old naturally regenerating forests occurred because there was a greater abundance of late successional species such as *P. virens* and *M. canadense* in these sites and this offset the decreasing cover of species such as *V. angustifolium* and *A. uva-ursi* that generally occurred at this stage. However this does not account for the very large differences between regeneration types in 50-year-old forests. If higher shrub cover was common to all 25- to 35-year-old planted sites, perhaps suppression of the summer herb layer at this stage will contribute to lower cover in older sites if plant species are unable to establish effectively in these forests.

Differences in community composition related to regeneration type were only evident in the 15-year-old sites. Similar to the trends in the community composition of the spring vegetation, this primarily occurred because of differing abundances of the

dominant species in sites of differing regeneration types. There was a higher abundance of *A. uva-ursi* and *V. angustifolium* in the planted sites and a greater abundance of A. *gerardii* in naturally regenerating sites. *Andropogon gerardi* is species typical of grasslands (Scott 1995) and as such is particularly adept at re-establishing after fire (USDA Forest Service). This would be expected to favour the establishment of this species in naturally sites. However, this trend was not apparent in these sites in 1992 (Lafrenière 1994). This difference may be an artefact of sampling; in the current study much of the grass within the summer assemblage could not be identified as it was not in a flowering stage and this may have included *A. gerardii*.

SUMMARY

For each of the components analysed, a summary of the main findings follows:

- Canopy closure increased significantly with forest age. There was no statistical difference in canopy closure between regeneration types. Canopy variability was not significantly different but showed a trend to higher variability in 15-year-old naturally regenerating forests.
- Light attenuation to 20 cm and to 2 m was not significantly influenced by forest age or regeneration type, however, tended to increase with forest age. Light attenuation in the understory was close to being significantly influenced by the interaction of forest age and regeneration type. Light attenuation in the understory (between 2 m and 20 cm) tended to be higher in 15- and 35-year-old planted sites.
- Jack pine diameter and height increased with age but did not differ between regeneration types. The number of jack pine stems per ha was significantly influenced by forest age, regeneration type and the interaction of the two. This was a result of the high density of jack pine stems in 15-year-old naturally regenerating forests.
- Per cent ground cover of herbs was significantly greater in natural sites. There was a trend to higher per cent cover of shrubs in mid-aged planted sites. Neither of these components was statistically influenced by forest age. Per cent cover of moss and lichen was not significantly influenced by forest age, regeneration type or the interaction of the two. Of the non-living ground cover components, there was a significant decrease in grass litter cover and increase in conifer litter cover with forest age. There was no significant influence of regeneration type or the

interaction of age and regeneration type on conifer or grass litter cover. The amount of bare ground decreased with forest age but was not significantly influenced by regeneration type or the interaction of the two factors. Other ground cover components such as per cent cover of fine woody debris and deciduous litter were not significantly different between forests of different ages or regeneration types.

- The number of pieces of downed, coarse woody debris was affected by forest age and regeneration type. This was a result of the large number of pieces in 15-year-old naturally regenerating sites. There was a significant interaction of decay stage and forest age but not of decay stage and regeneration type.
- Snag density and diameter were not significantly different between forests of different ages and regeneration types. There was a trend to greater snag density in naturally regenerating sites.
- Per cent cover of spring ground vegetation increased with forest age and was higher in natural forests. Species richness was greater in naturally regenerating stands. Species richness tended to increase with forest age in the natural sites but not significantly so. Alpha diversity and species evenness were not significantly influenced by forest age, regeneration type or the interaction of the two. Both alpha diversity and species evenness tended to increase with forest age. Beta diversity was not significantly affected by regeneration type. Assemblage composition in the 15-year-old sites was distinct from that in older sites. Composition differed somewhat between natural and planted sites within this age group.

- Per cent cover of summer ground vegetation was greater in naturally regenerating stands. Cover was not significantly influenced by age but tended to increase with forest age in natural forests and decrease with age in planted forests. Species richness, alpha diversity and species evenness were not significantly influenced by forest age or regeneration type. Species richness, alpha diversity and species evenness tended to increase with forest age. Beta diversity was not significantly affected by regeneration type. Assemblage composition in the 15-year-old sites was distinct from that in older sites. Composition differed somewhat between natural and planted sites within this age group.
- Species evenness of the shrub assemblage increased with forest age but was not affected by regeneration type. Per cent cover, species richness and alpha diversity were not significantly affected forest age or regeneration type or the interaction of the two. Regeneration type had no significant influence on beta diversity. The shrub assemblage of 15-year-old sites differed in composition from that of older sites.
- Species richness, alpha diversity and species evenness of mosses were affected by age but not regeneration type or the interaction of age and regeneration type. Species richness tended to increase with forest age, alpha diversity and species evenness decreased with forest age to 35 year and then increased. Per cent cover, was not significantly different but tended to increase with forest age. Moss assemblage composition in 15-year-old sites differed from that of older sites.

Table 3.1.1 Site origin, age and location

Site	Year of origin	Age class	Regeneration type	Latitude (degrees/ minutes)	Longitude (degrees/ minutes)	Elevation (m)
B46A	1946	50	Natural	49°14.138 N	95°52.923 W	374
B52B	1952	50	Natural	49°18.629 N	96°07.185 W	363
B64A	1964	35	Natural	49°19.215 N	96°07.673 W	382
B63B	1963	35	Natural	49°12.687 N	96°19.211 W	345
B74A	1974	25	Natural	49°18.376 N	96°07.506 W	392
B76B	1976	25	Natural	49°07.146 N	96°04.374 W	376
B87A	1987	15	Natural	49°24.659 N	96°07.457 W	351
B87B	1987	15	Natural	49°23.636 N	96°09.858 W	374
PL52A	1952	50	Planted	49°18.330 N	96°10.495 W	382
PL52B	1952	50	Planted	49°16.415 N	96°05.781 W	379
PL65A	1965	35	Planted	49°22.002 N	96°17.490 W	382
PL64B	1964	35	Planted	49°20.821N	96°16.425 W	381
PL78A	1978	25	Planted	49°29.204 N	96°07.633 W	334
PL76B	1976	25	Planted	49°20.056 N	96°16.155 W	376
PL89A	1989	15	Planted	49°24.790 N	96°11.582 W	373
PL89B	1989	15	Planted	49°23.416 N	96°11.413 W	379

Table 3.1.2 Decay classification of coarse woody debris

Decay class	Wood texture	Portion on ground	Twigs < 3 cm	Bark	Shape
Class 1	many small pieces, soft portions	all of log on ground, partly sunken	no twigs	no bark	oval
Class 2	small, blocky pieces	all of log on ground, sinking	no twigs	no bark	round to oval
Class 3	hard, large pieces, partly decaying	sagging near ground, or broken	no twigs	trace bark	round
Class 4	intact, hard to partly decaying	elevated but sagging slightly	no twigs	intact or partly missing	round
Class 5	intact, hard	elevated on support points	twigs present	bark intact	round

Classification system after British Columbia Ministry of Sustainable Resource Management (2004)

Table 3.1.3 Analysis of variance results for forest structure measures

Measure	Effect	df	F-ratio	P
Canopy closure	Age	3	10.057	0.00
	Regeneration	1	0.181	0.68
	Age*Regeneration	3	0.432	0.74
	Error	8		
Canopy variability (CV)	Age	3	0.064	0.98
	Regeneration	1	0.347	0.57
	Age*Regeneration	3	1.309	0.34
	Error	8		
Light attenuation to 20 cm	Age	3	2.743	0.11
	Regeneration	1	0.033	0.86
	Age*Regeneration	3	0.317	0.81
	Error	8		
Light attenuation to 2 m	Age	3	2.849	0.11
	Regeneration	1	0.258	0.63
	Age*Regeneration	3	0.271	0.85
	Error	8		
Light attenuation between 2 m and 20 cm	Age	3	2.609	0.12
	Regeneration	1	4.595	0.06
	Age*Regeneration	3	0.790	0.53
	Error	8		
Tree stems per ha	Age	3	1.432	0.30
	Regeneration	1	2.300	0.17
	Age*Regeneration	3	3.541	0.07
	Error	8		
Jack pine stems per ha	Age	3	8.487	0.01
	Regeneration	1	13.706	0.01
	Age*Regeneration	3	6.519	0.02
	Error	8		
Mean stem diameter	Age	3	1.119	0.40
	Regeneration	1	1.886	0.21
	Age*Regeneration	3	0.502	0.69
	Error	8		

Measure	Effect	df	F-ratio	P
Mean jack pine stem diameter	Age	3	22.497	0.00
	Regeneration	1	4.494	0.07
	Age*Regeneration	3	0.432	0.74
	Error	8		
Mean tree height	Age	3	54.809	0.00
	Regeneration	1	1.357	0.28
	Age*Regeneration	3	0.605	0.63
Snags per ha	Age	3	0.530	0.67
	Regeneration	1	3.860	0.09
	Age*Regeneration	3	0.901	0.48
	Error	8		
Mean snag diameter	Age	3	12.612	0.00
	Regeneration	1	1.569	0.25
	Age*Regeneration	3	1.256	0.35
	Error	8		
Number of coarse woody debris pieces	Age	3	33.529	0.00
	Regeneration	1	31.572	0.00
	Age*Regeneration	3	11.637	0.00
	Error	8		

Table 3.1.4 Univariate analysis of variance results for ground cover

	Measure	Effect	df	F-ratio	P
Living plants	Shrub (log)	Age	3	1.83	0.22
		Regeneration	1	0.799	0.40
		Age*Regeneration	3	0.422	0.74
		Error	8		
	Herb	Age	3	0.484	0.70
		Regeneration	1	6.106	0.04
		Age*Regeneration	3	1.570	0.27
		Error	8		
	Moss (log)	Age	3	1.680	0.25
		Regeneration	1	0.059	0.81
		Age*Regeneration	3	0.689	0.58
		Error			
	Lichen	Age	3	0.426	0.74
		Regeneration	1	0.009	0.93
		Age*Regeneration	3	0.674	0.59
		Error	8		
Non-plant cover	Coarse woody debris	Age	3	6.909	0.01
		Regeneration	1	1.824	0.21
		Age*Regeneration	3	1.720	0.24
		Error	8		
	Fine woody debris	Age	3	1.496	0.29
		Regeneration	1	0.880	0.38
		Age*Regeneration	3	0.933	0.47
		Error	8		
	Conifer litter	Age	3	4.006	0.05
		Regeneration	1	0.003	0.96
		Age*Regeneration	3	0.794	0.53
		Error	8		
	Deciduous litter (log x+1)	Age	3	0.198	0.89
		Regeneration	1	0.000	0.98
		Age*Regeneration	3	2.273	0.16
		Error	8		

Measure	Effect	df	F-ratio	P
Grass litter	Age	3	6.196	0.02
	Regeneration	1	2.308	0.17
	Age*Regeneration	3	0.461	0.72
	Error	8		
Bare ground (log x+1)	Age	3	5.375	0.03
	Regeneration	1	0.001	0.98
	Age*Regeneration	3	0.140	0.93
	Error	8		

Table 3.1.5 Per cent cover of domiant spring ground vegetation species

Species	Regeneration type	Mean % cover ± SE 15 years	25 years	35years	50 years
Vaccinium angustifolium	Natural	5.8 ± 2.5	25.2 ± 7.6	10.1 ± 3.2	7.1 ± 2.4
	Planted	8.8 ± 1.0	11.9 ± 7.1	3.4 ± 1.9	8.5 ± 3.4
Arctostaphylos uva-ursi	Natural	8.1 ± 7.6	17.6 ± 2.1	16.2 ± 2.4	6.6 ± 6.6
	Planted	14.4 ± 3.6	7.3 ± 3.5	1.1 ± 0.6	7.1 ± 3.4
Anemone quinquefolia	Natural	0.6 ± 0.6	9.3 ± 3.4	7.2 ± 0.1	10.4 ± 3.1
	Planted	0.2 ± 0.2	6.1 ± 4.5	5.9 ± 3.8	9.5 ± 9.4
Maianthemum canadense	Natural	1.0 ± 0.8	3.4 ± 0.4	5.4 ± 3.8	10.3 ± 0.9
	Planted	0.4 ± 0.2	2.6 ± 2.4	4.8 ± 4.8	5.0 ± 1.9
Pyrola virens	Natural	3.1 ± 0.6	0	5.3 ± 5.2	8.0 ± 5.9
	Planted	0.6 ± 0.6	0	0.1 ± 0.1	13.0 ± 4.9
Oryzopsis asperifolia	Natural	0	2.0 ± 2.0	3.9 ± 3.9	2.8 ± 0.4
	Planted	0	2.6 ± 0.2	4.3 ± 0.6	5.1 ± 5.1
Antennaria neglecta	Natural	5.2 ± 3.4	2.6 ± 2.1	4.0 ± 4.0	0.5 ± 0.5
	Planted	0	0	2.7 ± 1.9	4.7 ± 4.7
Fragaria virginiana	Natural	1.2 ± 1.2	2.0 ± 0.6	1.4 ± 0.4	3.3 ± 0.2
	Planted	0.3 ± 0.3	3.2 ± 2.6	2.4 ± 1.1	1.4 ± 0.4
Symphoricarpos albus	Natural	0	1.5 ± 1.3	0.5 ± 0.3	0.4 ± 0.4
	Planted	0.3 ± 0.3	2.4 ± 2.4	5.1 ± 2.2	0.1 ± 0.1
Galium boreale	Natural	0.1 ± 0.1	1.3 ± 0.6	1.5 ± 0.5	0.7 ± 0.4
	Planted	0.4 ± 0.4	2.0 ± 0.6	1.8 ± 0.7	0.2 ± 0.2

Table 3.1.6 Analysis of variance results for understory vegetation

			Spring		Summer		Shrub*		Moss*	
Measure	Effect	df	F-ratio	P	F-ratio	P	F-ratio	P	F-ratio	P
Total cover	Age	3	5.132	0.03	0.746	0.55	1.635	0.26	3.523	0.07
	Regeneration	1	6.467	0.03	11.476	0.01	0.583	0.47	0.069	0.80
	Age*Regeneration	3	1.531	0.28	2.669	0.12	0.719	0.57	0.121	0.95
	Error	8								
Number of species	Age	3	1.739	0.24	0.983	0.45	1.048	0.42	7.178	0.01
	Regeneration	1	12.333	0.01	0.117	0.74	0.095	0.77	3.267	0.11
	Age*Regeneration	3	1.258	0.35	1.987	0.19	0.540	0.67	0.600	0.63
	Error	8								
Shannon-Wiener diversity	Age	3	2.355	0.15	1.060	0.33	2.635	0.12	9.019	0.01
	Regeneration	1	2.175	0.18	2.275	0.16	1.051	0.34	2.993	0.12
	Age*Regeneration	3	1.822	0.22	1.435	0.30	1.708	0.24	2.887	0.10
	Error									
Shannon-Wiener evenness	Age	3	1.409	0.31	1.836	0.22	4.856	0.03	7.740	0.01
	Regeneration	1	0.054	0.82	1.251	0.30	1.240	0.30	0.135	0.72
	Age*Regeneration	3	1.557	0.27	2.274	0.16	1.781	0.23	0.475	0.71
	Error	8								

* Total cover of shrubs and mosses was log transformed prior to analysis

Table 3.1.7 Per cent cover of dominant summer ground vegetation species

Species	Regeneration type	Mean % cover ± SE 15 years	25 years	35 years	50 years
Vaccinium angustifolium	Natural	6.0 ± 1.9	18.7 ± 8.6	6.8 ± 2.5	5.8 ± 4.0
	Planted	11.8 ± 3.3	10.3 ± 8.5	7.7 ± 5.8	6.3 ± 6.3
Arctostaphylos uva-ursi	Natural	6.9 ± 5.1	13.3 ± 1.6	15.1 ± 3.5	3.4 ± 3.4
	Planted	16.3 ± 5.3	6.1 ± 3.9	1.9 ± 1.7	4.7 ± 3.8
Maianthemum canadense	Natural	1.9 ± 1.3	7.1 ± 0.1	14.8 ± 6.9	17.9 ± 8.7
	Planted	0.3 ± 0.3	2.9 ± 0.1	8.0 ± 7.9	14.0 ± 0.4
Andropogon gerardii	Natural	22.5 ± 3.2	0.5 ± 0.5	0	0
	Planted	18.9 ± 1.8	0	0	0
Pyrola virens	Natural	3.7 ± 1.5	0	4.4 ± 4.4	6.4 ± 5.6
	Planted	0.8 ± 0.8	0	0	3.5 ± 2.5
Fragaria virginiana	Natural	3.8 ± 3.8	2.4 ± 0.1	2.9 ± 1.5	2.6 ± 0.7
	Planted	0.7 ± 0.7	2.4 ± 2.4	3.1 ± 0.6	0.8 ± 0.3
Melampyrum lineare	Natural	0.9 ± 0.7	2.8 ± 2.4	1.2 ± 1.1	1.5 ± 1.5
	Planted	0.3 ± 0.1	4.8 ± 4.7	0.1 ± 0.1	4.0 ± 0.7
Antennaria neglecta	Natural	3.3 ± 2.6	2.2 ± 2.2	2.8 ± 2.0	0.9 ± 0.9
	Planted	0	1.6 ± 1.6	3.0 ± 2.3	1.3 ± 1.3
Galium boreale	Natural	0	1.5 ± 0.1	3.8 ± 0.9	1.7 ± 0.4
	Planted	1.8 ± 1.8	1.6 ± 0.1	2.7 ± 0.5	1.0 ± 1.0

Table 3.1.8 Per cent cover of dominant shrub species

Species	Regeneration type	Mean % cover ± SE 15 years	25 years	35 years	50 years
Amelanchier alnifolia	Natural	2.2 ± 2.1	3.3 ± 2.0	9.4 ± 6.3	3.9 ± 2.9
	Planted	1.2 ± 1.2	8.7 ± 5.1	14.3 ± 3.0	3.2 ± 1.5
Prunus virginiana	Natural	0.1 ± 0.1	3.7 ± 0.2	11.8 ± 2.3	2.7 ± 0.4
	Planted	2.0 ± 0.3	10.8 ± 10.4	7.2 ± 4.3	5.5 ± 0.3
Symphoricarpos albus	Natural	0	4.8 ± 1.6	1.0 ± 0.3	4.4 ± 2.3
	Planted	0.9 ± 0.4	3.8 ± 3.6	13.9 ± 12.4	2.1 ± 2.1
Rosa acicularis	Natural	1.1 ± 0.7	2.0 ± 1.8	1.6 ± 0.9	6.9 ± 2.6
	Planted	0.9 ± 0.7	1.1 ± 1.1	4.7 ± 0.9	4.1 ± 1.3
Vaccinium angustifolium	Natural	0.1 ± 0.1	2.7 ± 1.5	1.1 ± 0.1	4.2 ± 0.3
	Planted	0.9 ± 0.7	2.4 ± 1.4	1.7 ± 1.0	2.8 ± 0.5
Corylus cornuta	Natural	0	0	0	5.6 ± 5.6
	Planted	0	0	8.3 ± 8.3	0
Prunus pensylvanica	Natural	1.0 ± 1.0	0.1 ± 0.1	0.7 ± 0.5	1.4 ± 1.0
	Planted	2.1 ± 0.7	0	1.9 ± 0.6	1.2 ± 0.8

Table 3.1.9 Per cent cover of dominant moss species

Species	Regeneration type	Mean % cover ± SE			
		15 years	25 years	35 years	50 years
Pleurozium schreberi	Natural	0.6 ± 0.6	20.9 ± 9.6	25.3 ± 5.5	29.4 ± 11.3
	Planted	0.5 ± 0.5	9.1 ± 3.1	27.4 ± 20.7	30.4 ± 3.7
Dicranum polysetum	Natural	0	6.7 ± 0.7	1.4 ± 0.1	3.8 ± 3.2
	Planted	0.2 ± 0.1	4.7 ± 4.3	0.6 ± 0.4	2.4 ± 0.8
Ceratodon purpureus	Natural	6.4 ± 3.5	0.1 ± 0.1	0	0.1 ± 0.1
	Planted	3.1 ± 1.6	0	0	0.1 ± 0.1
Hylocomium splendens	Natural	0	0	1.1 ± 1.1	0.4 ± 0.4
	Planted	0	0	0	6.0 ± 5.8
Hypnum revolutum	Natural	1.3 ± 1.1	0	0	0
	Planted	3.2 ± 0.3	0	0	0

Figure 3.1.1 Location of study sites in Sandilands Provincial Forest.

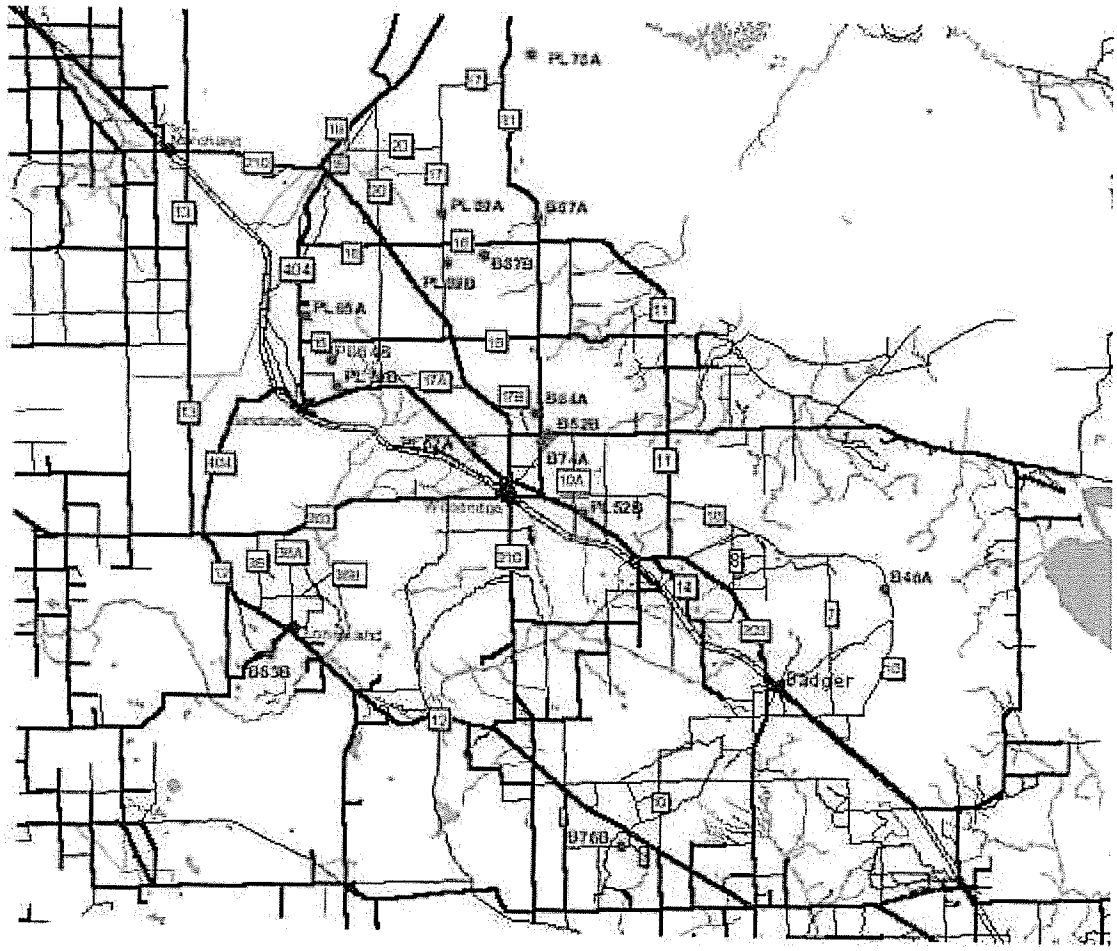


Figure 3.1.2 Arrangement of sampling points for canopy closure and light attenuation measurements and pitfall trap locations.

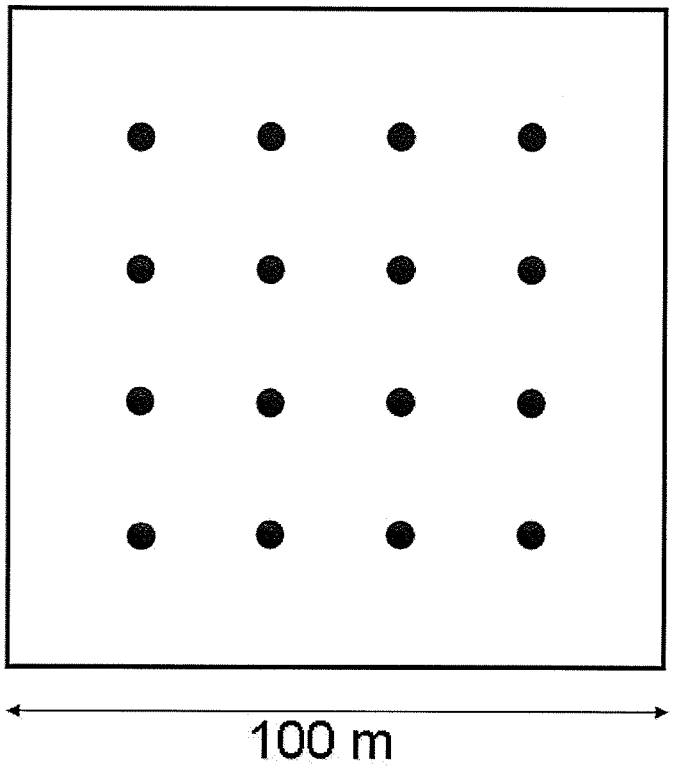
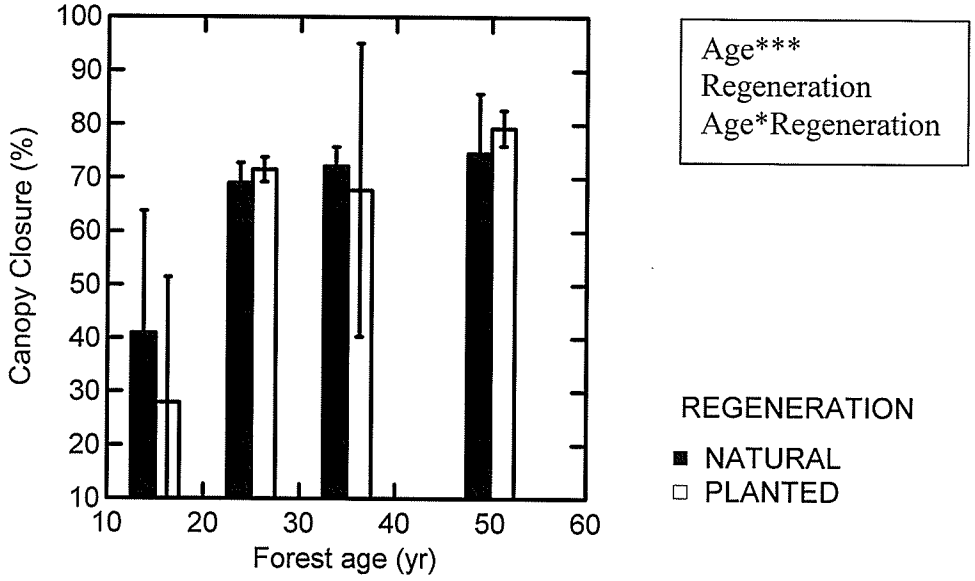


Figure 3.1.3 Fifteen-year-old naturally regenerating site (B87A)

Figure 3.1.4 Fifteen-year-old planted site (PL89A)

Figure 3.1.5 Per cent canopy closure (mean ± SE); patterns related to forest age and regeneration type.



Significance values: * $p \leq 0.05$, ** $p \leq 0.01$, *** $p \leq 0.005$

Figure 3.1.6 Canopy variability (mean ± SE); patterns related to forest age and regeneration type.

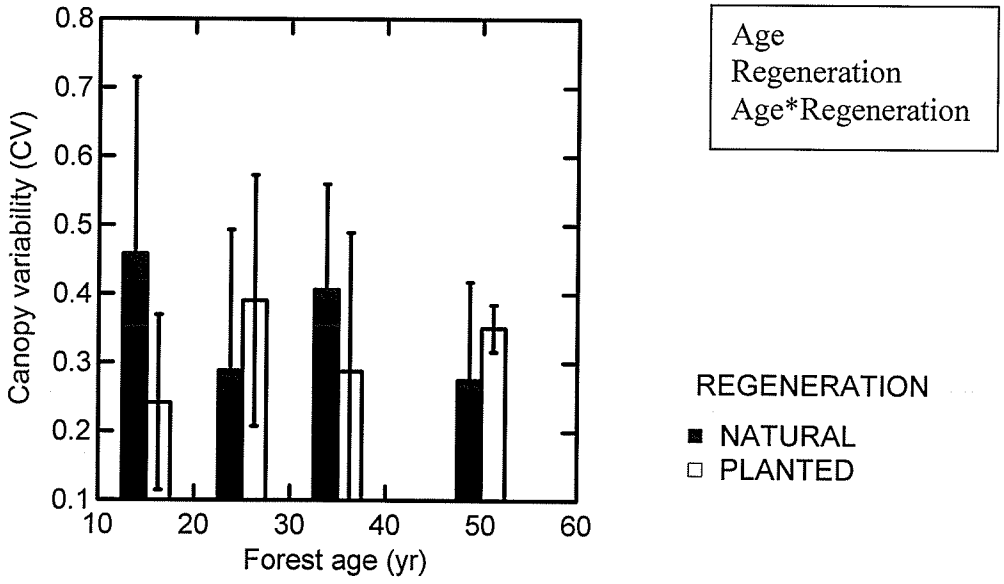


Figure 3.1.7 Light attenuation to 20 cm above ground (mean ± SE); patterns related to forest age and regeneration type.

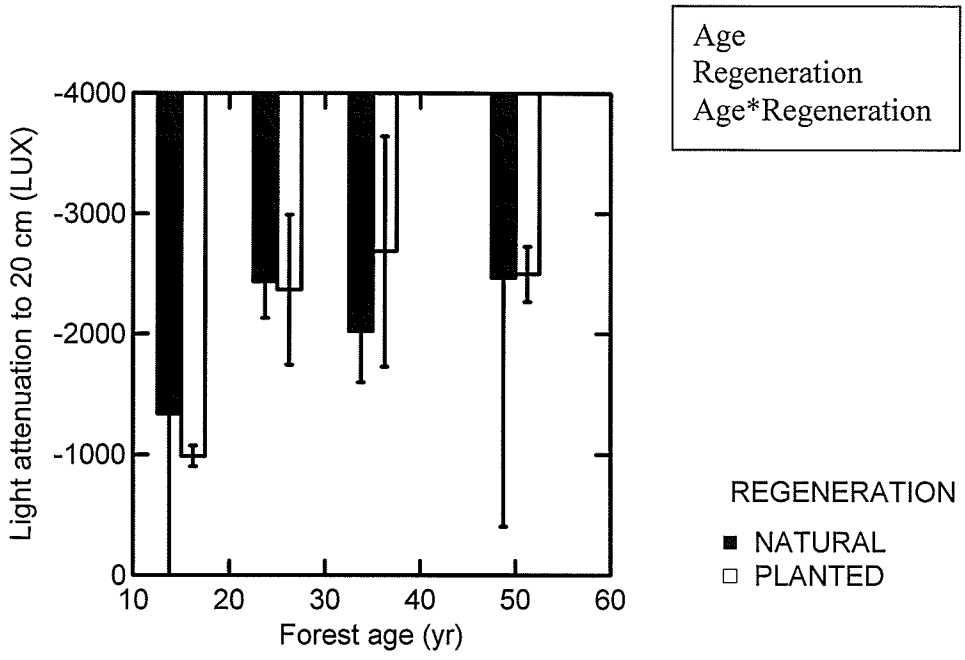


Figure 3.1.8 Light attenuation to 2 m above ground (mean ± SE); patterns related to forest age and regeneration type.

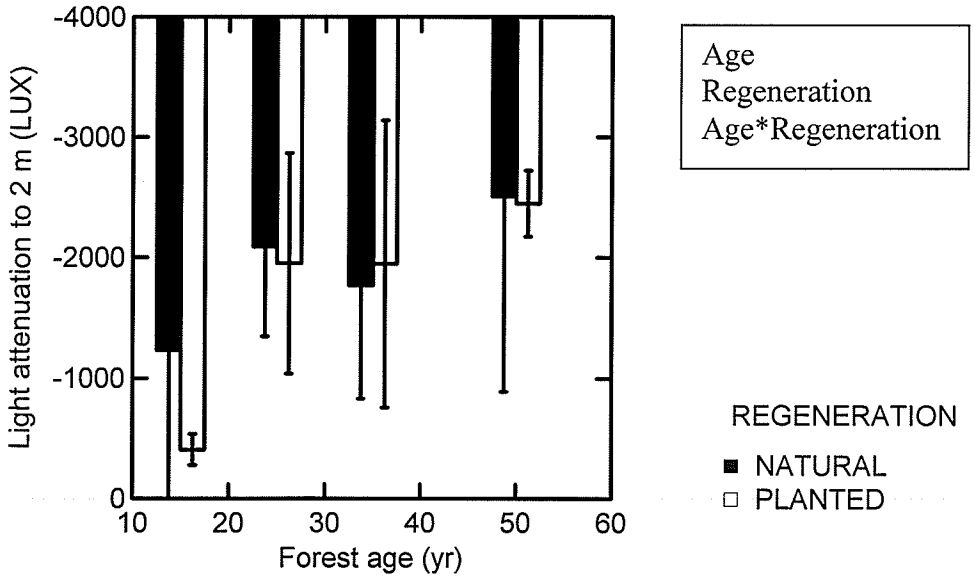


Figure 3.1.9 Light attenuation between 2 m and 20 cm (mean ± SE); patterns related to forest age and regeneration type.

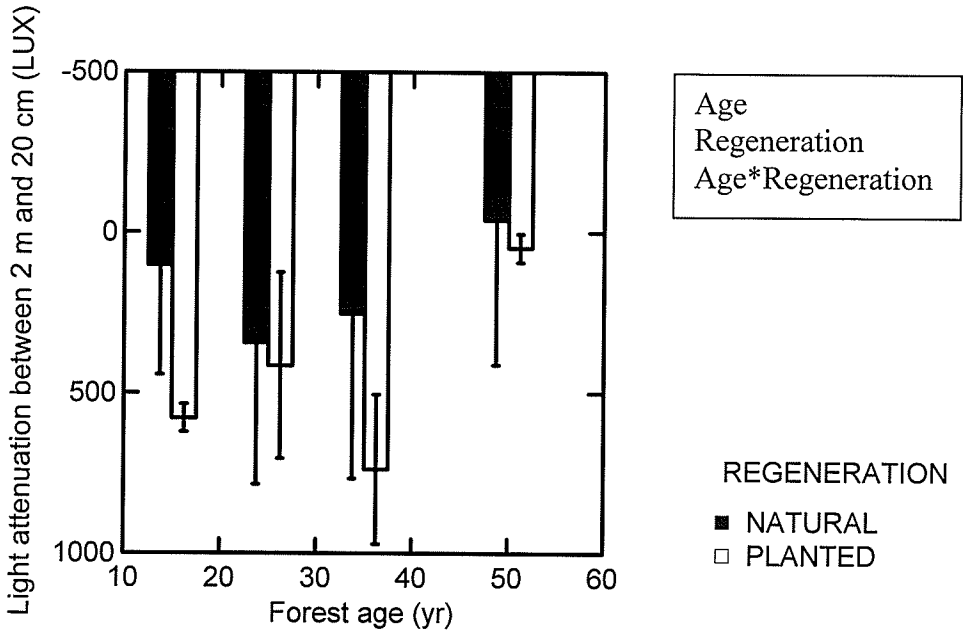


Figure 3.1.10 Per cent cover of shrubs (mean ± SE); patterns related to forest age and regeneration type.

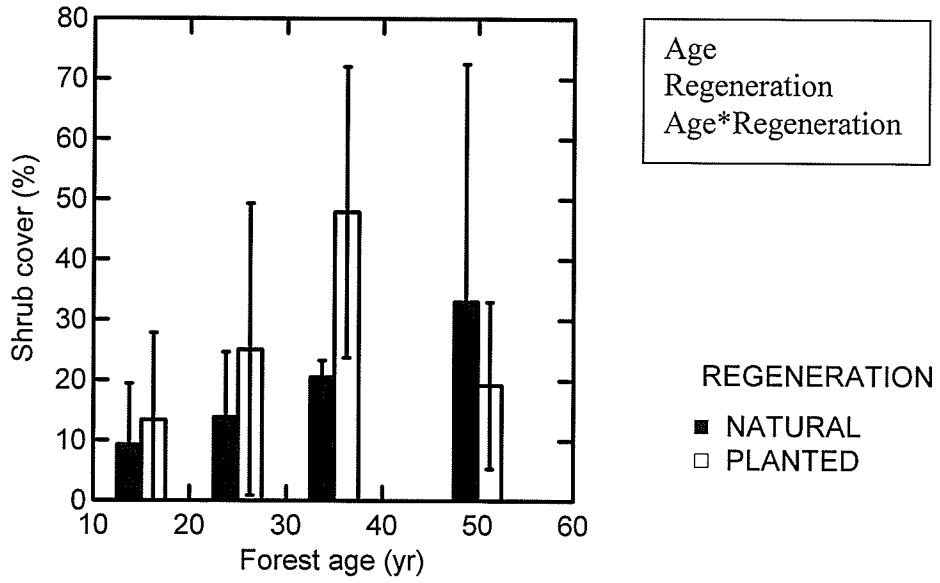


Figure 3.1.11 Per cent cover of herbs (mean ± SE); patterns related to forest age and regeneration type.

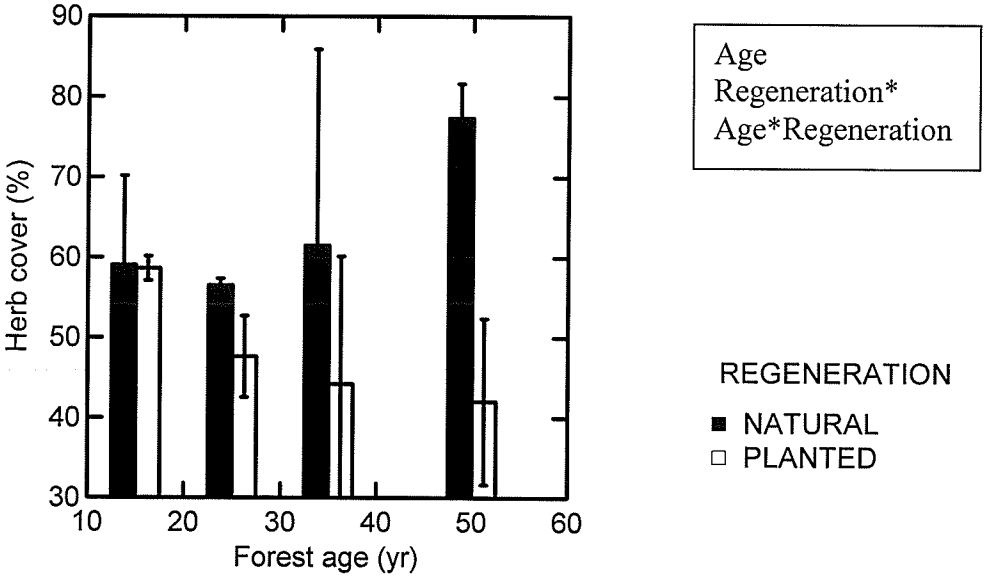


Figure 3.1.12 Per cent cover of moss (mean ± SE); patterns related to forest age and regeneration type.

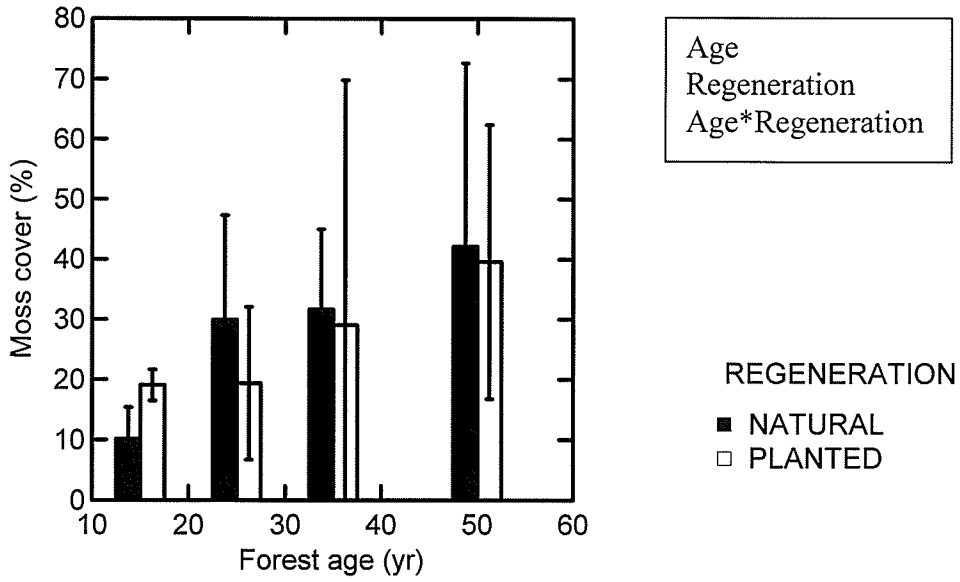


Figure 3.1.13 Per cent cover of lichen (mean ± SE); patterns related to forest age and regeneration type.

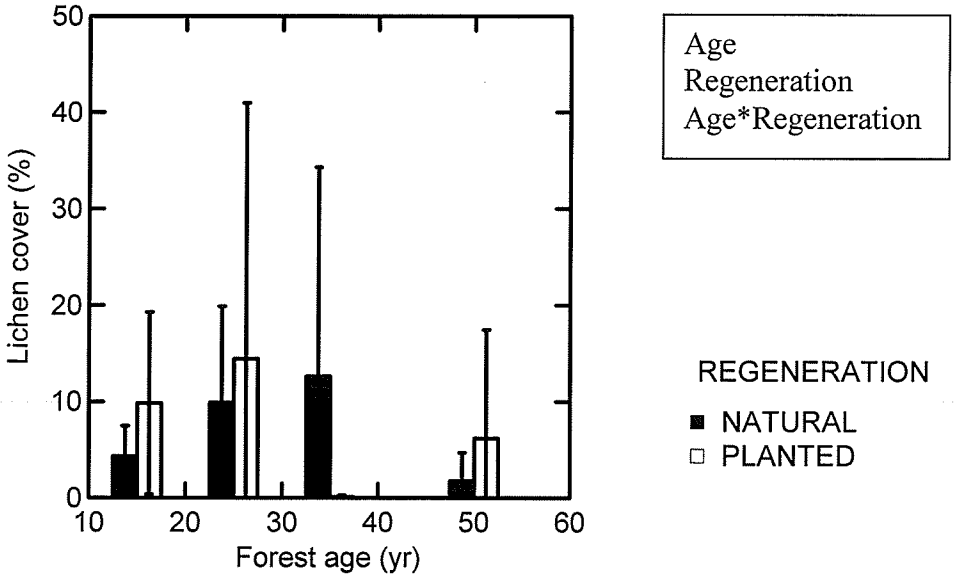


Figure 3.1.14 Per cent cover of coarse woody debris (mean ± SE); patterns related to forest age and regeneration type.

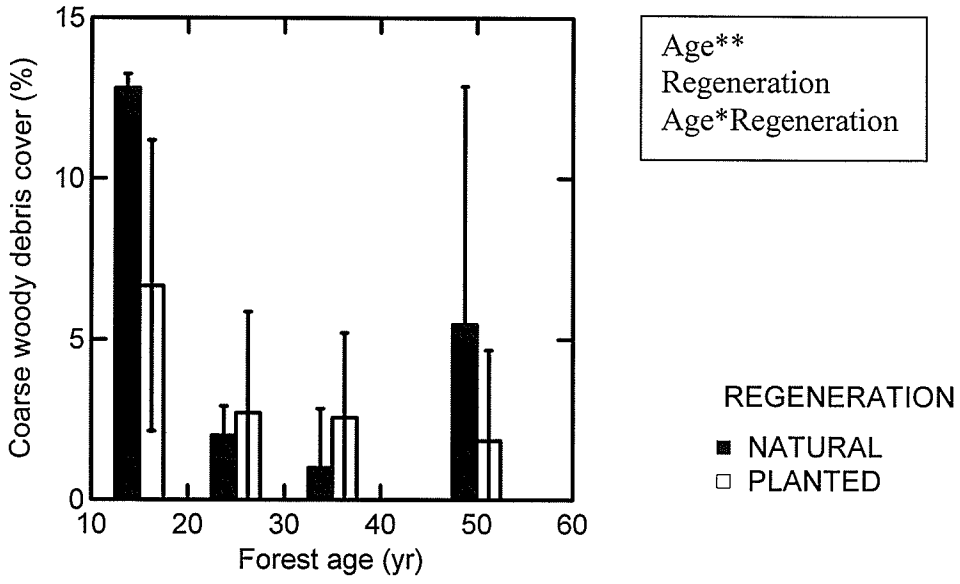


Figure 3.1.15 Per cent cover of fine woody debris (mean ± SE); patterns related to forest age and regeneration type.

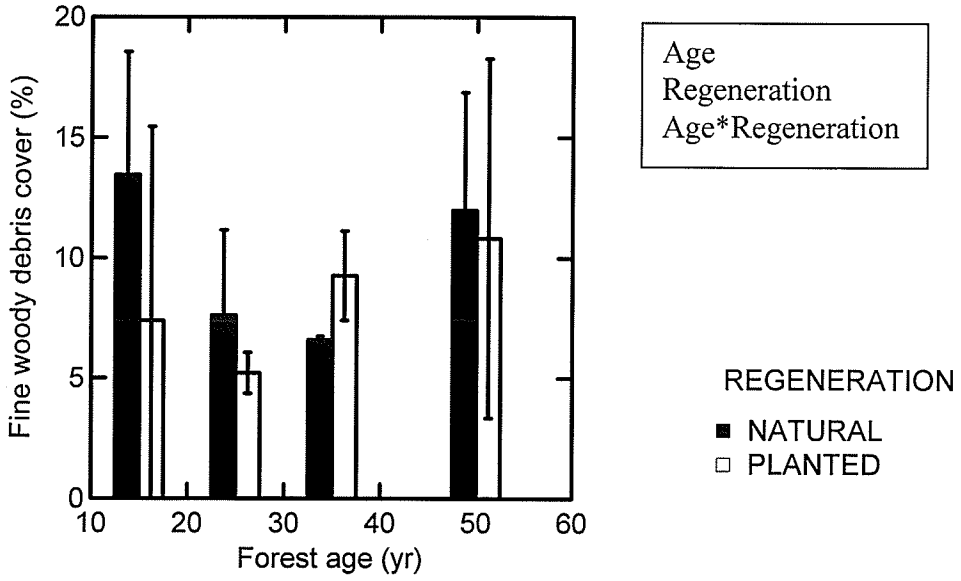


Figure 3.1.16 Per cent cover of grass litter (mean ± SE); patterns related to forest age and regeneration type.

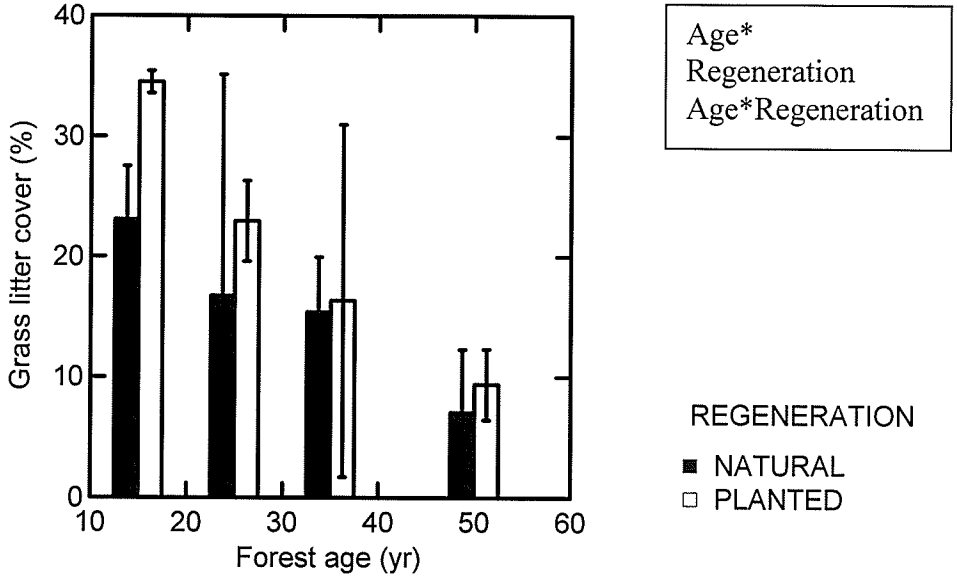


Figure 3.1.17 Per cent cover of conifer litter (mean ± SE); patterns related to forest age and regeneration type.

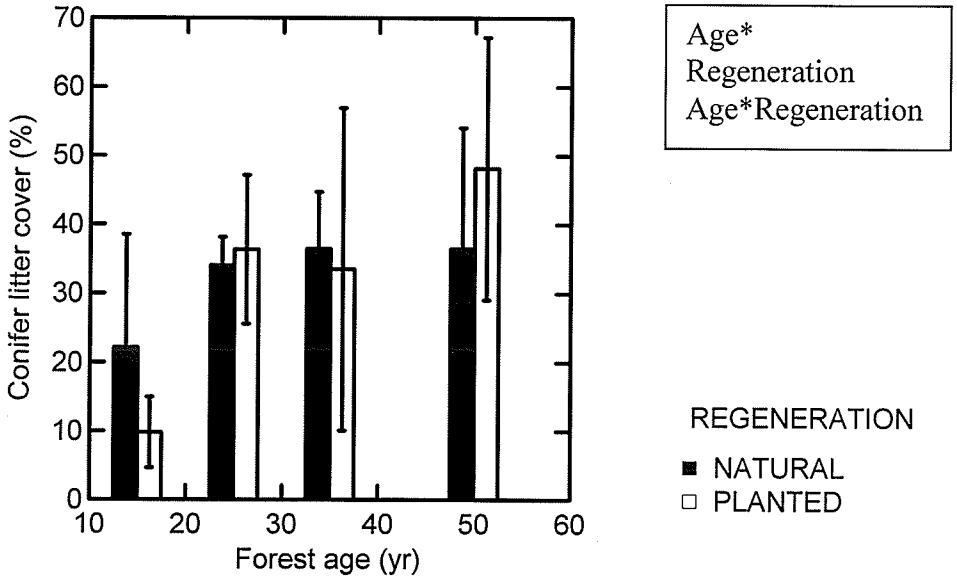


Figure 3.1.18 Per cent cover of deciduous litter (mean ± SE); patterns related to forest age and regeneration type.

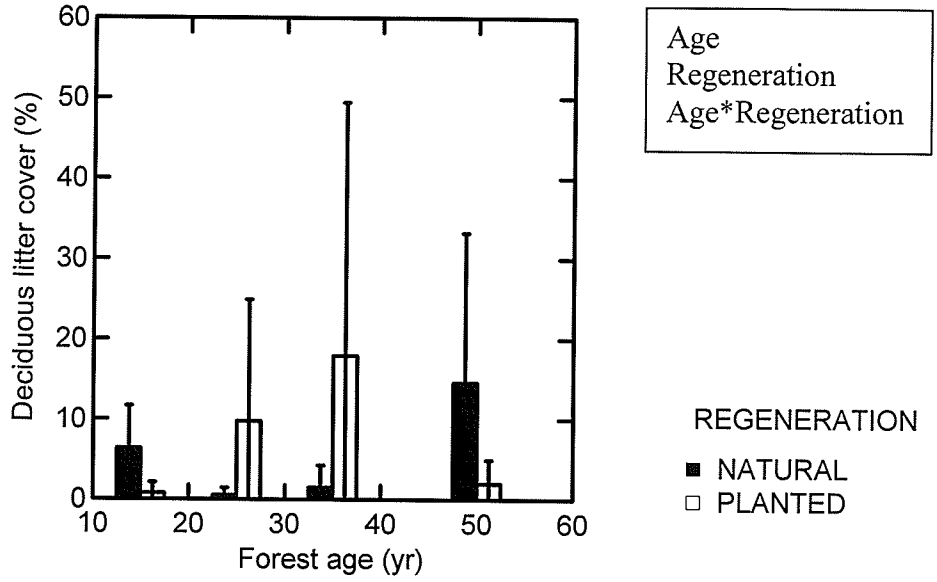


Figure 3.1.19 Per cent cover of bare ground (mean ± SE); patterns related to forest age and regeneration type.

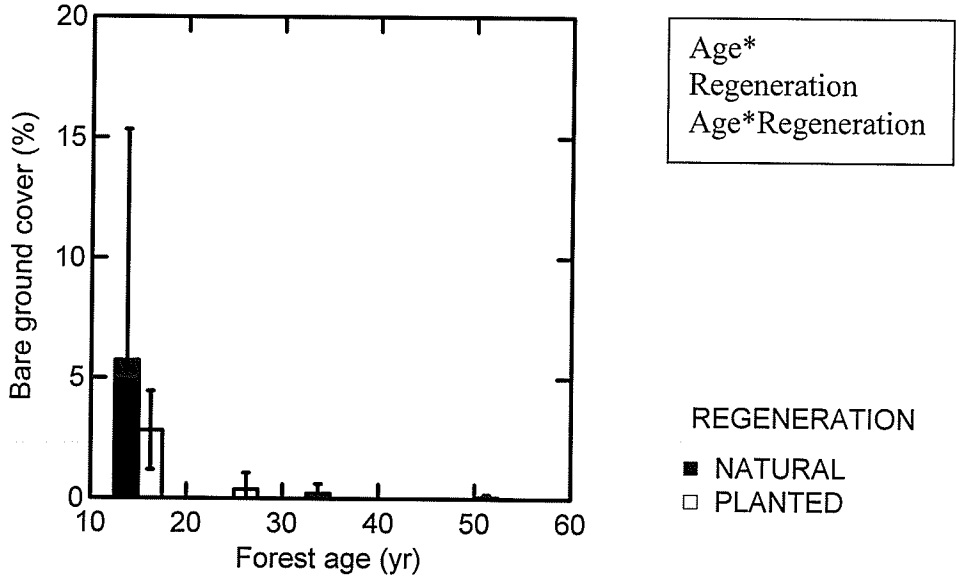


Figure 3.1.20 Number of tree stems per ha (mean ± SE); patterns related to forest age and regeneration type.

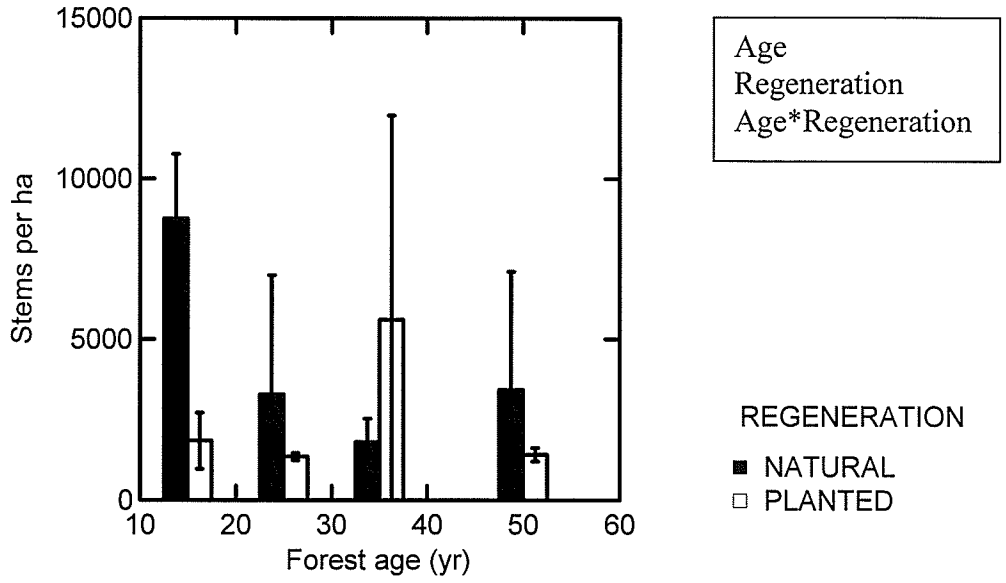


Figure 3.1.21 Number of jack pine stems per ha (mean ± SE); patterns related to forest age and regeneration type.

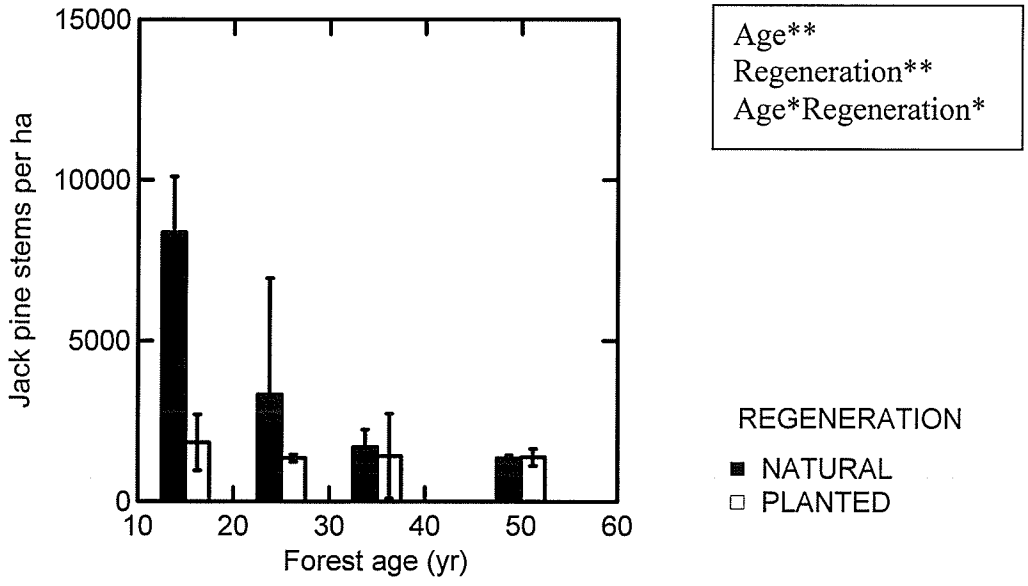


Figure 3.1.22 Stem diameter of trees at breast height (mean ± SE); patterns related to forest age and regeneration type.

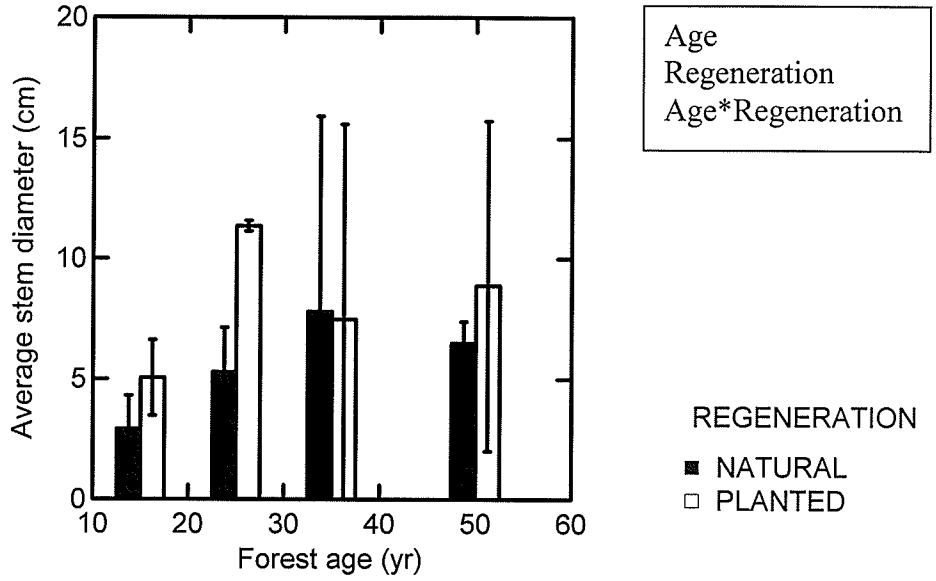


Figure 3.1.23 Jack pine stem diameter (mean ± SE); patterns related to forest age and regeneration type.

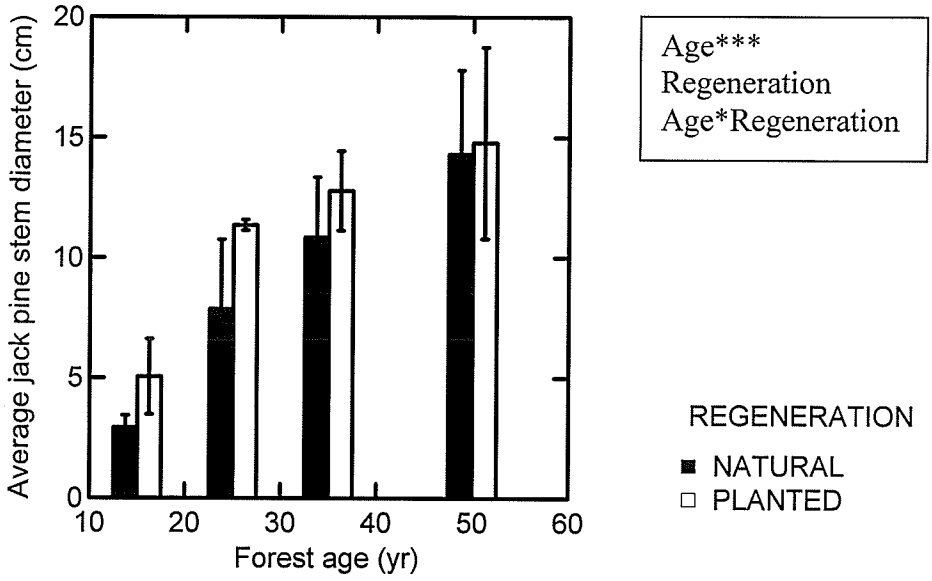


Figure 3.1.24 Jack pine height (mean ± SE); patterns related to forest age and regeneration type.

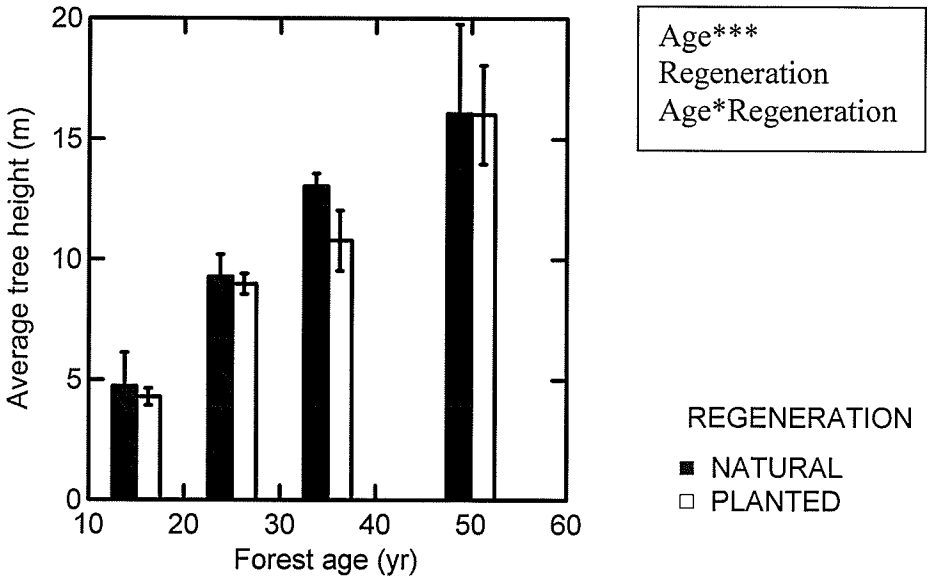


Figure 3.1.25 Number of coarse woody debris pieces sampled over 4, 100 m transects (mean ± SE); patterns related to forest age and regeneration type.

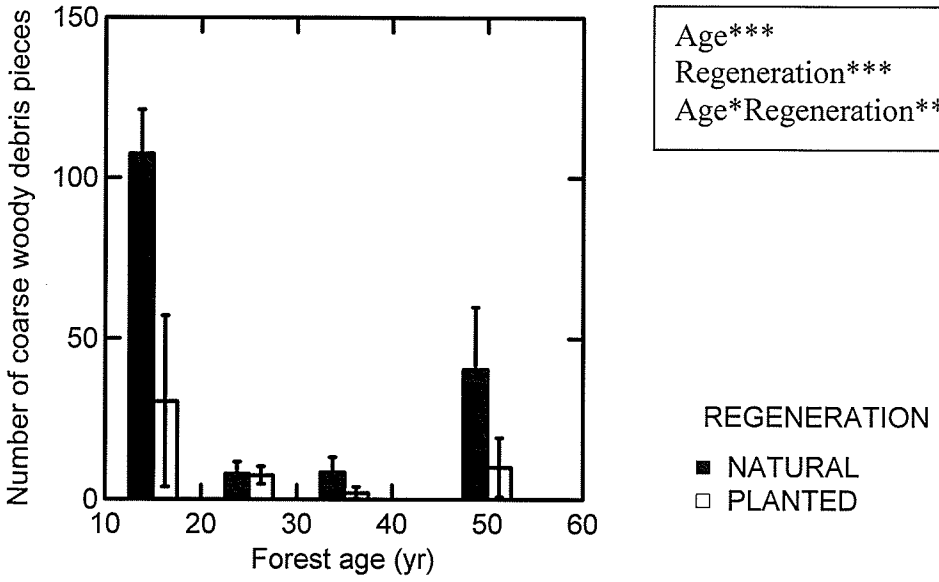


Figure 3.1.26a Number of coarse woody debris pieces per decay class sampled over 4, 100 m transects in naturally regenerating forests (mean ± SE); patterns related to forest age. Note vertical scale differs from that in figure 3.1.26a.

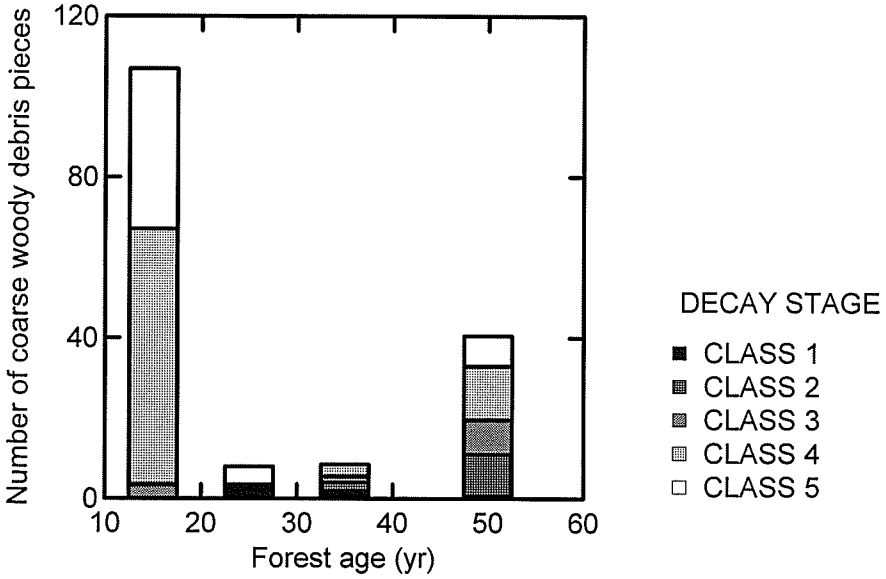


Figure 3.1.26b Number of coarse woody debris pieces per decay class over 4, 100 m transects in planted forests (mean ± SE); patterns related to forest age.

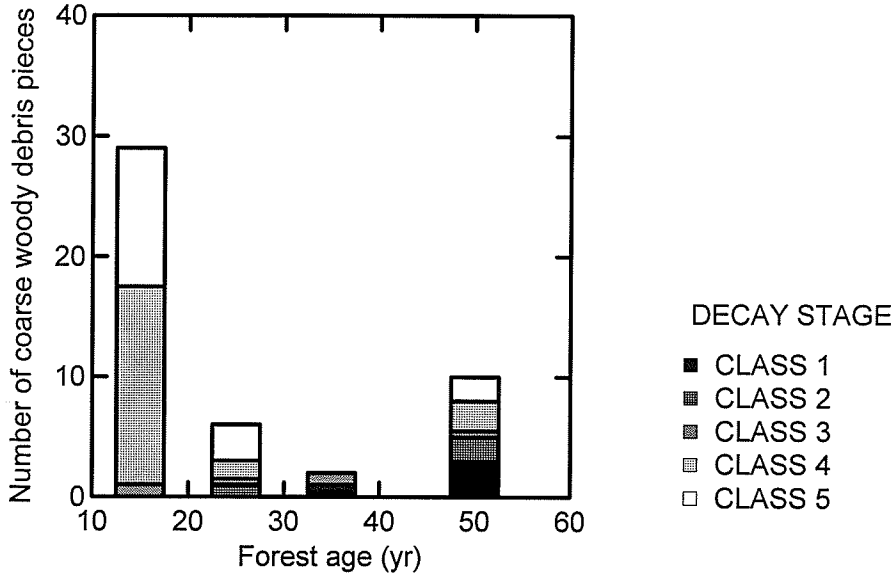


Figure 3.1.27 Number of snags per ha (mean ± SE); patterns related to forest age and regeneration type.

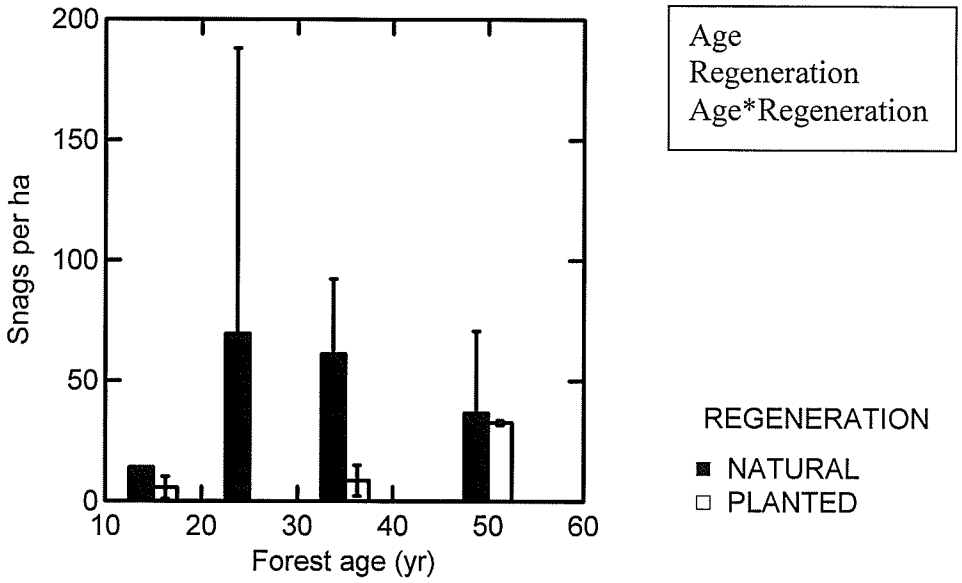


Figure 3.1.28 Snag diameter at breast height (mean ± SE); patterns related to forest age and regeneration type.

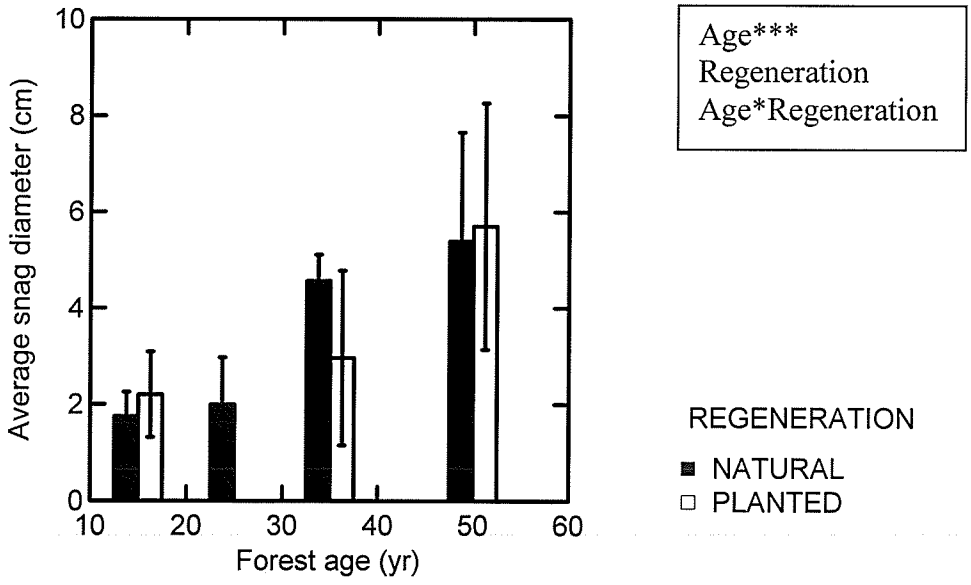


Figure 3.1.29 Per cent cover of spring ground vegetation (mean ± SE); patterns related to forest age and regeneration type.

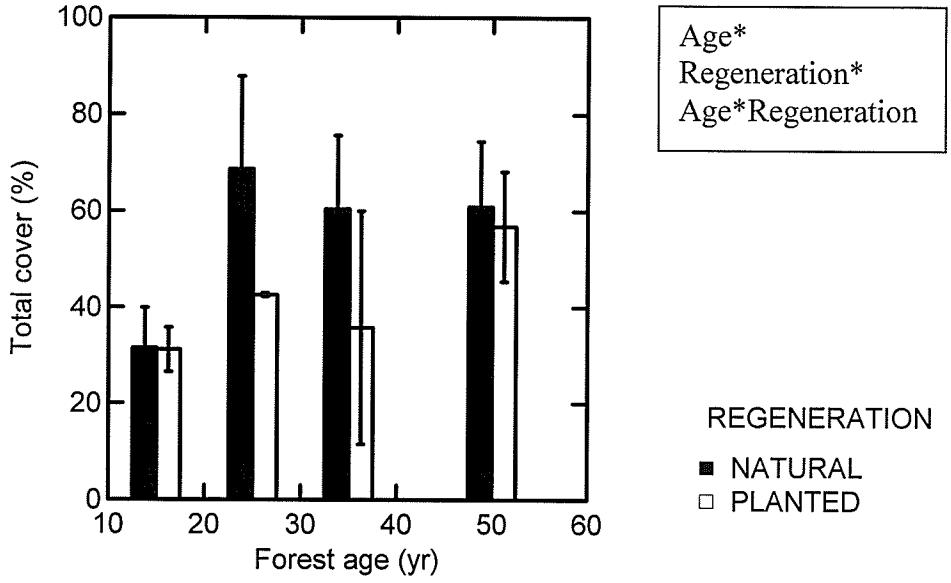


Figure 3.1.30 Number of spring ground vegetation species sampled per site (mean ± SE); patterns related to forest age and regeneration type.

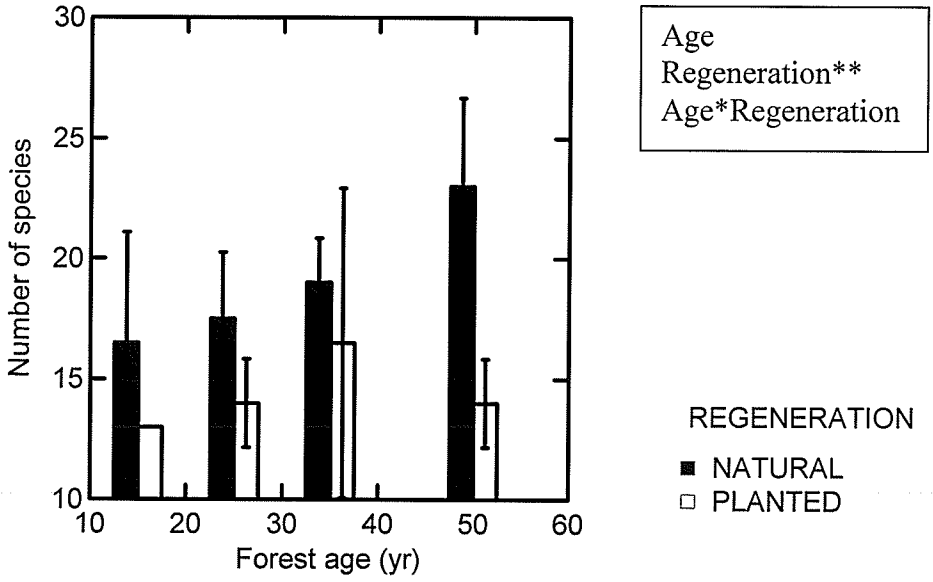


Figure 3.1.31 Alpha diversity of spring ground vegetation assemblages (mean ± SE); patterns related to forest age and regeneration type.

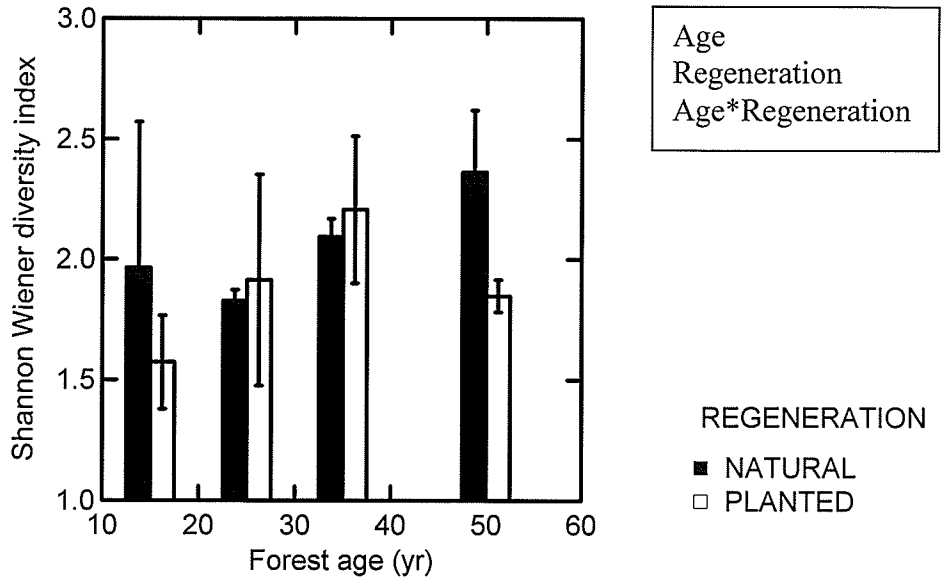


Figure 3.1.32 Species evenness of spring ground vegetation assemblages (mean ± SE); patterns related to forest age and regeneration type.

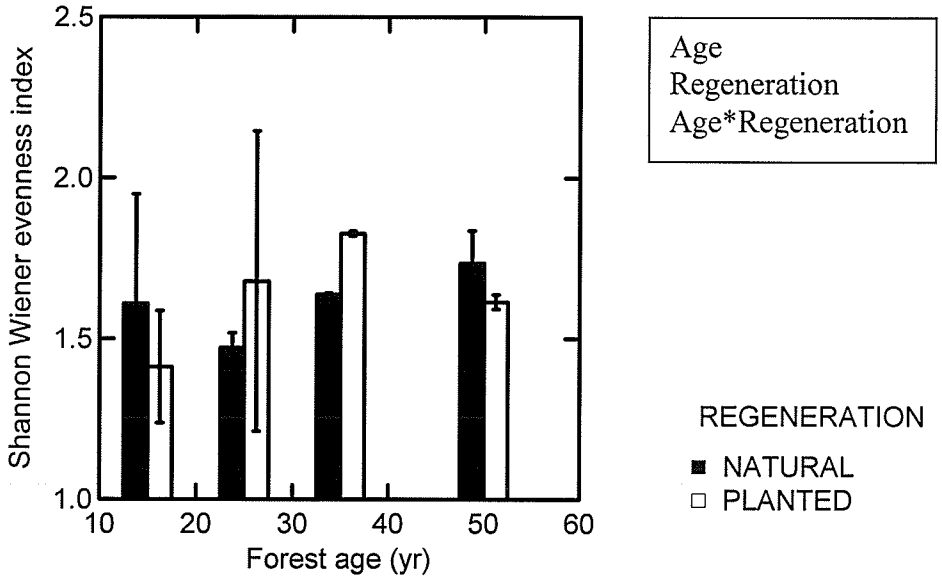


Figure 3.1.33 Kendall's index of beta diversity of spring ground vegetation assemblages; patterns related to forest age and regeneration type

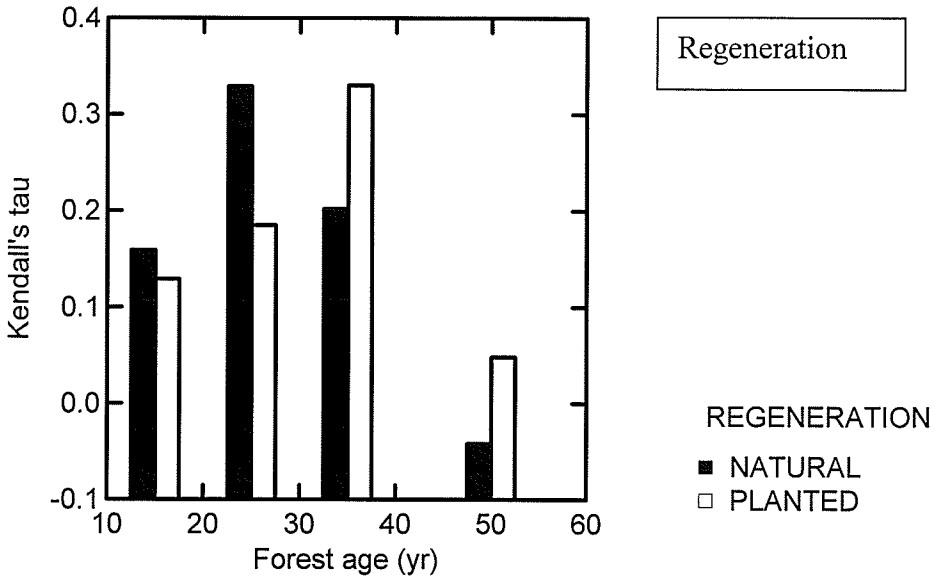


Figure 3.1.34 Jaccard's index of beta diversity of spring ground vegetation assemblages; patterns related to forest age and regeneration type

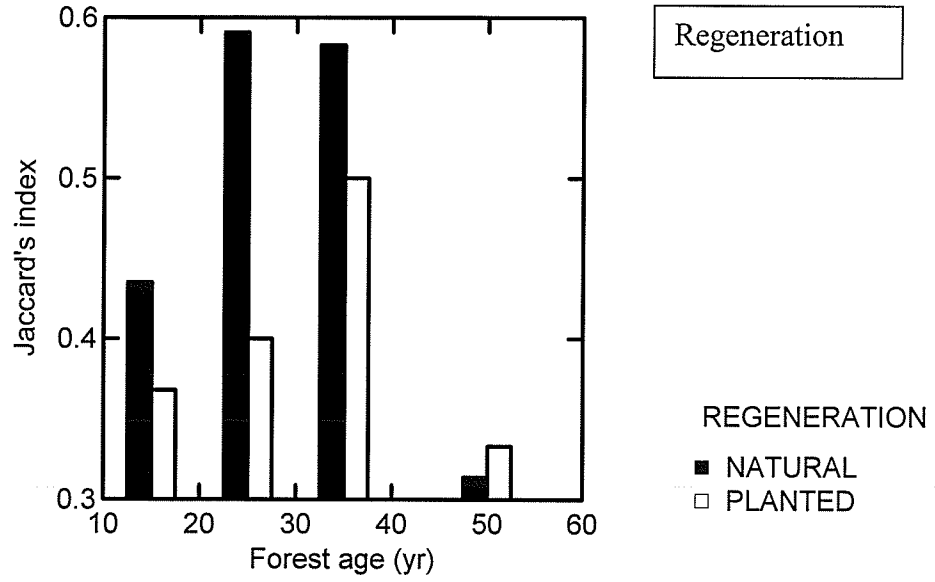
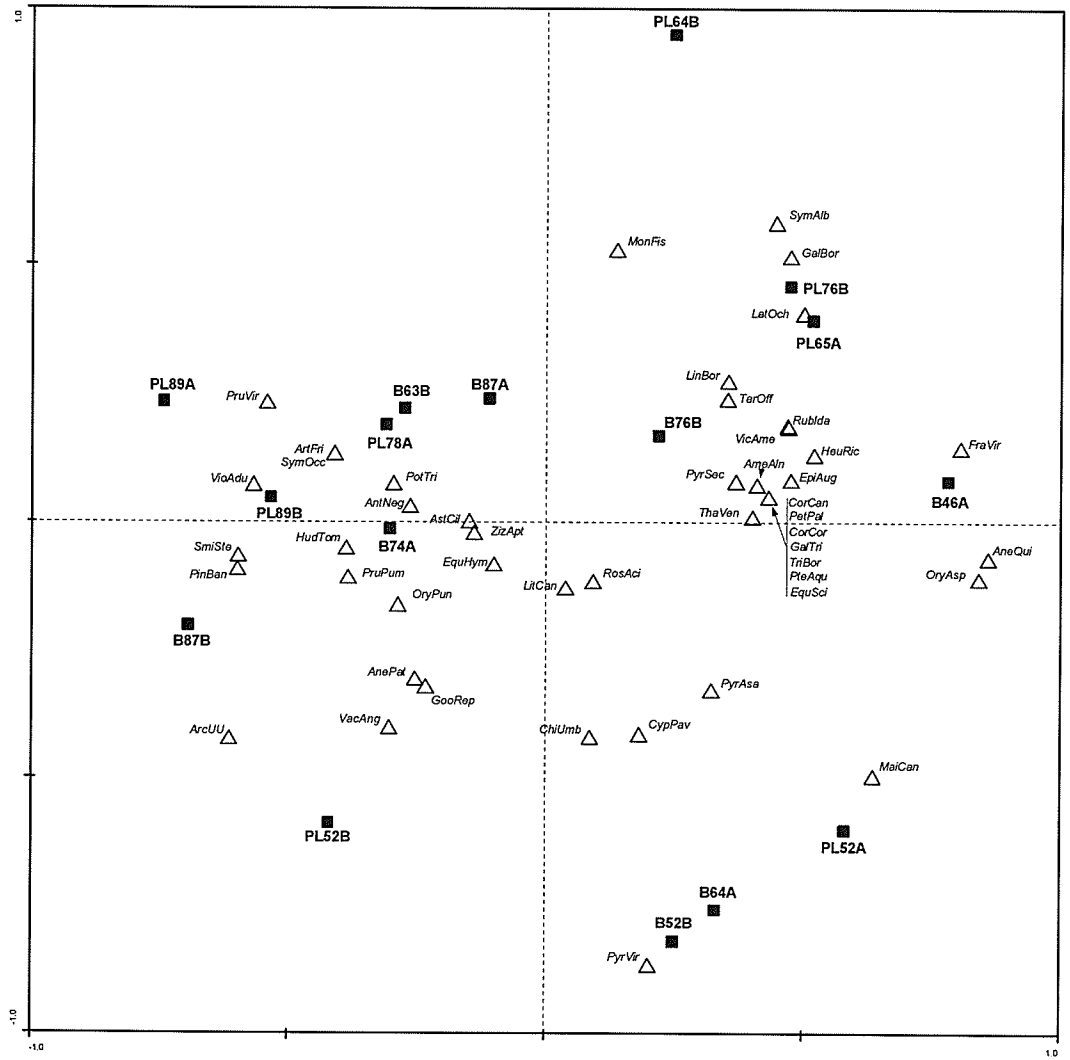


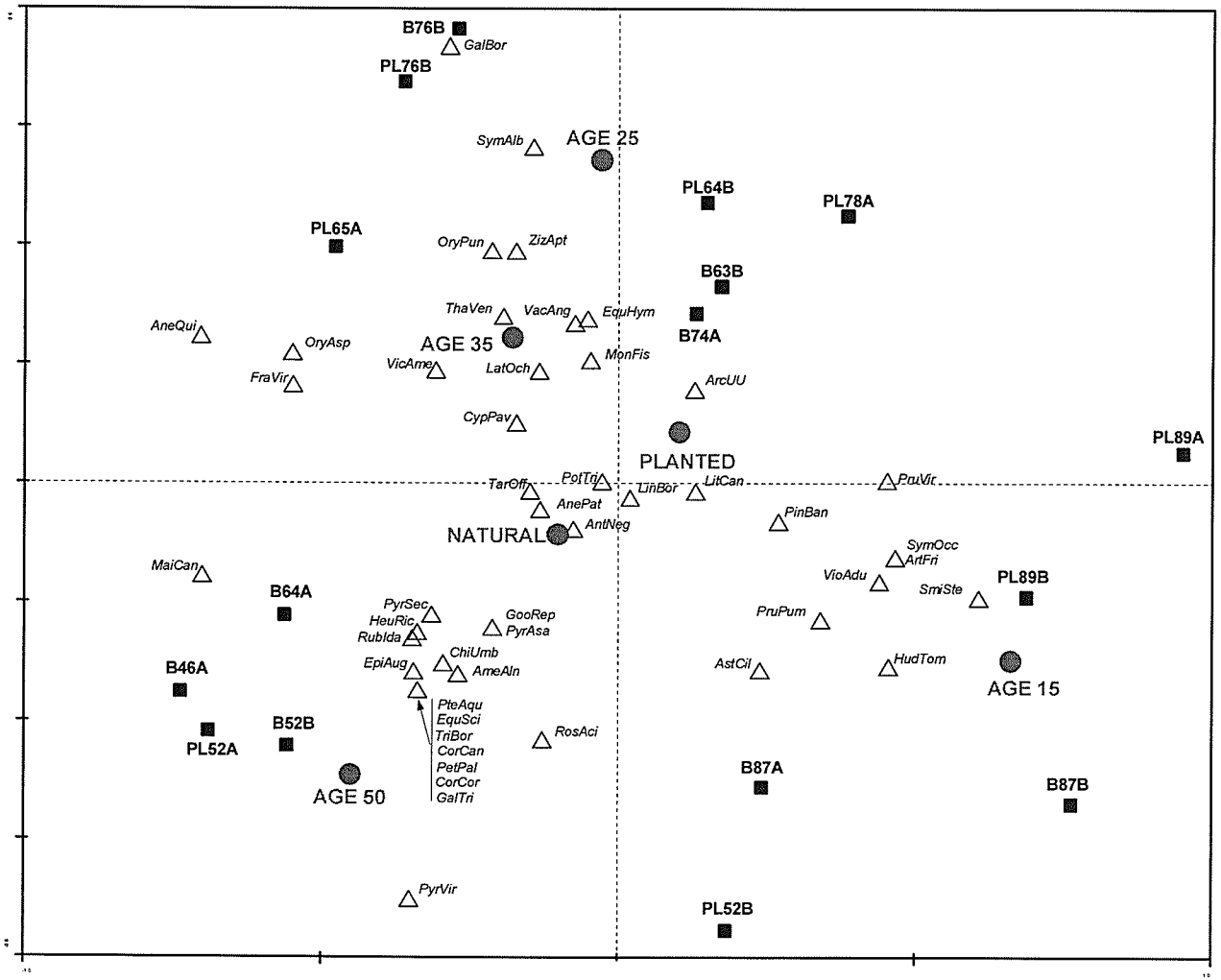
Figure 3.1.35 Principal Components Analysis ordination diagram of spring ground vegetation species (Δ) and sites (■). Species codes: AMEALN = *Amelanchier alnifolia*, ANECYL = *Anemone cylindrica*, ANEPAT = *Anemone patens*, ANEQUI = *Anemone quinquefolia*, ANTNEG = *Antennaria neglecta*, ARCUU = *Arctostaphylos uva-ursi*, ARTFRI = *Artemisia frigida*, ASTCIL = *Aster ciliolatus*, CHIUMB = *Chimaphila umbellata*, CORCAN = *Cornus canadensis*, CORCOR = *Corylus cornuta*, CYPPAV = *Cypripedium pavriflorus*, EPIANG = *Epilobium angustifolium*, EQUHYM = *Equisetum hymenale*, EQUSCI = *Equisetum scripoides*, FRAVIR = *Fragaria virginiana*, GALBOR = *Galium boreale*, GALTRI = *Galium triflorum*, GOOREP = *Goodyera repens*, HEURIC = *Heuchera richardsonii*, HUDTOM = *Hudsonia tomentosa*, LATOCH = *Lathyrus ochroleucus*, LINBOR = *Linnaea borealis*, LITCAN = *Lithospermum canescens*, MAICAN = *Maianthemum canadense*, MONFIS = *Monarda fistulosa*, ORYASP = *Oryzopsis asperifolia*, ORYPUN = *Oryzopsis pungens*, PINBAN = *Pinus banksiana*, PETPAL = *Petasites palmatus*, POTTRI = *Potentilla tridentata*, PRUPUM = *Prunus pumila*, PRUVIR = *Prunus virginiana*, PTEAQU = *Pteridium aquilinum*, PYRASA = *Pyrola asarafolia*, PYRSEC = *Pyrola secunda*, PYRVIR = *Pyrola virens*, ROSACI = *Rosa acicularis*, RUBIDA = *Rubus idaeus*, RUBPUB = *Rubus pubescens*, SMISTE = *Smilacina stellata*, SYMALB = *Symphoricarpos albus*, SYMOCC = *Symphoricarpos occidentalis*, TAROFF = *Taraxacum officinale*, THAVEN = *Thalictrum venulosum*, TRIBOR = *Trientalis borealis*, VACANG = *Vaccinium angustifolium*, VICAME = *Vicia americana*, VIOADU = *Viola adunca*, ZIZAPT = *Zizia aptera*



Axis 1 λ = 0.317

Axis 2 λ = .183

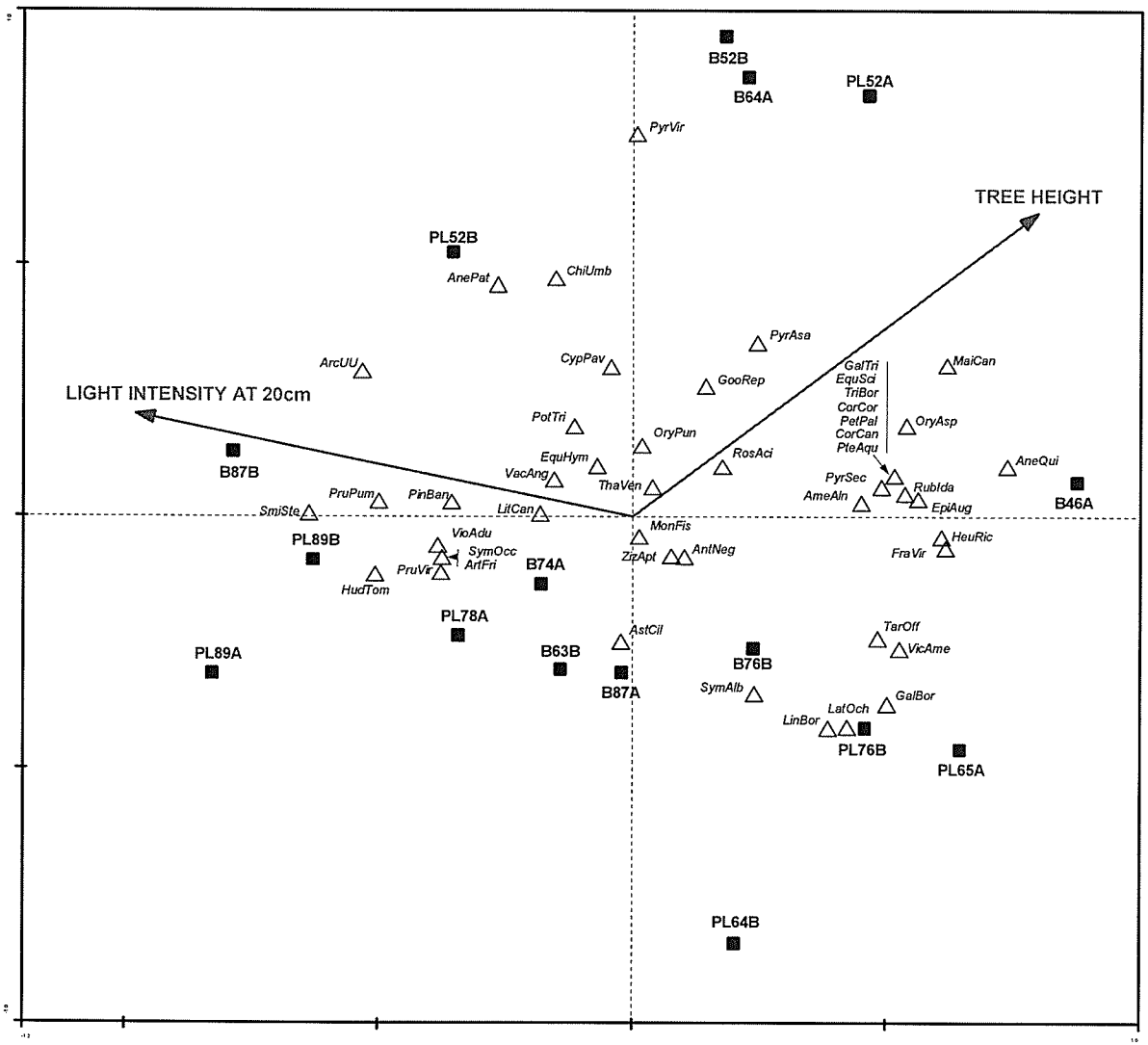
Figure 3.1.36 Redundancy Analysis ordination diagram of spring ground vegetation species (Δ) and sites (■) constrained by forest age and regeneration type. Species codes: AMEALN = *Amelanchier alnifolia*, ANECYL = *Anemone cylindrica*, ANEPAT = *Anemone patens*, ANEQUI = *Anemone quinquefolia*, ANTNEG = *Antennaria neglecta*, ARCUU = *Arctostaphylos uva-ursi*, ARTFRI = *Artemisia frigida*, ASTCIL = *Aster ciliolatus*, CHIUMB = *Chimaphila umbellata*, CORCAN = *Cornus canadensis*, CORCOR = *Corylus cornuta*, CYPPAV = *Cypripedium pavriflorus*, EPIANG = *Epilobium angustifolium*, EQUHYM = *Equisetum hymenale*, EQUSCI = *Equisetum scripoides*, FRAVIR = *Fragaria virginiana*, GALBOR = *Galium boreale*, GALTRI = *Galium triflorum*, GOOREP = *Goodyera repens*, HEURIC = *Heuchera richardsonii*, HUDTOM = *Hudsonia tomentosa*, LATOCH = *Lathyrus ochroleucus*, LINBOR = *Linnaea borealis*, LITCAN = *Lithospermum canescens*, MAICAN = *Maianthemum canadense*, MONFIS = *Monarda fistulosa*, ORYASP = *Oryzopsis asperifolia*, ORYPUN = *Oryzopsis pungens*, PINBAN = *Pinus banksiana*, PETPAL = *Petasites palmatus*, POTTRI = *Potentilla tridentata*, PRUPUM = *Prunus pumila*, PRUVIR = *Prunus virginiana*, PTEAQU = *Pteridium aquilinum*, PYRASA = *Pyrola asarafolia*, PYRSEC = *Pyrola secunda*, PYRVIR = *Pyrola virens*, ROSACI = *Rosa acicularis*, RUBIDA = *Rubus idaeus*, RUBPUB = *Rubus pubescens*, SMISTE = *Smilacina stellata*, SYMALB = *Symphoricarpos albus*, SYMOCC = *Symphoricarpos occidentalis*, TAROFF = *Taraxacum officinale*, THAVEN = *Thalictrum venulosum*, TRIBOR = *Trientalis borealis*, VACANG = *Vaccinium angustifolium*, VICAME = *Vicia americana*, VIOADU = *Viola adunca*, ZIZAPT = *Zizia aptera*



Axis 1 λ = 0.182

Axis 2 λ = 0.128

Figure 3.1.37 Redundancy Analysis ordination diagram of spring ground vegetation species (Δ) and sites (■) constrained by environmental variables. Species codes: AMEALN = *Amelanchier alnifolia*, ANECYL = *Anemone cylindrica*, ANEPAT = *Anemone patens*, ANEQUI = *Anemone quinquefolia*, ANTNEG = *Antennaria neglecta*, ARCUU = *Arctostaphylos uva-ursi*, ARTFRI = *Artemisia frigida*, ASTCIL = *Aster ciliolatus*, CHIUMB = *Chimaphila umbellata*, CORCAN = *Cornus canadensis*, CORCOR = *Corylus cornuta*, CYPPAV = *Cypripedium pavriflorus*, EPIANG = *Epilobium angustifolium*, EQUHYM = *Equisetum hymenale*, EQUSCI = *Equisetum scripoides*, FRAVIR = *Fragaria virginiana*, GALBOR = *Galium boreale*, GALTRI = *Galium triflorum*, GOOREP = *Goodyera repens*, HEURIC = *Heuchera richardsonii*, HUDTOM = *Hudsonia tomentosa*, LATOCH = *Lathyrus ochroleucus*, LINBOR = *Linnaea borealis*, LITCAN = *Lithospermum canescens*, MAICAN = *Maianthemum canadense*, MONFIS = *Monarda fistulosa*, ORYASP = *Oryzopsis asperifolia*, ORYPUN = *Oryzopsis pungens*, PINBAN = *Pinus banksiana*, PETPAL = *Petasites palmatus*, POTTRI = *Potentilla tridentata*, PRUPUM = *Prunus pumila*, PRUVIR = *Prunus virginiana*, PTEAQU = *Pteridium aquilinum*, PYRASA = *Pyrola asarafolia*, PYRSEC = *Pyrola secunda*, PYRVIR = *Pyrola virens*, ROSACI = *Rosa acicularis*, RUBIDA = *Rubus idaeus*, RUBPUB = *Rubus pubescens*, SMISTE = *Smilacina stellata*, SYMALB = *Symphoricarpos albus*, SYMOCC = *Symphoricarpos occidentalis*, TAROFF = *Taraxacum officinale*, THAVEN = *Thalictrum venulosum*, TRIBOR = *Trientalis borealis*, VACANG = *Vaccinium angustifolium*, VICAME = *Vicia americana*, VIOADU = *Viola adunca*, ZIZAPT = *Zizia aptera*



Axis 1 λ = 0.226

Axis 2 λ = 0.116

Figure 3.1.38 Per cent cover of summer ground vegetation (mean ± SE); patterns related to forest age and regeneration type.

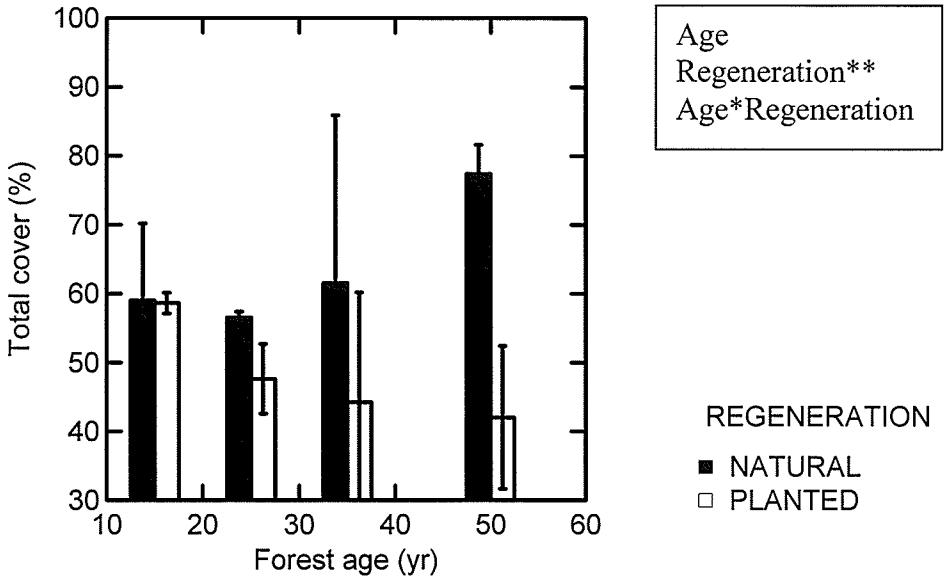


Figure 3.1.39 Number of summer ground vegetation species sampled per site (mean ± SE); patterns related to forest age and regeneration type.

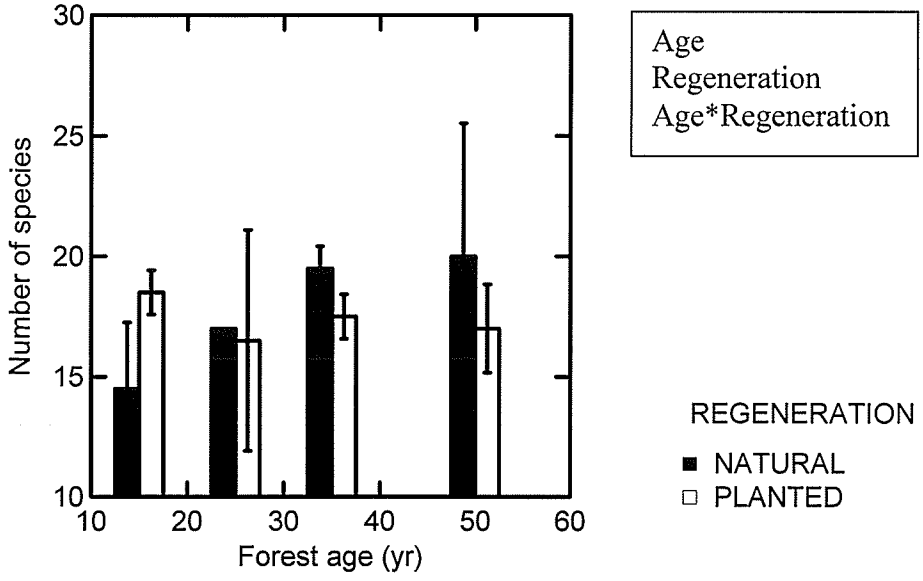


Figure 3.1.40 Alpha diversity of summer ground vegetation assemblages (mean ± SE); patterns related to forest age and regeneration type.

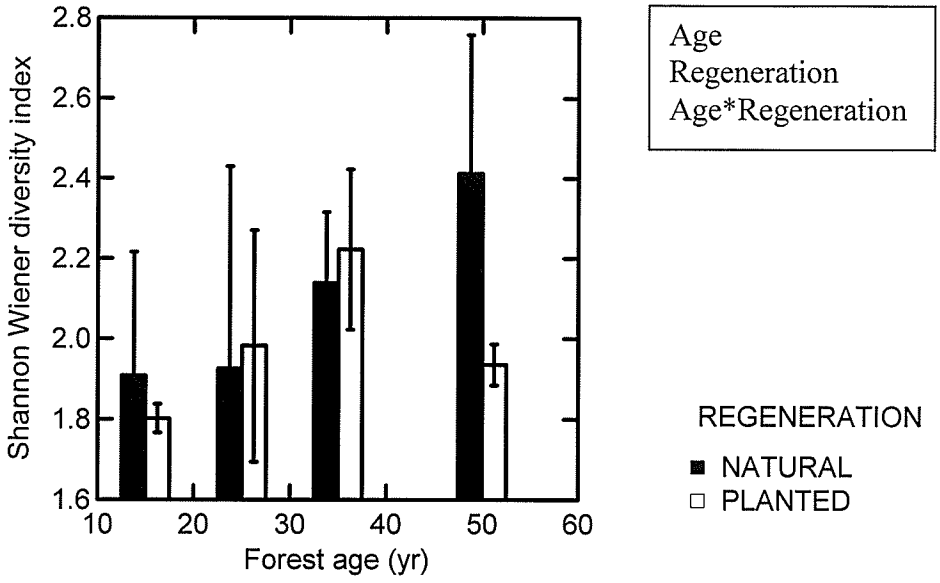


Figure 3.1.41 Species evenness of summer ground vegetation assemblages (mean ± SE); patterns related to forest age and regeneration type.

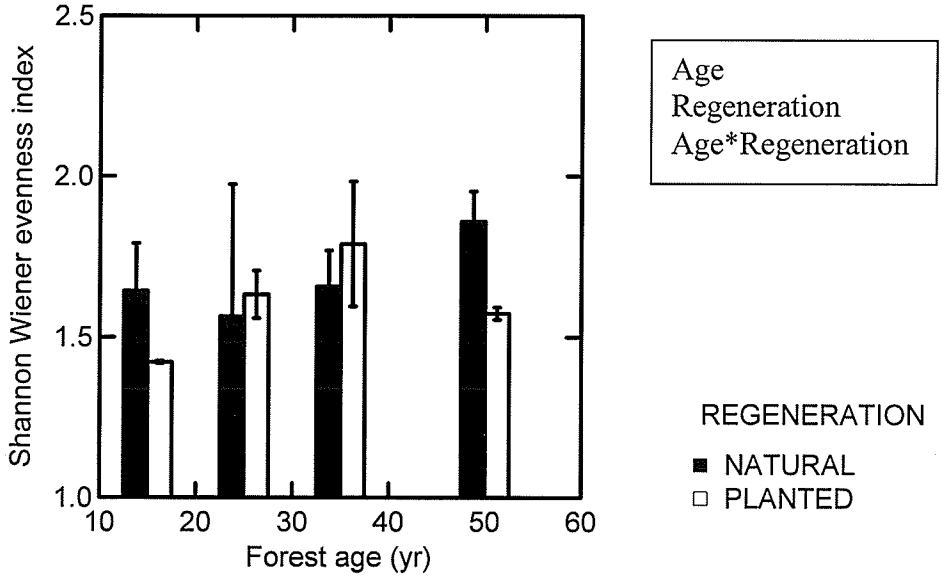


Figure 3.1.42 Kendall's index of beta diversity of summer ground vegetation assemblages; patterns related to forest age and regeneration type

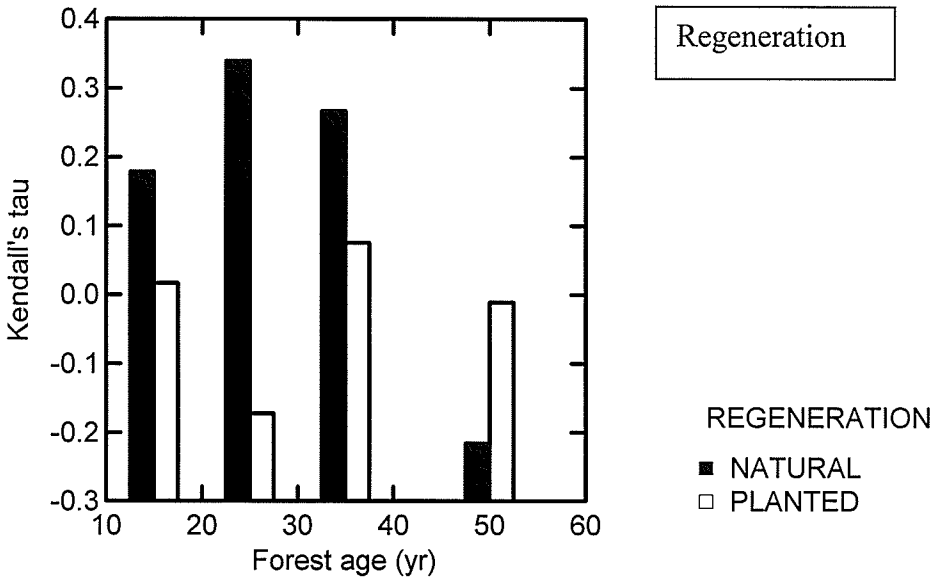


Figure 3.1.43 Jaccard's index of beta diversity of summer ground vegetation assemblages; patterns related to forest age and regeneration type

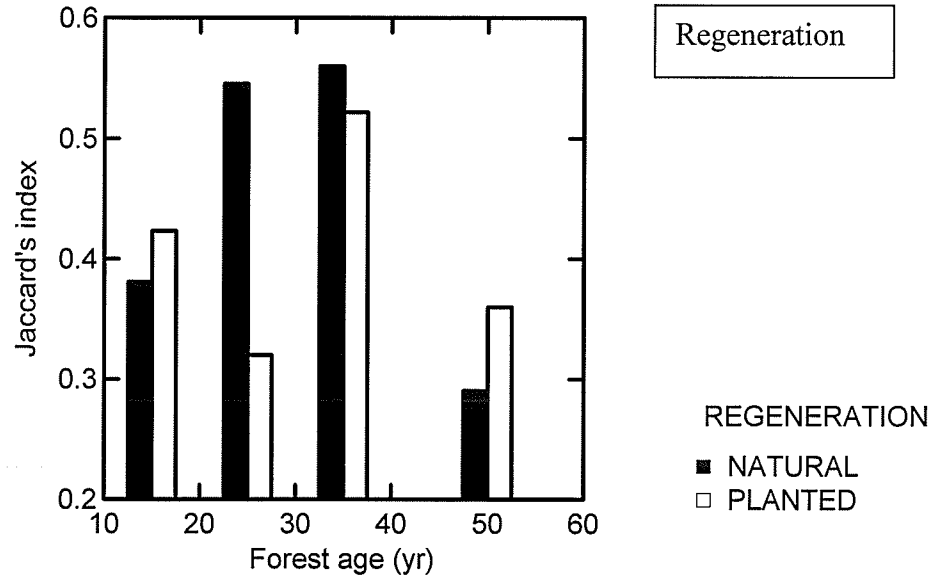
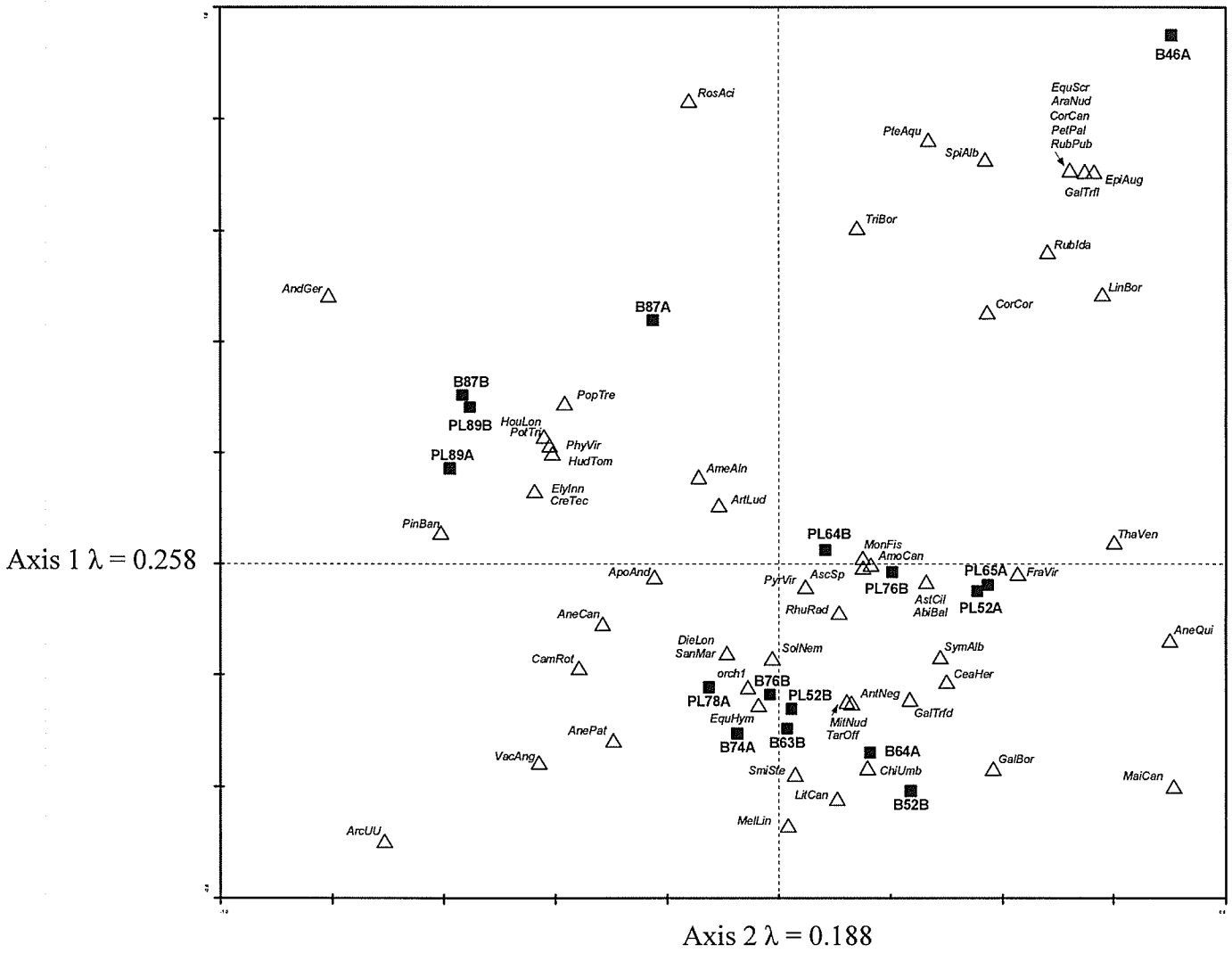


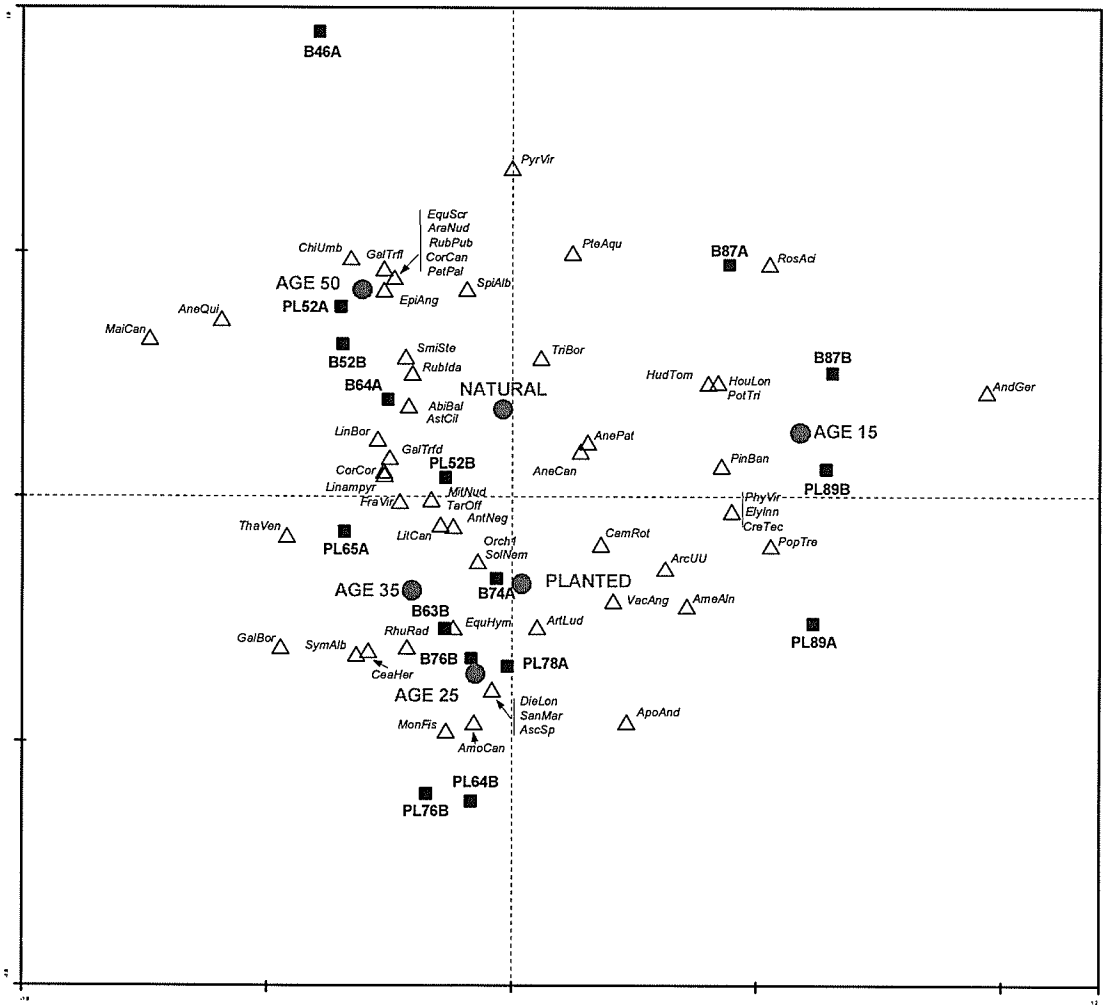
Figure 3.1.44 Principal Components Analysis ordination diagram of summer ground vegetation species (Δ) and sites (■). Species codes: ABIBAL = *Abies balsamea*, AMEALN = *Amelanchier alnifolia*, AMOCAN = *Amorpha canescens*, ANDGER = *Andropogon gerardii*, ANECAN = *Anemone canadensis*, ANEPAT = *Anemone patens*, ANEQUI = *Anemone quinquefolia*, ANTNEG = *Antennaria neglecta*, APOAND = *Apocynum androsaemifolium*, ARANUD = *Aralia nudicaulis*, ARCUU = *Arctostaphylos uva-ursi*, ARTLUD = *Artemisia ludoviciana*, ASCSP = *Asclepias* spp., ASTCIL = *Aster ciliolatus*, CAMROT = *Campanula rotundifolia*, CEAHER = *Ceanothus herbaceous*, CHIUMB = *Chimaphila umbellata*, CORCAN = *Cornus canadensis*, CORCOR = *Corylus cornuta*, CRETEC = *Crepis tectorum*, DIELON = *Diervilla lonicera*, ELYINN = *Elynus innovatus*, EPIANG = *Epilobium angustifolium*, EQUHYM = *Equisetum hymenale*, EQUSCI = *Equisetum scripoides*, FRAVIR = *Fragaria virginiana*, GALBOR = *Galium boreale*, GALTRD = *Galium trifidum,* GALTRI = *Galium triflorum*, HOULON = *Houstonia longifolia*, HUDTOM = *Hudsonia tomentosa*, LINBOR = *Linnaea borealis*, LITCAN = *Lithospermum canescens*, MAICAN = *Maianthemum canadense*, MELLIN = *Melampyrum lineare*, MITNUD = *Mitella nuda,* MONFIS = *Monarda fistulosa*, ORCH1 = Orchid 1, PETPAL = *Petasites palmatus,* PHYVIR = *Physalis virginiana*, PINBAN = *Pinus banksiana*, POPTRE = *Populus tremuloides*, POTTRI = *Potentilla tridentata*, PTEAQU = *Pteridium aquilinum*, PYRVIR = *Pyrola virens*, RHURAD = *Rhus radicans*, ROSACI = *Rosa acicularis*, RUBIDA = *Rubus idaeus*, RUBPUB = *Rubus pubescens*, SANMAR = *Sanicula marilandica*, SMISTE = *Smilacina stellata*, SOLNEM = *Solidago nemoralis*, SPIALB = *Spiraea alba*, SYMALB = *Symphoricarpos albus*, TAROFF = *Taraxacum officinale*, THAVEN = *Thalictrum venulosum*, TRIBOR = *Trientalis borealis*, VACANG = *Vaccinium angustifolium*, VIOADU = *Viola adunca*, ZIZAPT = *Zizia aptera*



Axis 1 λ = 0.258

Axis 2 λ = 0.188

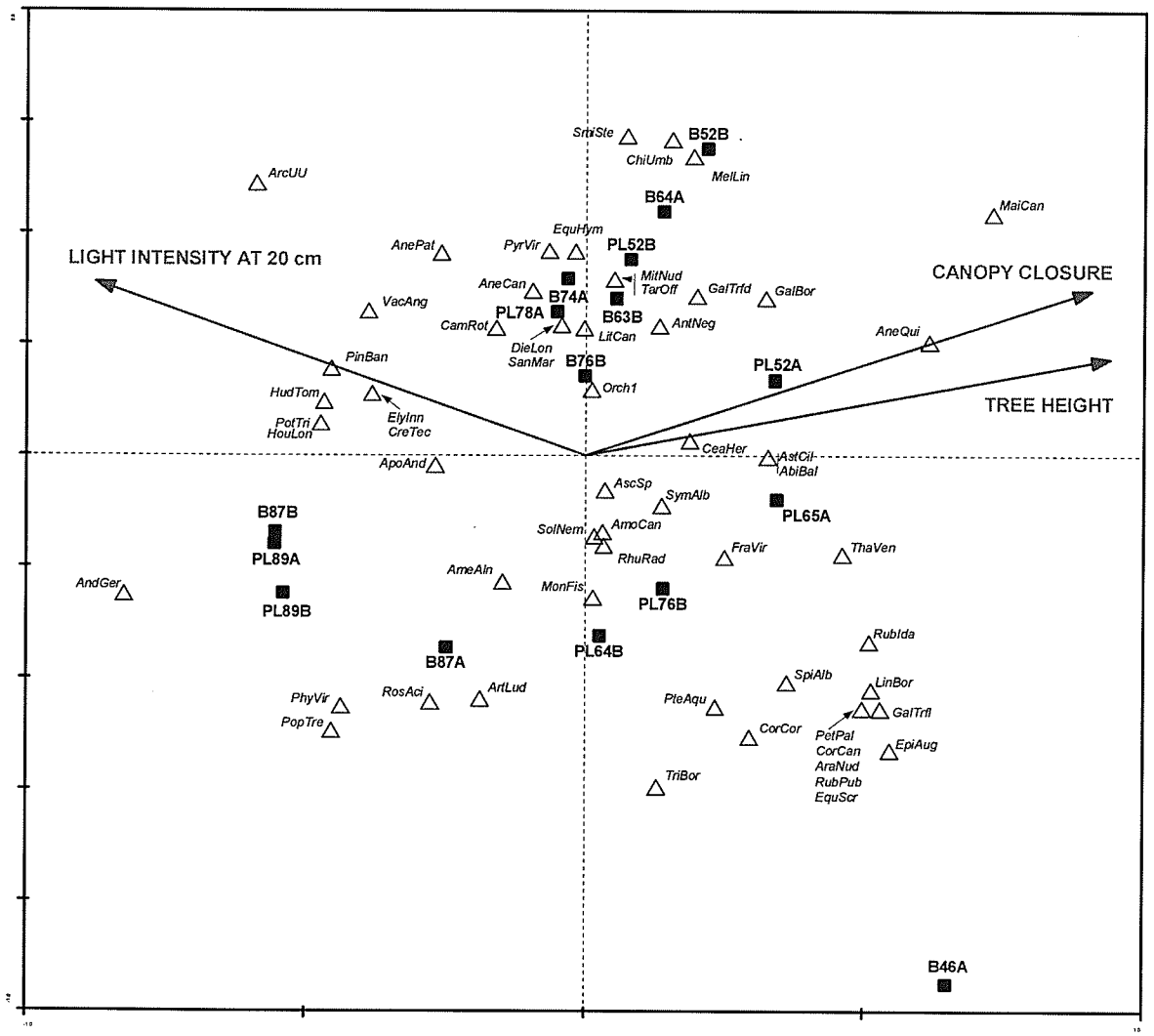
Figure 3.1.45 Redundancy Analysis ordination diagram of summer ground vegetation species (Δ) and sites (■) constrained by forest age and regeneration type. Species codes: ABIBAL = *Abies balsamea*, AMEALN = *Amelanchier alnifolia*, AMOCAN = *Amorpha canescens*, ANDGER = *Andropogon gerardii*, ANECAN = *Anemone canadensis*, ANEPAT = *Anemone patens*, ANEQUI = *Anemone quinquefolia*, ANTNEG = *Antennaria neglecta*, APOAND = *Apocynum androsaemifolium*, ARANUD = *Aralia nudicaulis*, ARCUU = *Arctostaphylos uva-ursi*, ARTLUD = *Artemisia ludoviciana*, ASCSP = *Asclepias* spp., ASTCIL = *Aster ciliolatus*, CAMROT = *Campanula rotundifolia*, CEAHER = *Ceanothus herbaceous*, CHIUMB = *Chimaphila umbellata*, CORCAN = *Cornus canadensis*, CORCOR = *Corylus cornuta*, CRETEC = *Crepis tectorum*, DIELON = *Diervilla lonicera*, ELYINN = *Elynus innovatus*, EPIANG = *Epilobium angustifolium*, EQUHYM = *Equisetum hymenale*, EQUSCI = *Equisetum scripoides*, FRAVIR = *Fragaria virginiana*, GALBOR = *Galium boreale*, GALTRD = *Galium trifidum,* GALTRI = *Galium triflorum*, HOULON = *Houstonia longifolia*, HUDTOM = *Hudsonia tomentosa*, LINBOR = *Linnaea borealis*, LITCAN = *Lithospermum canescens*, MAICAN = *Maianthemum canadense*, MELLIN = *Melampyrum lineare*, MITNUD = *Mitella nuda,* MONFIS = *Monarda fistulosa*, ORCH1 = Orchid 1, PETPAL = *Petasites palmatus,* PHYVIR = *Physalis virginiana*, PINBAN = *Pinus banksiana*, POPTRE = *Populus tremuloides*, POTTRI = *Potentilla tridentata*, PTEAQU = *Pteridium aquilinum*, PYRVIR = *Pyrola virens*, RHURAD = *Rhus radicans*, ROSACI = *Rosa acicularis*, RUBIDA = *Rubus idaeus*, RUBPUB = *Rubus pubescens*, SANMAR = *Sanicula marilandica*, SMISTE = *Smilacina stellata*, SOLNEM = *Solidago nemoralis*, SPIALB = *Spiraea alba*, SYMALB = *Symphoricarpos albus*, TAROFF = *Taraxacum officinale*, THAVEN = *Thalictrum venulosum*, TRIBOR = *Trientalis borealis*, VACANG = *Vaccinium angustifolium*, VIOADU = *Viola adunca*, ZIZAPT = *Zizia aptera*



Axis 1 λ = 0.230

Axis 2 λ = 0.108

Figure 3.1.46 Redundancy Analysis ordination diagram of summer ground vegetation species (Δ) and sites (■) constrained by environmental variables. Species codes: ABIBAL = *Abies balsamea*, AMEALN = *Amelanchier alnifolia*, AMOCAN = *Amorpha canescens*, ANDGER = *Andropogon gerardii*, ANECAN = *Anemone canadensis*, ANEPAT = *Anemone patens*, ANEQUI = *Anemone quinquefolia*, ANTNEG = *Antennaria neglecta*, APOAND = *Apocynum androsaemifolium*, ARANUD = *Aralia nudicaulis*, ARCUU = *Arctostaphylos uva-ursi*, ARTLUD = *Artemisia ludoviciana*, ASCSP = *Asclepias* spp., ASTCIL = *Aster ciliolatus*, CAMROT = *Campanula rotundifolia*, CEAHER = *Ceanothus herbaceous*, CHIUMB = *Chimaphila umbellata*, CORCAN = *Cornus canadensis*, CORCOR = *Corylus cornuta*, CRETEC = *Crepis tectorum*, DIELON = *Diervilla lonicera*, ELYINN = *Elynus innovatus*, EPIANG = *Epilobium angustifolium*, EQUHYM = *Equisetum hymenale*, EQUSCI = *Equisetum scripoides*, FRAVIR = *Fragaria virginiana*, GALBOR = *Galium boreale*, GALTRD = *Galium trifidum,* GALTRI = *Galium triflorum*, HOULON = *Houstonia longifolia*, HUDTOM = *Hudsonia tomentosa*, LINBOR = *Linnaea borealis*, LITCAN = *Lithospermum canescens*, MAICAN = *Maianthemum canadense*, MELLIN = *Melampyrum lineare*, MITNUD = *Mitella nuda,* MONFIS = *Monarda fistulosa*, ORCH1 = Orchid 1, PETPAL = *Petasites palmatus,* PHYVIR = *Physalis virginiana*, PINBAN = *Pinus banksiana*, POPTRE = *Populus tremuloides*, POTTRI = *Potentilla tridentata*, PTEAQU = *Pteridium aquilinum*, PYRVIR = *Pyrola virens*, RHURAD = *Rhus radicans*, ROSACI = *Rosa acicularis*, RUBIDA = *Rubus idaeus*, RUBPUB = *Rubus pubescens*, SANMAR = *Sanicula marilandica*, SMISTE = *Smilacina stellata*, SOLNEM = *Solidago nemoralis*, SPIALB = *Spiraea alba*, SYMALB = *Symphoricarpos albus*, TAROFF = *Taraxacum officinale*, THAVEN = *Thalictrum venulosum*, TRIBOR = *Trientalis borealis*, VACANG = *Vaccinium angustifolium*, VIOADU = *Viola adunca*, ZIZAPT = *Zizia aptera*



Axis 1 λ = 0.235

Axis 2 λ = 0.127

Figure 3.1.47 Per cent cover of shrubs (mean ± SE); patterns related to forest age and regeneration type.

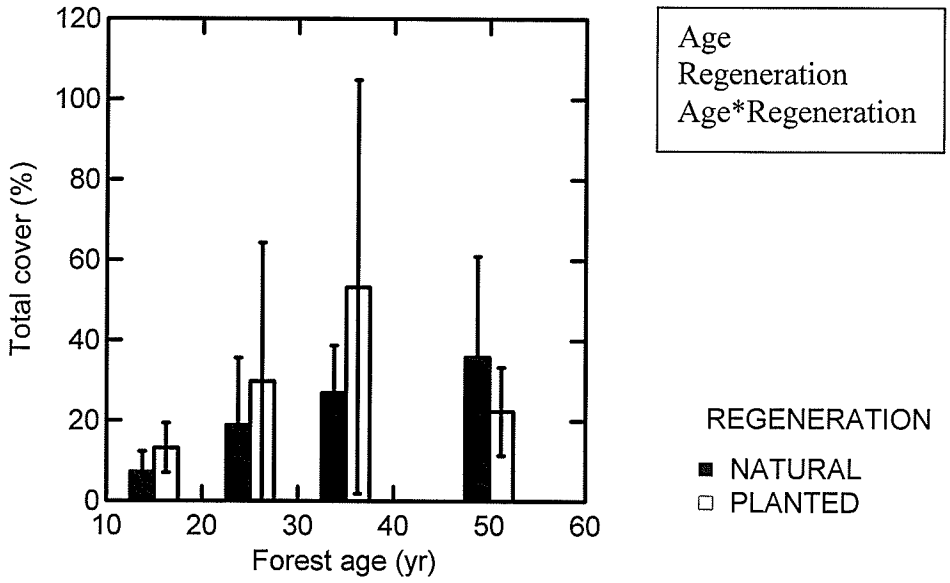


Figure 3.1.48 Number of shrub species sampled per site (mean ± SE); patterns related to forest age and regeneration type.

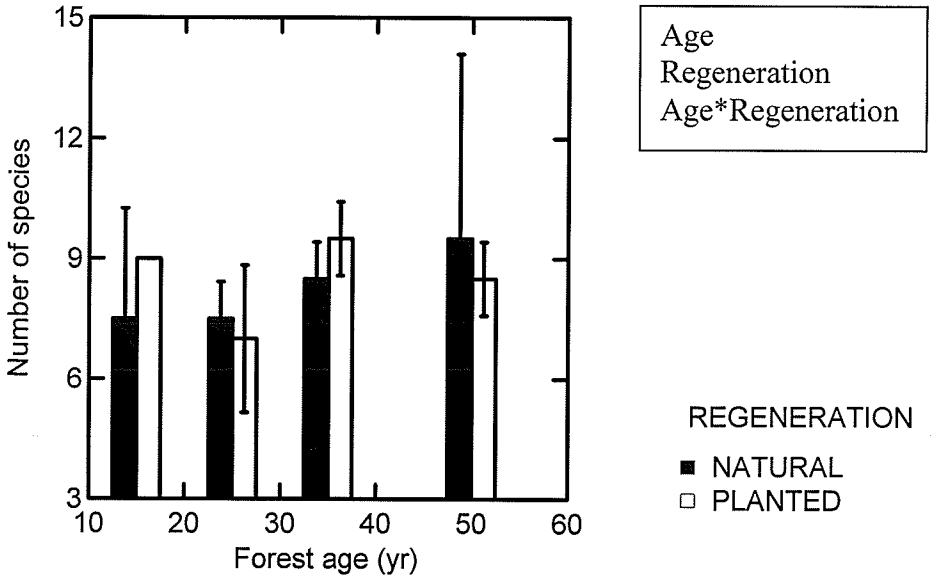


Figure 3.1.49 Alpha diversity of the shrub assemblages (mean ± SE); patterns related to forest age and regeneration type.

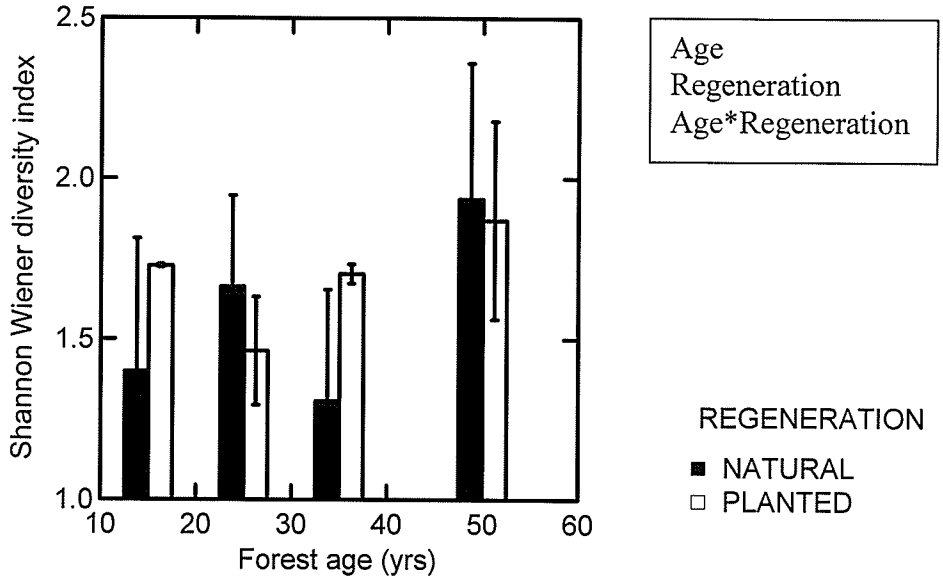


Figure 3.1.50 Species evenness of the shrub assemblages (mean ± SE); patterns related to forest age and regeneration type.

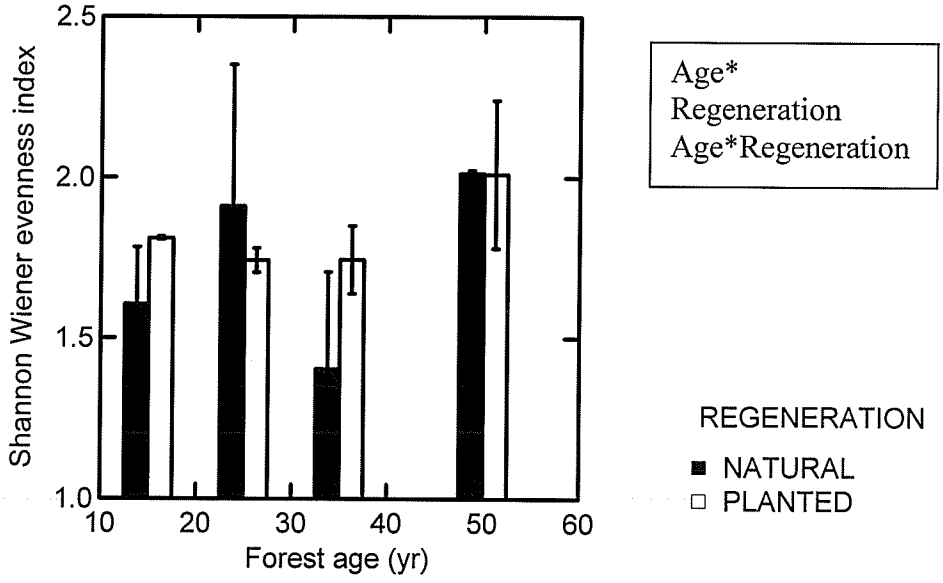


Figure 3.1.51 Kendall's index of beta diversity of shrub assemblages; patterns related to forest age and regeneration type

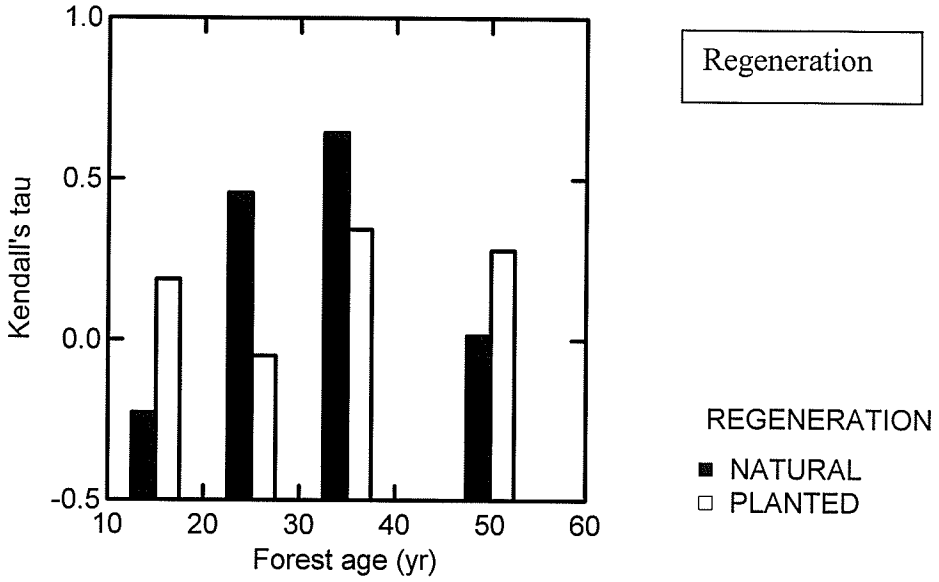


Figure 3.1.52 Jaccard's index of beta diversity of shrub assemblages; patterns related to forest age and regeneration type

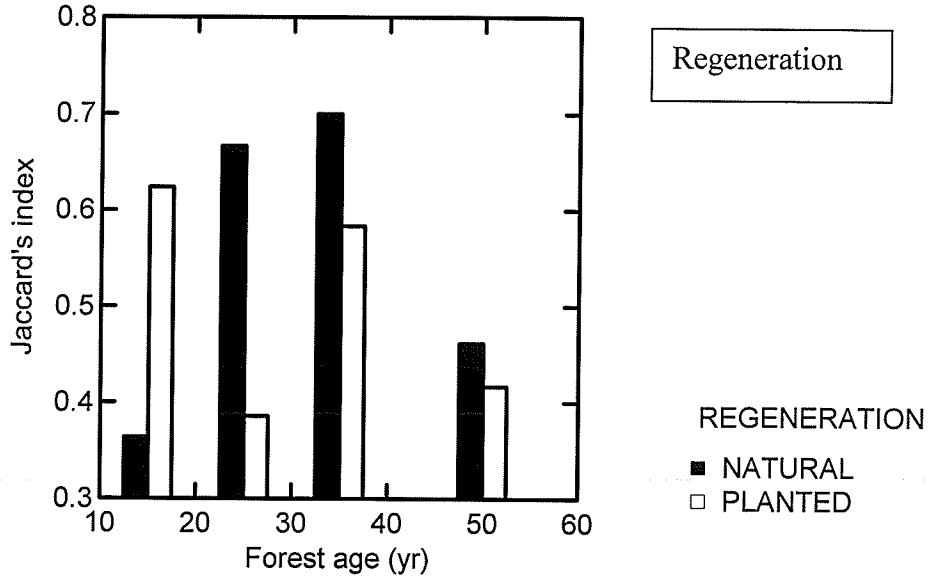
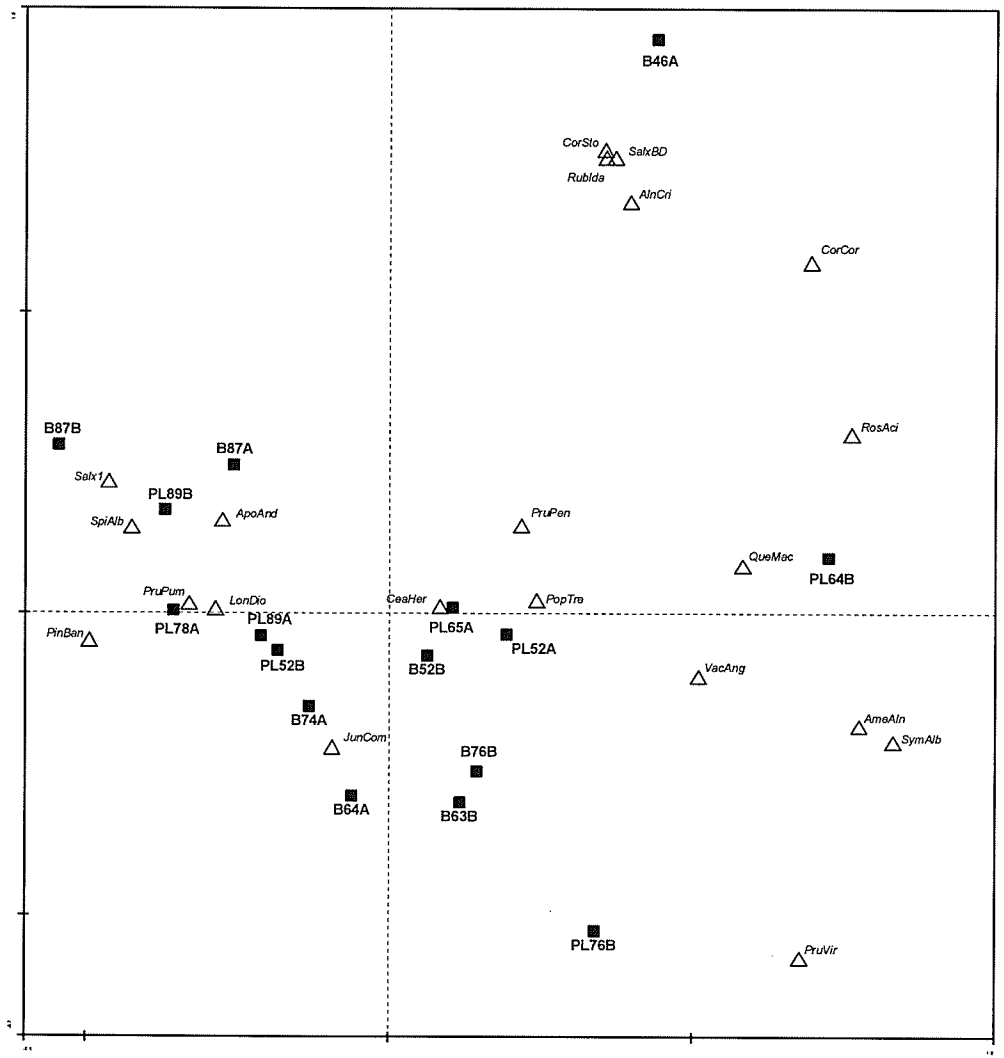


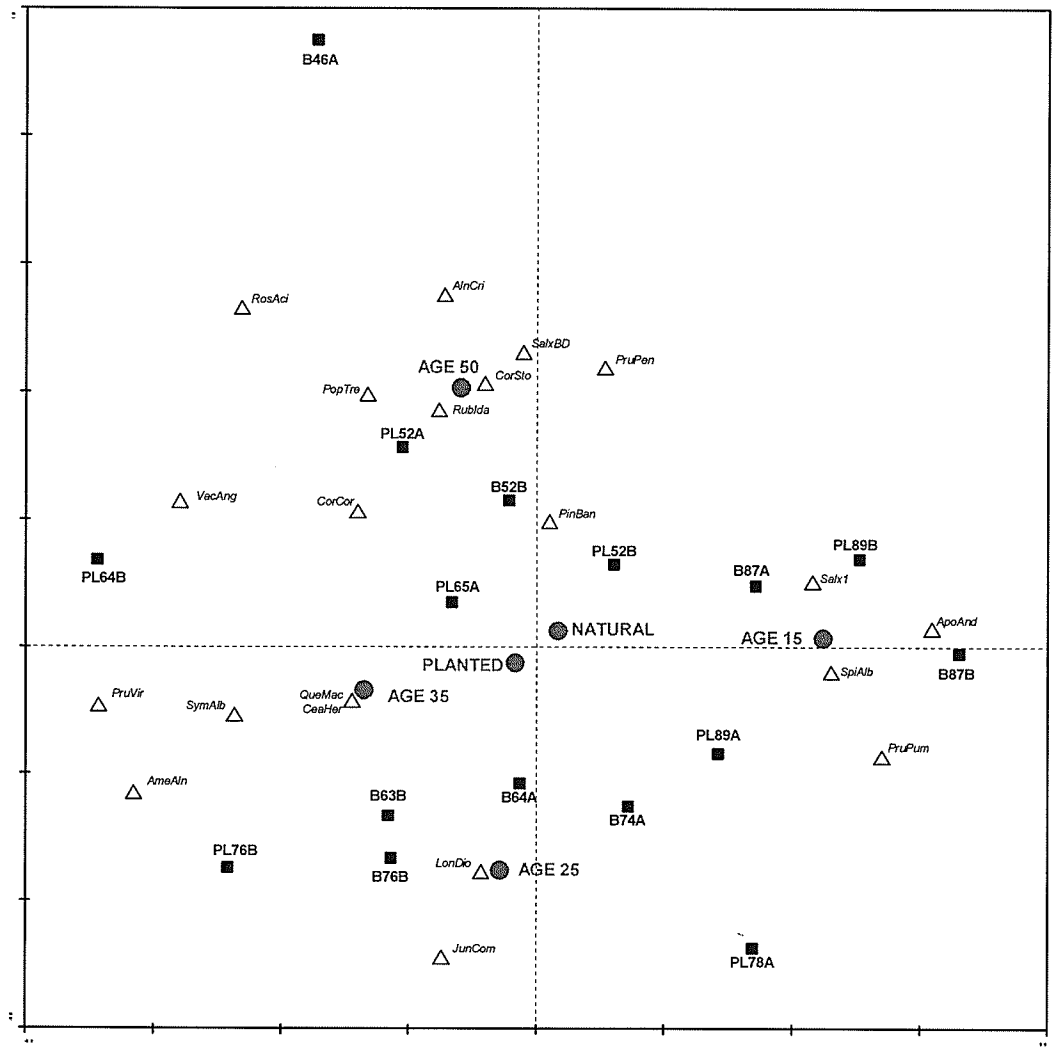
Figure 3.1.53 Principal Components Analysis ordination diagram of shrub species (Δ) and sites (■). Species codes: ALNCRI = *Alnus crispa*, AMEALN = *Amelanchier alnifolia*, APOAND = *Apocynum androsaemifolium*, CEAHER = *Ceanothus herbaceous*, CORSTO = *Cornus stolonifera*, CORCOR = *Corylus cornuta*, DIELONG = *Diervilla lonicera*, JUNCOM = *Juniperus communis*, LONDIO = *Lonicera dioica*, PINBAN = *Pinus banksiana*, POPTRE = *Populus tremuloides*, PRUPEN = *Prunus pensylvanica*, PRUPUM = *Prunus pumila*, PRUVIR = *Prunus virginiana*, QUEMAC = *Quercus macrocarpa*, ROSACI = *Rosa acicularis*, RUBIDA = *Rubus idaeus*, SALX1 = *Salix* 1, SALXBD = *Salix bebbiana/discolor*, SPIALB = *Spiraea alba*, SYMALB = *Symphoricarpos albus*, VACANG = *Vaccinium angustifolium*.



Axis 1 λ = 0.409

Axis 2 λ = 0.168

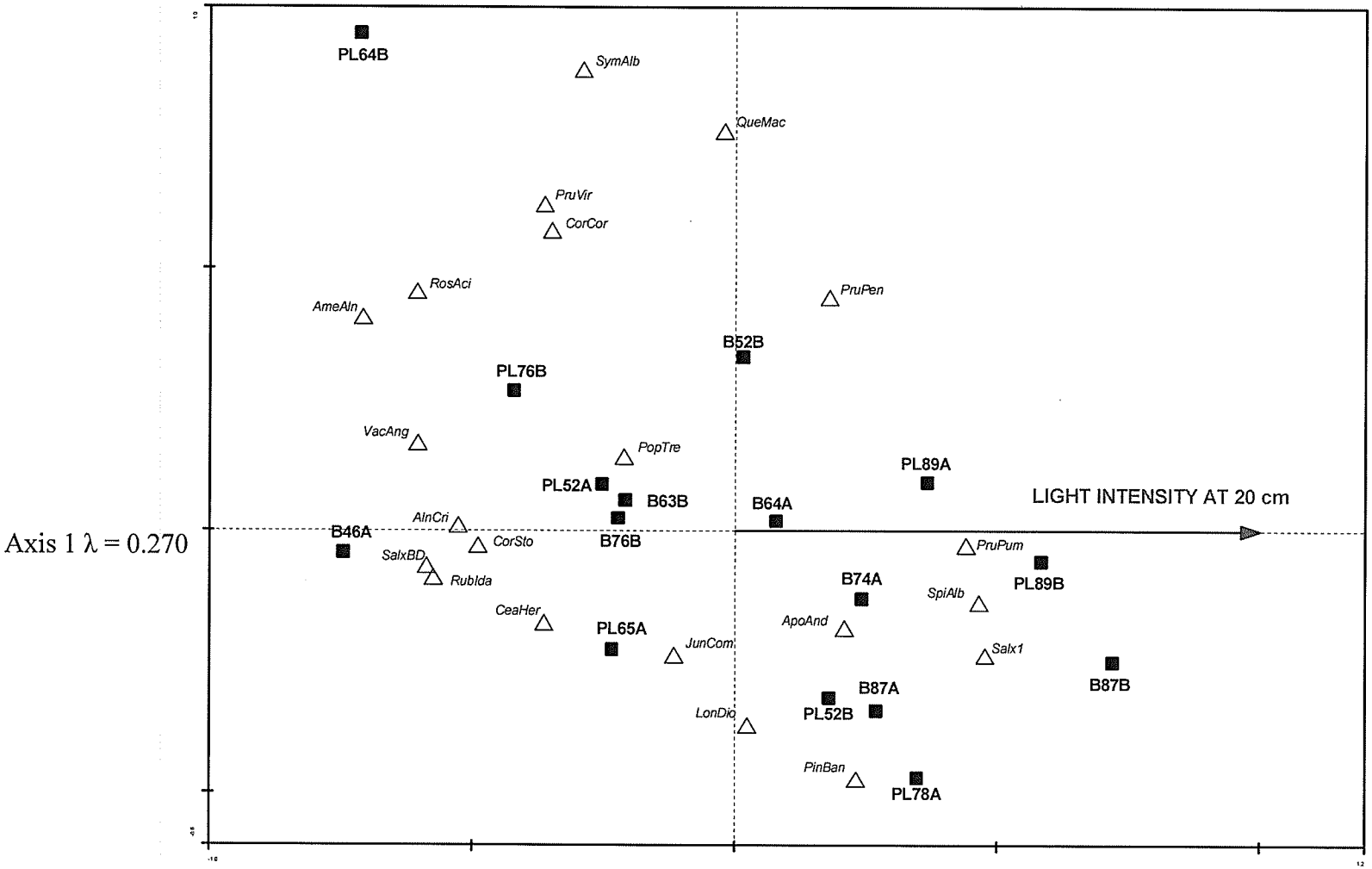
Figure 3.1.54 Redundancy Analysis ordination diagram of shrub species (Δ) and sites (■) constrained by forest age and regeneration type. Species codes: ALNCRI = *Alnus crispa*, AMEALN = *Amelanchier alnifolia*, APOAND = *Apocynum androsaemifolium*, CEAHER = *Ceanothus herbaceous*, CORSTO = *Cornus stolonifera*, CORCOR = *Corylus cornuta*, DIELONG = *Diervilla lonicera*, JUNCOM = *Juniperus communis*, LONDIO = *Lonicera dioica*, PINBAN = *Pinus banksiana*, POPTRE = *Populus tremuloides*, PRUPEN = *Prunus pensylvanica*, PRUPUM = *Prunus pumila*, PRUVIR = *Prunus virginiana*, QUEMAC = *Quercus macrocarpa*, ROSACI = *Rosa acicularis*, RUBIDA = *Rubus idaeus*, SALX1 = *Salix* 1, SALXBD = *Salix bebbiana/discolor*, SPIALB = *Spiraea alba*, SYMALB = *Symphoricarpos albus*, VACANG = *Vaccinium angustifolium*.



Axis 1 λ = 0.214

Axis 2 λ = 0.086

Figure 3.1.55 Redundancy Analysis ordination diagram of shrub species (Δ) and sites (■) constrained by environmental variables. Species codes: ALNCRI = *Alnus crispa*, AMEALN = *Amelanchier alnifolia*, APOAND = *Apocynum androsaemifolium*, CEAHER = *Ceanothus herbaceous*, CORSTO = *Cornus stolonifera*, CORCOR = *Corylus cornuta*, DIELONG = *Diervilla lonicera*, JUNCOM = *Juniperus communis*, LONDIO = *Lonicera dioica*, PINBAN = *Pinus banksiana*, POPTRE = *Populus tremuloides*, PRUPEN = *Prunus pensylvanica*, PRUPUM = *Prunus pumila*, PRUVIR = *Prunus virginiana*, QUEMAC = *Quercus macrocarpa*, ROSACI = *Rosa acicularis*, RUBIDA = *Rubus idaeus*, SALX1 = *Salix* 1, SALXBD = *Salix bebbiana/discolor*, SPIALB = *Spiraea alba*, SYMALB = *Symphoricarpos albus*, VACANG = *Vaccinium angustifolium*.



Axis 1 λ = 0.270

Axis 2 λ = 0.214

Figure 3.1.56 Per cent cover of moss (mean ± SE); patterns related to forest age and regeneration type.

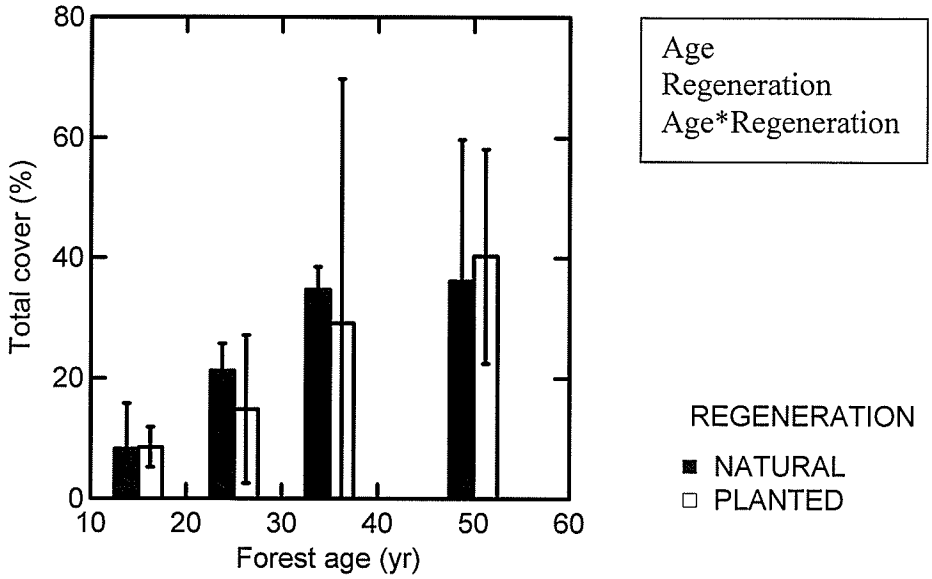


Figure 3.1.57 Number of moss species sampled per site (mean ± SE); patterns related to forest age and regeneration type.

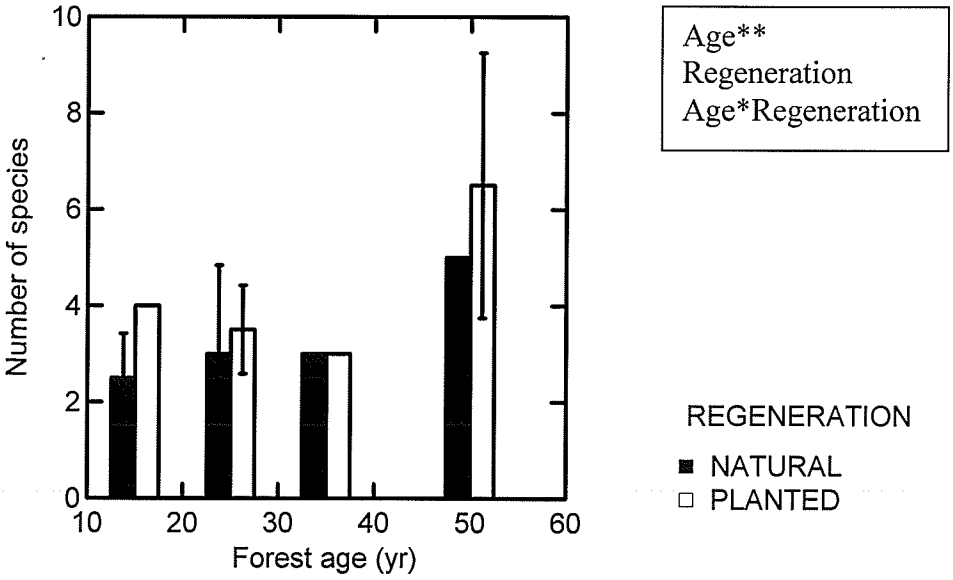


Figure 3.1.58 Alpha diversity of the moss assemblages (mean ± SE); patterns related to forest age and regeneration type.

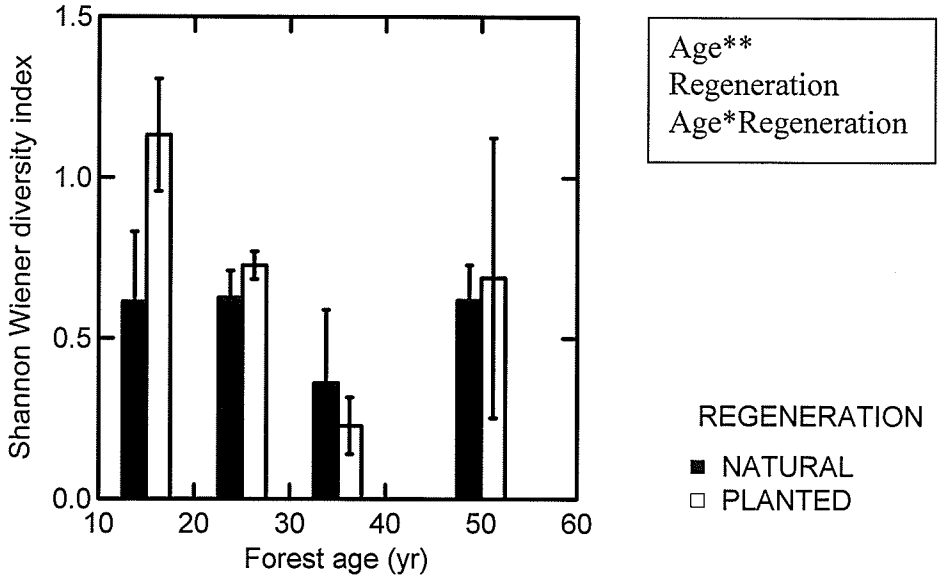


Figure 3.1.59 Species evenness of the moss assemblages (mean ± SE); patterns related to forest age and regeneration type.

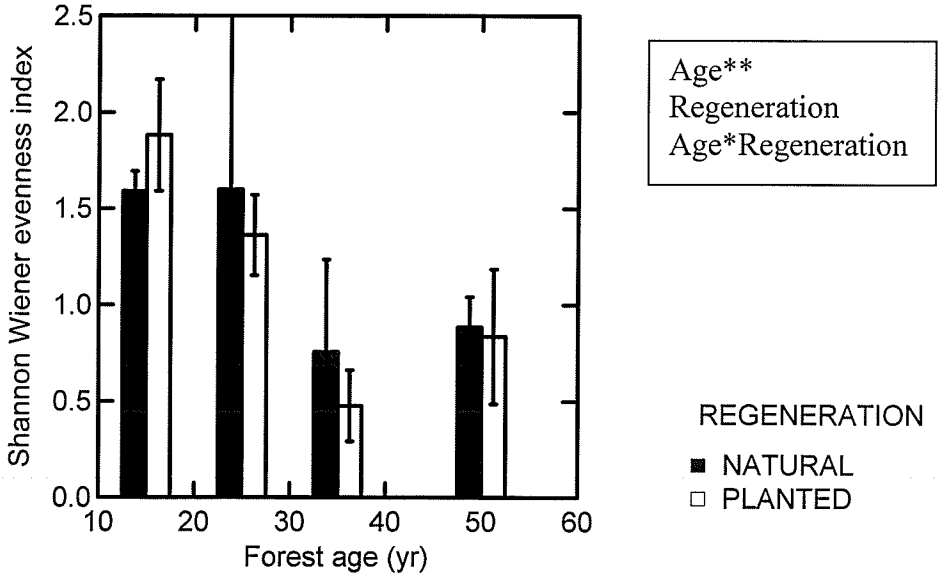


Figure 3.1.60 Kendall's index of beta diversity of the moss assemblages; patterns related to forest age and regeneration type

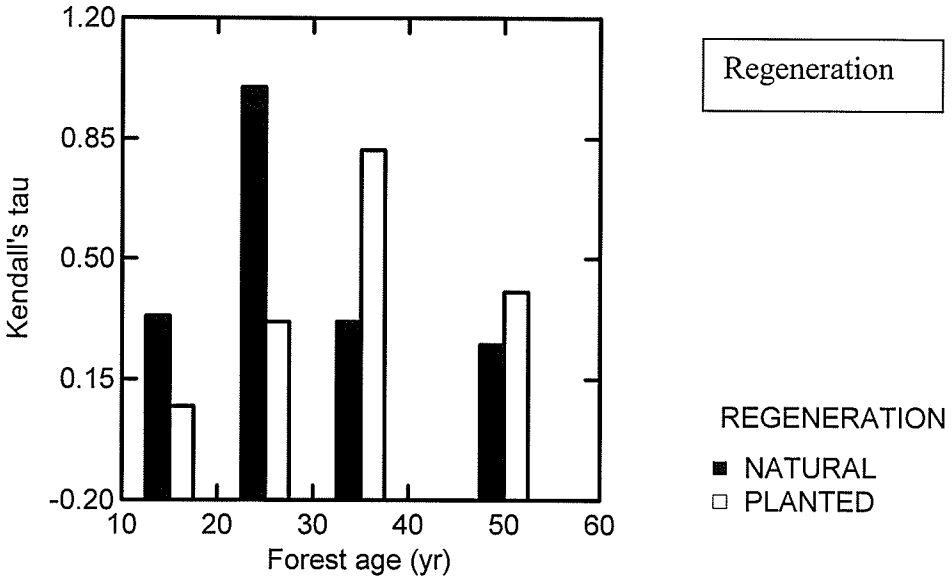


Figure 3.1.61 Jaccard's index of beta diversity of the moss assemblages; patterns related to forest age and regeneration type

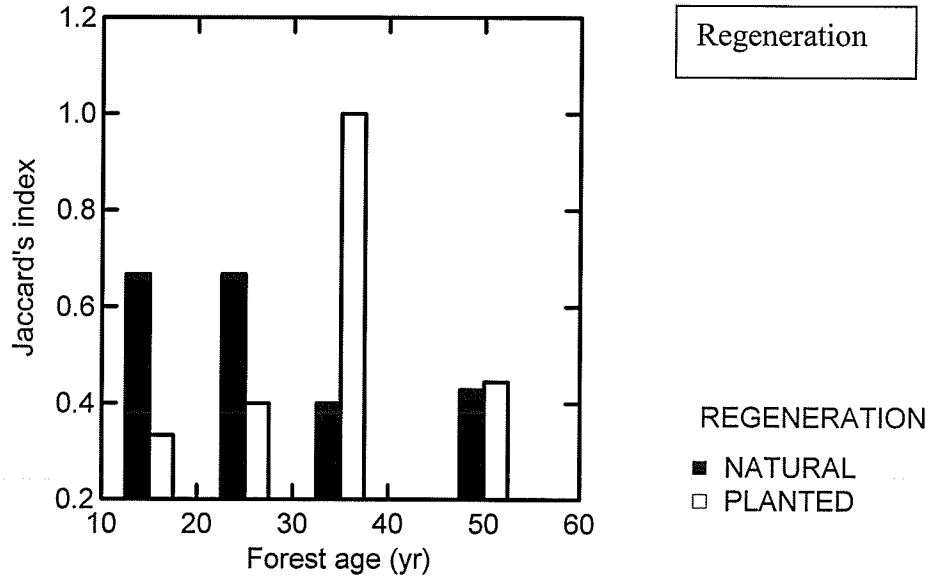
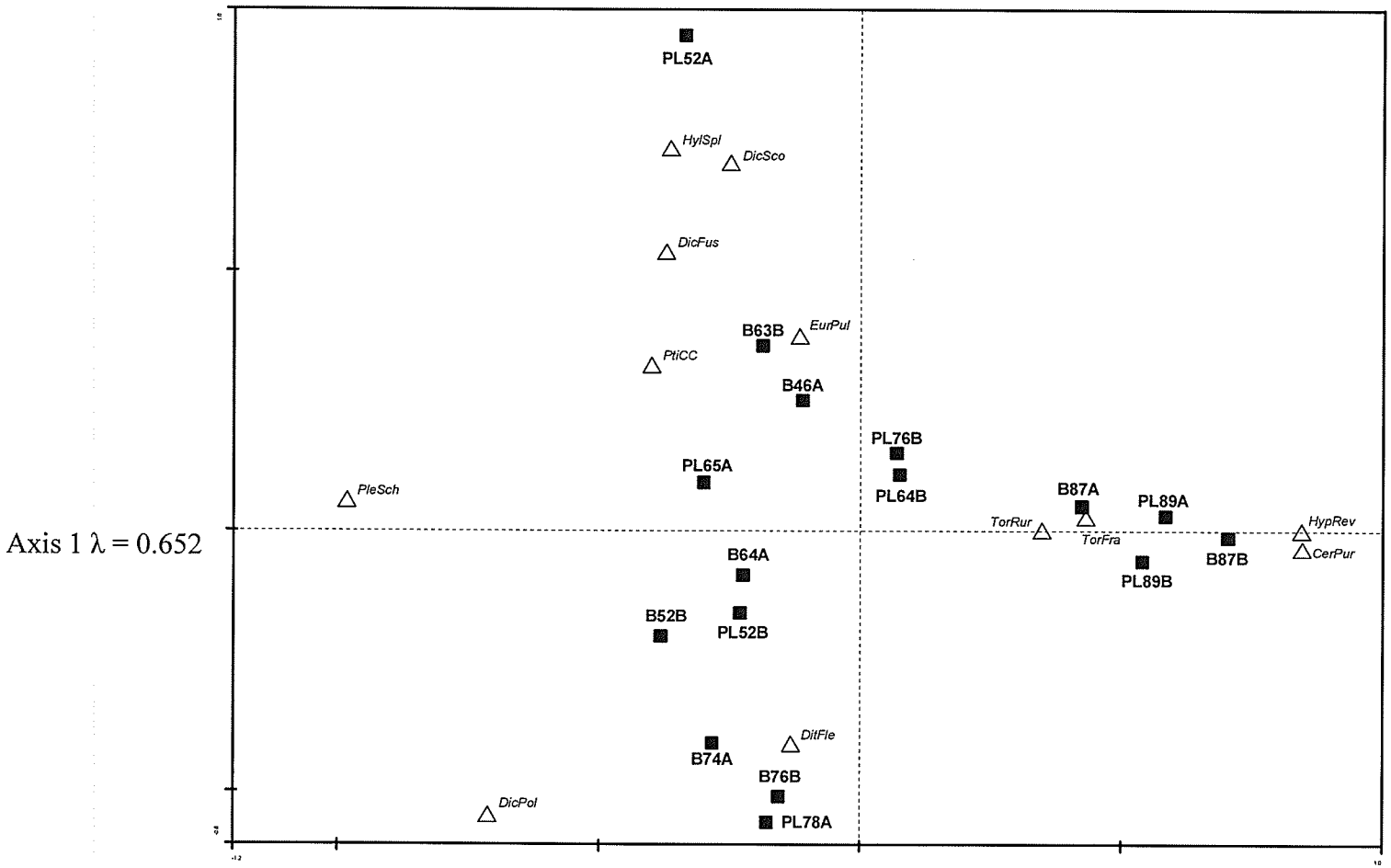


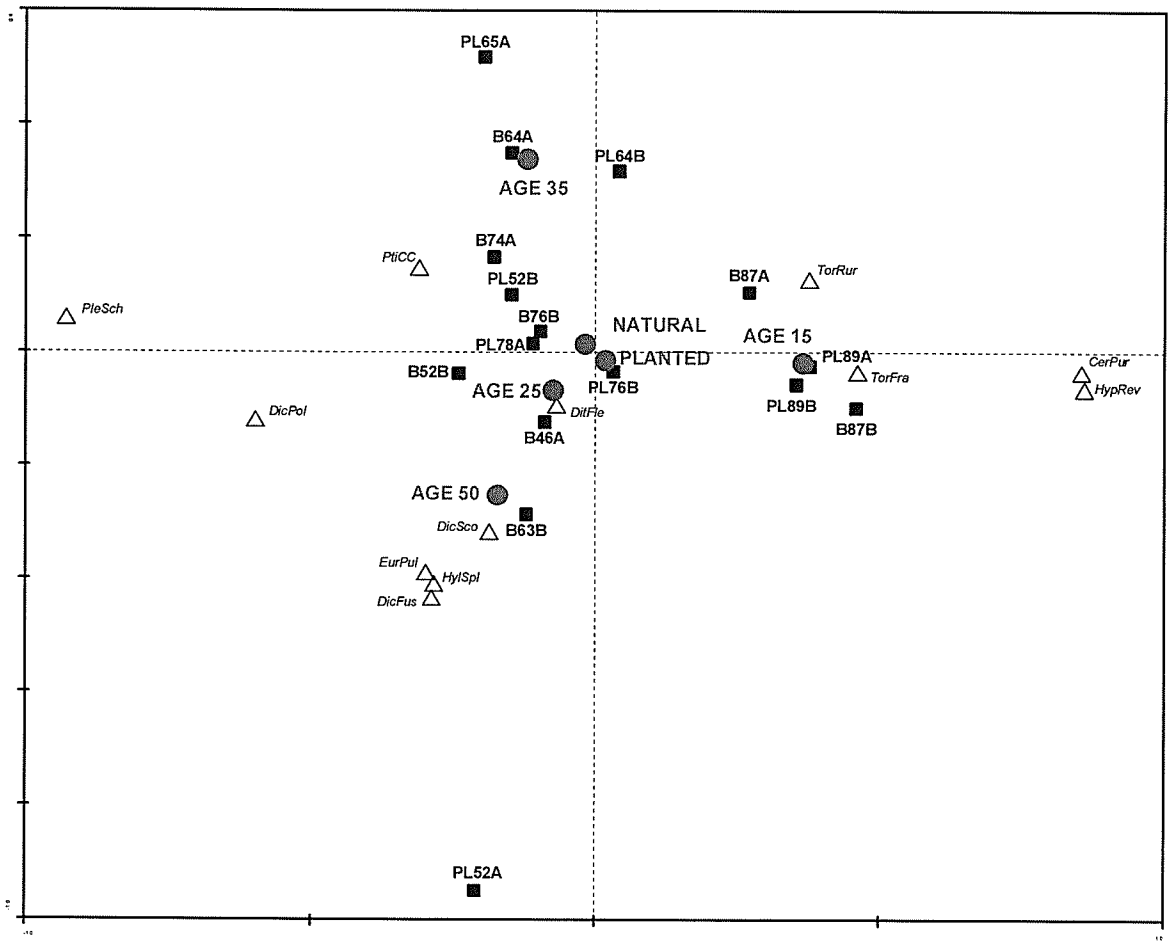
Figure 3.1.62 Principal Components Analysis ordination diagram of shrub species (Δ) and sites (■). Species codes: CERPUR = *Ceratodon purpureus*, DICFUS = *Dicranum fuscescens*, DICPOL = *Dicranum polysetum*, DICSCO = *Dicranum scoparium*, DITFLE = *Ditrichum flexicaule*, EURPUL = *Eurhynchium pulchellum*, HYLSPL = *Hylocomium splendens*, HYPREV = *Hypmum revolutum*, PLESCH = *Pleurozium schreberi*, PTICC = *Ptilium crista-castrensis*, TORFRA = *Tortula fragilis*, TORRUR = *Tortula ruralis*.



Axis 1 λ = 0.652

Axis 2 λ = 0.122

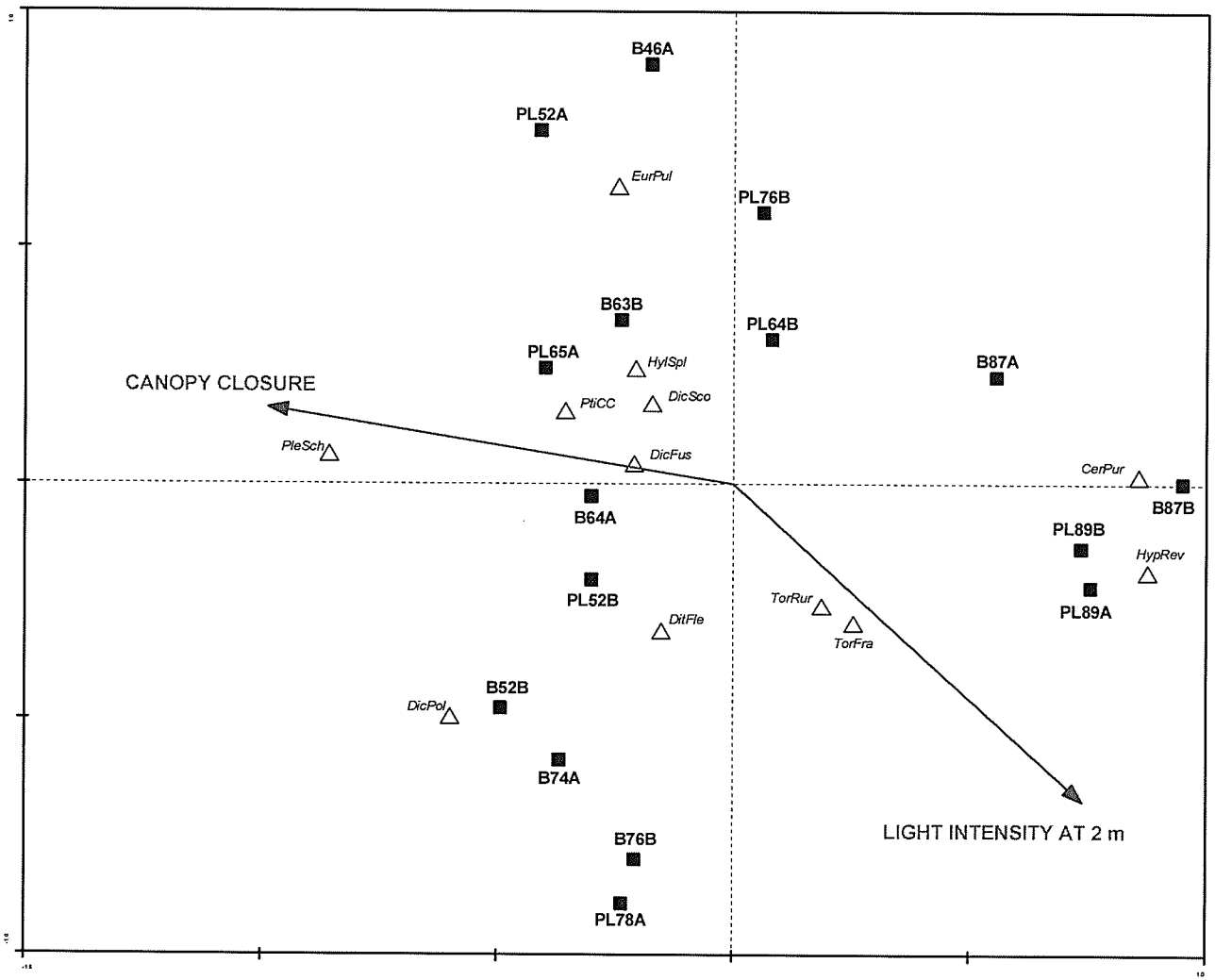
Figure 3.1.63 Redundancy Analysis ordination diagram of shrub species (Δ) and sites (■) constrained by forest age and regeneration type. Species codes: CERPUR = *Ceratodon purpureus*, DICFUS = *Dicranum fuscescens*, DICPOL = *Dicranum polysetum*, DICSCO = *Dicranum scoparium*, DITFLE = *Ditrichum flexicaule*, EURPUL = *Eurhynchium pulchellum*, HYLSPL = *Hylocomium splendens*, HYPREV = *Hypmum revolutum*, PLESCH = *Pleurozium schreberi*, PTICC = *Ptilium crista-castrensis*, TORFRA = *Tortula fragilis*, TORRUR = *Tortula ruralis*.



Axis 1 λ = 0.587

Axis 2 λ = 0.032

Figure 3.1.64 Redundancy Analysis ordination diagram of shrub species (Δ) and sites (■) constrained by environmental variables. Species codes: CERPUR = *Ceratodon purpureus*, DICFUS = *Dicranum fuscescens*, DICPOL = *Dicranum polysetum*, DICSCO = *Dicranum scoparium*, DITFLE = *Ditrichum flexicaule*, EURPUL = *Eurhynchium pulchellum*, HYLSPL = *Hylocomium splendens*, HYPREV = *Hypmum revolutum*, PLESCH = *Pleurozium schreberi*, PTICC = *Ptilium crista-castrensis*, TORFRA = *Tortula fragilis*, TORRUR = *Tortula ruralis*.



Axis 1 λ = 0.527

Axis 2 λ = 0.073

3.2 Effect of forest management on the diversity of butterfly (Lepidoptera) assemblages in jack pine (*Pinus banksiana*) forests in southeastern Manitoba

Abstract

The health of biological communities may be affected by forest management practices including reforestation strategies. The response of the butterfly assemblage to stand level changes associated with regeneration type and with forest age was evaluated. Butterflies were sampled by hand-netting along prescribed transects in planted and naturally regenerating forests of 15, 25, 35, and 50 years of age. Total catch, species richness, alpha diversity, species evenness and species dominance measures were examined for the influence of forest age and regeneration type and beta diversity between replicates was compared. No significant effect of forest age or regeneration type was found for any of the summary measures, however, the small number of butterflies collected over the two study years limited the conclusions that could be drawn from these analyses. In addition, year to year differences in weather influenced the results and may have obscured age and regeneration type patterns in the data. Recommended modifications to the sampling methods used in this study are outlined.

INTRODUCTION

A heterogeneous forest structure is characteristic of natural post-fire regeneration in the boreal zone (Nilsson et al. 2001). Structurally, spatial patterns may be altered by reforestation, which tends to increase the uniformity of a stand (Hansen et al. 1991). In addition, the understory plant community may be influenced by stand management and reforestation techniques. Both diversity and community composition may be different in managed and natural stands, especially in young forests (Abrams and Dickmann 1982; Reich et al. 2001). For example, burned stands tend to be occupied by unique, colonizing species (Abrams and Dickmann 1982); other understory species are favoured by management, increasing in abundance after harvest and in some cases out-competing other plant species (Esseen et al. 1997). These structural and floral differences may in turn influence the faunal community of the forest, therefore, the effect of forest management on sensitive fauna must be evaluated.

The primary factors influencing butterfly distribution are the availability of an adequate and appropriate food source for both larvae and adults (Ehrlich 1984). Butterflies display some degree of host-specificity, especially in larval stages (Howe 1975), therefore they should be expected to respond to an alteration in the understory plant community. Habitat selection by adult butterflies may also be influenced by the degree of canopy cover (Warren 1985). Butterflies in forested areas exhibit preferences for different levels of shade (Pollard 1977). Members of a few species, such as the Satyrinae, favour more heavily shaded, closed forests (Warren 1985; Rudolph and Ely 2000). Adults of other species are typically found in open glades; Papilionidae and

Pieridae especially tend to favour open habitats, where their thermal and nectar requirements are met (Rudolph and Ely 2000).

On these grounds, the butterfly assemblage is expected to respond to elements of stand structure and to floral diversity or quality, specific ecosystem characteristics that are important in the evaluation of forest management. Therefore butterflies may have potential as biological indicators in forest ecosystems. Although Elliott (1997) found that the diversity of the butterfly assemblage did not show a consistent trend in planted and natural sites, the assemblage composition differed between planted and naturally regenerating forests. The use of butterflies as indicators to evaluate the health of managed forests is not well-documented in the boreal forest region however. Butterflies have been used more frequently to investigate the effect of forest management in tropical environments where they have been found to respond to forest management techniques such as selective harvesting and replanting (e.g. Willott et al. 2000; Stork et al. 2003).

The specific objectives of this study were as follows:

- To determine whether alpha diversity of the butterfly community differs between planted and naturally regenerated jack pine stands of a similar age.
- To determine whether alpha diversity of the butterfly community is influenced by forest age.
- To determine whether beta diversity of butterfly assemblages differs between planted and naturally regenerated stands.
- To compare the butterfly community occurring in planted jack pine stands to those occurring in naturally regenerated stands of a similar age.

- To investigate relationships between butterfly assemblages and habitat variables that may explain differences in these assemblages.

Materials and Methods

This study was conducted in the Sandilands Provincial Forest, situated in southeastern Manitoba. A full description of regional characteristics can be found in Chapter 3.1.

Sixteen sites were established, eight in forests regenerating naturally after fire and eight in planted forests. Two replicates representing each of four different forest ages in each regeneration type were used; the approximate ages of these forests were 15, 25, 35 and 50 years.

The sites were originally selected in 1991, and at the time of selection, the forests were approximately 5, 15, 25 and 40 years of age. Full details regarding site history, site selection and site characteristics are provided in Chapter 3.1, information on site locations can be found in Table 3.1.1 and Figure 3.1.1.

The study sites were 100 X 100 m, and were located in forest stands that were a minimum of 2 ha in size. Sites were located at least 20 m away from any major discontinuity such as a roadway or trail. All sites were dominated by jack pine, with a minimum of 75% of tree stems of that species. In addition, they were all located on well-drained upland regions.

Sites were given code names corresponding to regeneration type (B or PL), year of origin, and replicate (A or B). For example, B87A the first replicate of is a site that is regenerating naturally after an ecosystem-altering fire in 1987. Similarly, PL52B is the

second replicate of a site that that was planted in 1952. Replicate letters were assigned for convenience, they do not imply a blocked study design.

Environmental Characteristics

Site characteristics including flora were thoroughly investigated and the methods and results of this sampling are presented in Chapter 3.1. Temperature data were obtained from Environment Canada for Steinbach, MB (Environment Canada 2005) and precipitation data from Manitoba Conservation for Woodridge, MB (Manitoba Conservation 2005).

Butterfly Sampling

Butterflies and skippers were sampled bi-weekly at each site. Samples were obtained by netting all butterflies and skippers sighted along a prescribed route within a 30 minute time period (Elliott 1997). The prescribed route consisted of a series of 10, 100 m transects that were designed so that each area of the site was examined twice (Elliott 1997). All specimens were euthanized with ethyl acetate, placed in a labelled Petri dish, and kept in a cooler until they could be taken to the laboratory for preservation and identification. Sampling occurred between 10 AM and 4 PM and was deferred if it was raining or if the understory vegetation was wet. To control for the influence of time of day on the collection, each sampling day was equally divided into four sampling periods. A planted site was paired with a naturally regenerating site of the same age, and these sites were sampled in the same half of the same sampling day. Sites were rotated through

the four sampling periods over the sampling season. Sampling continued from 26 May to 29 August 2003 and 7 June to 24 August 2004.

All butterflies collected were identified to species with the aid of a local guide (Klassen et al. 1989) and JB Wallis Museum specimens. Nomenclature was updated following Layberry et al. (1998). *Speyeria electa* is now considered a subspecies of *Speyeria atlantis*, however, Elliott (1997) followed a previous classification system and counted *S. electa* as a separate species. Because this study was designed as a follow-up study to Elliott's, *S. electa* was counted as a separate species in this study. Voucher specimens are deposited at the JB Wallis Museum, Winnipeg Manitoba. Species authorities are found in Appendix 7.

Host specific butterflies were defined as being those whose larvae feed exclusively on plants within one genus. These species were identified based on the food plant descriptions of Klassen et al. (1989).

Statistical Analysis

The number of individuals collected was used as a general indicator of relative butterfly abundance. The total number of species (species richness), and the log series alpha index were used to assess alpha diversity of each of butterfly community. The log series alpha index alpha (Southwood 2000) was calculated for the equation:

$$S = \alpha \log_e\left(1 + \frac{N}{\alpha}\right)$$

To accomplish this, the logarithmic series parameter x was estimated using iterative least squares minimization from the following equation:

$$\frac{S}{N} = \frac{(1-x)}{x}\left[-\log_e(1-x)\right]$$

Where S is the total number of species and N is the total number of individuals in the sample.

The log series alpha was then derived from N and the estimate of x using the equation:

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

Species evenness for each site was characterized by calculating the slope of the log abundance of the constituent species against rank abundance. Species dominance was calculated using the Berger Parker Index (d) (Berger and Parker 1970) using the equation:

$$d = N_{max}/N$$

Where N_{max} equals the number of individuals of the most abundant species.

The effect of regeneration type, forest age, and the interaction of the two, on the each of the above measure was conducted using analysis of variance. A repeated measures analysis using the general linear model was used to evaluate the influence of field season bias on each of the preceding measures and to evaluate the interaction between collection year and the experimental design factors.

Data were tested for normality prior to analysis by graphing residuals from a general linear model estimate against the estimated values, and assessing for the

appropriate distribution pattern in the scattergram. When a heterogeneous distribution of residuals was noted, data was appropriately transformed and analyzed in that form.

Jaccard's index (C_J) and Kendall's τ correlation coefficient were used to measure the beta diversity of the butterfly community in each of the replicate pairs. These two measures were calculated using the methods described in Chapter 3.1.

Beta diversity measures were compared using a paired t-test. In order to evaluate the influence of collection year on beta diversity measures, a repeated measures model was used. Because there is no independent variable in this model, this tests functions as a multiple year version of a paired t-test.

All these analyses were performed using SYSTAT 10.2 (SYSTAT 2002). For all analysis, an alpha value of ≤ 0.05 was considered significant.

Ordination analysis of the butterfly assemblage was attempted however, this analysis could not be reliably interpreted, and no results are presented.

RESULTS

Monthly temperature means and monthly precipitation accumulations are presented in Table 3.2.1. The 2004 collection year was generally cooler than 2003, especially in May and August. Precipitation over the 2004 collection year was higher than in 2003; this was especially evident in April, May and August.

There was a significant effect of collection year on all of the site measures (Table 3.2.2), however there was no interaction between collection year and forest age, regeneration type or the interaction of the two. Because the two collection years were quite different in terms of weather, each year is described separately.

A total of 308 butterflies representing 32 different species were collected in 2003. In 2004, 189 individuals of 24 different species were collected. A summary of the most commonly collected species is presented in Table 3.2.3. Complete collection data from the 2003 and 2004 seasons can be found in Appendix 7. The most commonly collected species in both years were *Glaucopsyche lygdamus*, *Enodia anthedon*, *Colias interior* and *Celastrina ladon*. Collectively they made up 55% of the entire catch in 2003, and 58% in 2004. Species such as *E. anthedon* and *C. ladon* were more commonly collected in older forests, this trend was especially apparent for *E. anthedon* which was rarely collected in 15-year-old sites. Although *C. interior* was collected in a number of sites, it was most often collected in PL78A. *Megisto cymela* was more commonly collected in planted sites in both of the collection years, although this species did not occur in great frequency.

The number of butterflies collected was not significantly influenced by forest age, regeneration type or the interaction of the two in either collection year (Table 3.2.4). The number of butterflies collected in 2004 was less than two thirds that collected in 2003, however, the patterns related to forest age were similar in both years (Figure 3.2.1 and 3.2.2). The peak catch tended to occur in mid-aged stands in both regeneration types; in 25-year-old planted and 35-year-old natural sites.

The number of species collected was not significantly affected by forest age, regeneration type or by their interaction in either of the two collection years (Table 3.2.4). Fewer species were collected in the youngest and oldest sites in 2003. Twenty-five-year-old planted, and 35-year-old natural sites were more speciose than their counterparts; this non-significant trend was evident in both study years (Figure 3.2.3 and Figure 3.2.4).

The number of species demonstrating relative feeding specificity in the larval stage, i.e. those relying upon host plants within the same genus, was not significantly different between regeneration types or forest ages in either collection year (Table 3.2.4). In 2003, more host plant specialists were found in 35-year-old naturally regenerating sites, while the planted sites of the same age had the fewest (Figure 3.2.5). In 2004, most host plant specialist species were collected in the 15-year-old sites (Figure 3.2.6). In sites older than 15 years, there were similar regeneration related patterns of host plant specialists in both study years.

Species diversity, as indicated by the log series alpha index, was not significantly influenced by forest age, regeneration type or the interaction of the two in either collection year (Table 3.2.4), however different patterns emerged in each collection year (Figures 3.2.7 and 3.2.8). In 2003 there was a general trend, albeit subtle, to decreasing diversity with forest age. In 2004 a slight reduction in diversity was noted between 15-year-old and older natural sites and between 15-year-old and mid-aged planted sites, however, there was a high level of diversity 50-year-old planted sites. This was primarily due to the influence of one site, PL52A, in which a total of seven butterflies of six different species was collected in 2004.

Neither dominance nor evenness was significantly influenced by forest age, regeneration type or the interaction of the two (Table 3.2.4). No clear successional, or year to year trend in species evenness was evident for either measure (Figures 3.2.9 – 3.2.12). Overall, the butterfly assemblage in planted sites tended to be marginally more evenly distributed than that in naturally regenerating sites.

Beta diversity was not significantly different between collection years for either measure, nor was there an interaction between collection year and regeneration type (Table 3.2.2); therefore the statistical results presented for each of these measures reflect both years combined. There was no significant influence of regeneration type when either the Kendall's τ ($F_{1,3} = 0.292$, $p > 0.05$) or the Jaccard's index ($F_{1,3} = 0.018$, $p > 0.05$) was employed. Trends in these measures are illustrated in Figures 3.2.13 – 3.2.16. In 2003, beta diversity between planted replicates tended to be lowest in 15-year-old forests and increased with forest, while in natural sites it was lower in both the oldest and youngest sites. The beta diversity in young naturally regenerating sites generally exceeded that of the young planted sites. In 2004, beta diversity in planted sites followed a similar pattern to 2003, while in natural sites it was highest in the 15- and 25-year-old sites. Beta diversity between natural replicates tended to be lower than that between planted replicates in 2004.

Discussion

Sampling butterflies in boreal forest environments is fraught with problems. Hand-netting in particular biases the collection in favour of weaker fliers, as stronger fliers are more difficult to catch (Pollard and Yates 1993). In addition, the environment is often not conducive to effective netting. Thick underbrush hinders the movement of the sampler, making it difficult to give chase once a specimen is sighted. In addition understory elements often physically disrupt the netting process by hindering net swing.

Identification of species on the wing is an established method used in forest studies in tropical areas (e.g. Hill et al. 1995; Hamer et al. 1997; Willott et al. 2000).

However in the boreal region this method is not practical if species level identification is desired. For example, in this study, species of the genus *Speyeria* would not have been distinguishable from each other nor would species of the genus *Phyciodes*. There are an insufficient number of butterfly groups in boreal forests to warrant examination of higher taxonomic groups. In addition to uncertainties with species level identifications, there would be a high likelihood of mis-estimating the number of each species present, as it is not possible to monitor the location of each of the sighted specimens. Therefore counts based on sighting would either over- or under-estimate the number of individuals present.

Bait sampling on its own is also not a viable alternative as it biases the collection toward certain families such as the nymphalids (Kremen 1994). Again, due to the limited number of butterfly species inhabiting boreal forests, especially more mature stands, this technique on its own it not likely sufficient. In these study sites, over the two collection years of his study, Elliott (1997) collected a mere 20 species in bait traps, 14 of which were nymphalids. It is likely that bait sampling in combination with hand collection, as employed by Elliott (1997), would provide a better sampling method for butterflies in boreal forests if butterflies were deemed the best indicators for the question at hand.

The frequency with which butterflies are sampled is another consideration. For logistical reasons, butterflies were sampled on a bi-weekly basis in this study. This contributed to the low sample sizes however. In comparison, Elliott (1997) collected a total of 2158 individuals by hand netting over the two years of his study; 667 over 4 ½ months in the first year and 1491 in the second. Increasing the sampling frequency to weekly would help to mitigate the problem of low sample sizes.

In addition to immediate issues with collection technique, both weather and climate influence butterfly catch. Butterfly activity is influenced by weather conditions including temperature, precipitation and cloud cover (Pollard et al. 1975; Pollard and Yates 1993; Willott et al. 2000). Although sampling was deferred for rain, and was controlled for time of day, the structure of this project precluded deferring sampling when less than ideal temperatures or cloud cover may have suppressed butterfly activity. In addition to weather, larger scale trends influence the activity of butterflies. Abnormally cold or wet summers, such as that of 2004 (Table 3.2.1), will potentially influence butterfly catch for the entire collection year as counts of some species are higher with warm, sunny weather (Pollard et al. 1975). Over the course of a collection season the influence of poor weather will have a cumulative effect on the catch. For example, *G. lygdamus* was the most commonly collected species in 2003 but the catch of this species in 2004 was less than half of that in 2003 (Table 3.2.3). Catch of *E. anthedon* and *Callophrys niphon* followed a similar year to year pattern. The catch of other species, such as *C. interior* and *C. ladon*, were less influenced by collection year. Yet other species, such as *M. cymela* increase in abundance; catch of this species in 2004 was double that of 2003. The presence of biennial species, such as *Oeneis macounii*, also influenced the assemblage, although, as this species reached adulthood in this area in 2004, there was less influence of this species on year to year differences in total catch and species diversity measures.

As butterflies are more abundant in open areas, perhaps they may be of more utility in newly regenerating forests. It is in the youngest sites where many management related influences seem to be the most evident. Elliott (1997) did find differences in

butterfly assemblages between managed and natural forests of 5 and 15 years of age, supporting their use in these sites.

Collection methods, sampling frequency and weather related effects all limited butterfly collection in the two years of this study and these factors limited the sensitivity of the analyses that could be performed with this data set. The patterns for the butterfly catch from 2003 and 2004 (Table 3.2.3) differed and this is attributable to strong climatic differences from year to year (Table 3.2.1). Both year to year differences and the differences in sampling strategies make it difficult to compare patterns in these data to those of Elliott (1997). No clear, comparable patterns could be identified between these two studies.

CONCLUSIONS

The small number of butterflies collected over the two study years limited the analysis and interpretation of this data set. In addition, year to year differences in weather influenced the results. Modifications to the sampling methods used in this study are recommended if this group is employed to study boreal forest changes in the future.

Table 3.2.1 Mean monthly temperature and monthly precipitation accumulations for southeastern Manitoba

		Mean max (°C)	Mean (°C)	Mean min (°C)	Precipitation (mm)
November – March (2002/2003)					621.0*
2003	April	12.8	5.8	-1.3	20.5
	May	20.2	12.8	5.5	105.3
	June	23.6	17.0	10.5	102.3
	July	25.9	19.6	13.2	51.4
	August	27.8	21.1	14.4	83.6
	September	18.2	12.8	7.3	87.4
	October	12.6	6.9	1.2	28.6
November – March (2003/2004)					1109.0*
2004	April	9.5	3.8	-2.0	40.0
	May	13.6	7.8	2.0	145.8
	June	20.5	14.4	8.2	75.3
	July	24.4	18.2	11.9	58.2
	August	20.1	14.2	8.3	154.4
	September	20.4	15.1	9.7	118.0
	October	10.6	6.0	1.4	77.9

Temperature data from Environment Canada (2005) for Steinbach MB; precipitation data from Manitoba Conservation (2005) for Woodridge MB

*Snowfall accumulation

Table 3.2.2 Repeated measures analysis results for abundance and diversity measures of the butterfly assemblage

Measure	Effect	df	F-ratio	P
Total individuals	Year	1	17.082	0.00
	Year*age	3	0.883	0.49
	Year*regeneration	1	2.443	0.16
	Year*age*regeneration	3	1.002	0.44
	Error			
Species richness	Year	1	11.261	0.01
	Year*age	3	0.438	0.73
	Year*regeneration	1	0.072	0.80
	Year*age*regeneration	3	0.517	0.68
	Error			
Log series α	Year	1	98.578	0.00
	Year*age	3	1.356	0.32
	Year*regeneration	1	2.755	0.14
	Year*age*regeneration	3	0.186	0.90
	Error			
Berger Parker	Year	1	50.888	0.00
	Year*age	3	1.389	0.32
	Year*regeneration	1	0.169	0.69
	Year*age*regeneration	3	0.620	0.62
	Error			
Slope of log abundance	Year	1	31.696	0.00
	Year*age	3	1.442	0.30
	Year*regeneration	1	0.283	0.61
	Year*age*regeneration	3	1.823	0.22
	Error			
Jaccard's index	Year	1	0.624	0.49
	Year*regeneration	1	3.094	0.18
	Error	3		
Kendall's τ	Year	1	4.803	0.12
	Year*regeneration	1	4.982	0.11
	Error	3		

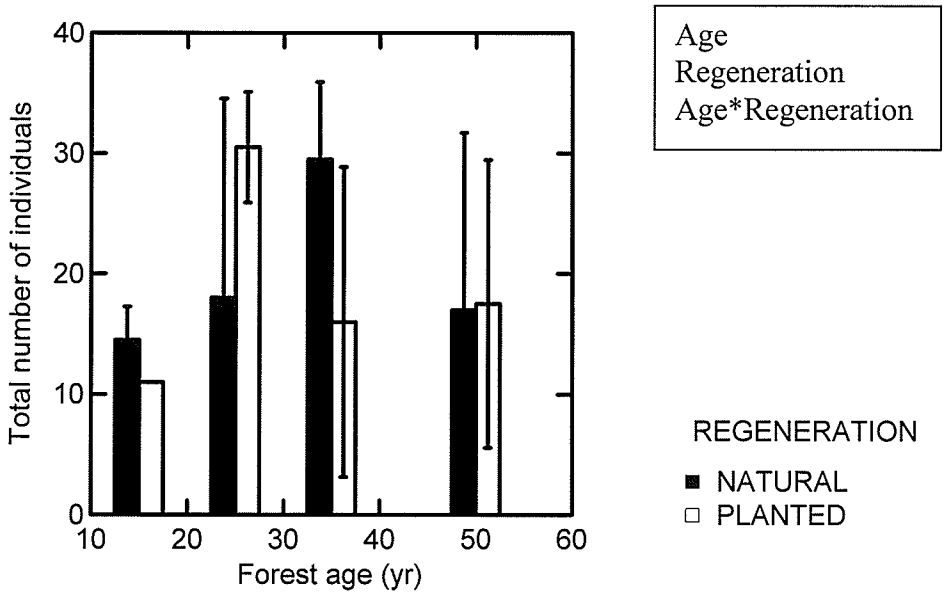
Table 3.2.3 Common butterfly species (at least 10 collected in one of two collection years)

	Species	Regeneration type	Mean catch ± SE 15 years	25 years	35 years	50 years
2003	*Glaucopsyche lygdamus*	Natural	5 ± 0.5	6 ± 2.5	4 ± 2.0	3 ± 1.0
		Planted	1 ± 0.5	3 ± 0.5	5 ± 4.0	4 ± 2.5
	Enodia anthedon	Natural	0	3 ± 3.0	6 ± 0.5	3 ± 3.0
		Planted	1 ± 0.5	5 ± 3.5	2 ± 1.0	4 ± 3.5
	Colias interior	Natural	1 ± 0.5	2 ± 1.0	1 ± 1.0	2 ± 1.5
		Planted	3 ± 0.5	# ± 9.5	0 ± 0.0	2 ± 1.0
	Celastrina ladon	Natural	1 ± 0.5	2 ± 1.5	5 ± 4.5	3 ± 0.5
		Planted	0 ± 0.0	2 ± 0.5	3 ± 1.0	2 ± 2.0
	Callophrys niphon	Natural	1 ± 0.5	2 ± 1.5	2 ± 2.0	0
		Planted	1	2 ± 0.5	1 ± 0.5	2 ± 0.0
	Megisto cymela	Natural	0	0	0	0
		Planted	0	2 ± 1.0	1 ± 0.5	1 ± 0.5
	Oeneis macounii	Natural	0	0	0	0
		Planted	0	0	0	0
2004	*Colias interior*	Natural	2 ± 0.5	4 ± 0.5	1 ± 0.5	0
		Planted	5 ± 0.0	6 ± 5.5	0	1 ± 0.5
	Celastrina ladon	Natural	1 ± 0.5	1 ± 0.5	4 ± 1.5	2 ± 0.0
		Planted	1 ± 0.5	3 ± 2.5	1 ± 1.0	3 ± 2.0
	Enodia anthedon	Natural	0	2 ± 2.0	1 ± 0.0	3 ± 2.5
		Planted	0	3 ± 2.5	5 ± 2.5	1 ± 0.0
	Glaucopsyche lygdamus	Natural	1 ± 1.0	2 ± 1.5	2 ± 1.5	2 ± 1.0
		Planted	1 ± 1.0	0	3 ± 3.0	1 ± 1.0
	Oeneis macounii	Natural	0	1 ± 0.5	4 ± 2.5	0
		Planted	1 ± 1.0	3 ± 1.5	0	1 ± 0.5
	Megisto cymela	Natural	1 ± 1.0	0	1 ± 0.5	1 ± 0.5
		Planted	0	2 ± 1.1	2 ± 1.4	1 ± 0.4
	Callophrys niphon	Natural	0	0	1 ± 0.0	1 ± 0.5
		Planted	1 ± 0.4	1 ± 0.4	1 ± 0.4	1 ± 0.7

Table 3.2.4 Analysis of variance results for abundance and diversity measures for the butterfly assemblage

			2003		2004		Repeated measures Between subjects	
Measure	Effect	df	F-ratio	P	F-ratio	P	F-ratio	P
Total individuals	Age	3	1.733	0.24	0.930	0.47	1.73	0.24
	Regeneration	1	0.062	0.81	3.133	0.11	0.40	0.55
	Age*Regeneration	3	1.800	0.22	0.637	0.61	1.63	0.26
	Error	8						
Number of species	Age	3	0.669	0.59	0.039	0.99	0.37	0.78
	Regeneration	1	0.194	0.67	0.871	0.38	0.88	0.38
	Age*Regeneration	3	1.744	0.24	0.642	0.61	2.05	0.19
	Error	8						
Number of host plant specialists	Age	3	0.275	0.84	1.222	0.36	0.37	0.78
	Regeneration	1	0.059	0.81	0.037	0.85	0.01	0.93
	Age*Regeneration	3	1.510	0.28	0.333	0.80	1.13	0.39
	Error	8						
Log series α	Age	3	1.461	0.30	1.449	0.30	1.59	0.27
	Regeneration	1	2.657	0.14	0.299	0.60	2.55	0.15
	Age*Regeneration	3	0.192	0.90	1.841	0.22	0.20	0.89
	Error	8						
Berger Parker	Age	3	0.396	0.76	0.227	0.88	2.67	0.12
	Regeneration	1	0.532	0.49	0.034	0.86	2.00	0.20
	Age*Regeneration	3	0.569	0.65	0.276	0.84	1.44	0.30
	Error	8						
Slope	Age	3	2.752	0.14	0.637	0.61	1.46	0.30
	Regeneration	1	0.391	0.76	0.027	0.87	0.32	0.59
	Age*Regeneration	3	0.306	0.82	1.081	0.41	1.86	0.22
	Error	8						

Figure 3.2.1 Total number of butterflies caught in the 2003 collection year; patterns associated with forest age and regeneration type.



Significance values: * $p \leq 0.05$, ** $p \leq 0.01$, *** $p \leq 0.005$

Figure 3.2.2 Total number of butterflies caught in the 2004 collection year; patterns associated with forest age and regeneration type.

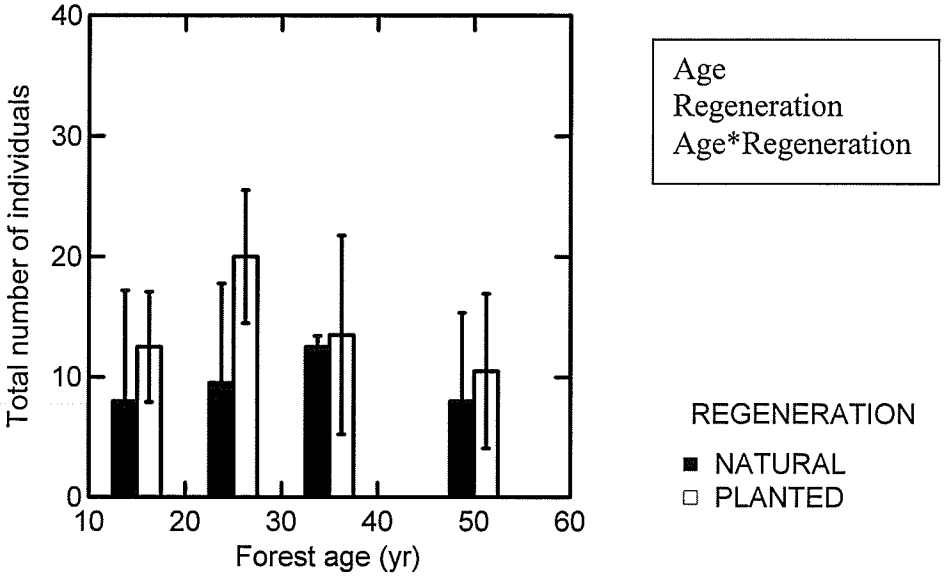


Figure 3.2.3 Total number of butterfly species caught in the 2003 collection year; patterns associated with forest age and regeneration type.

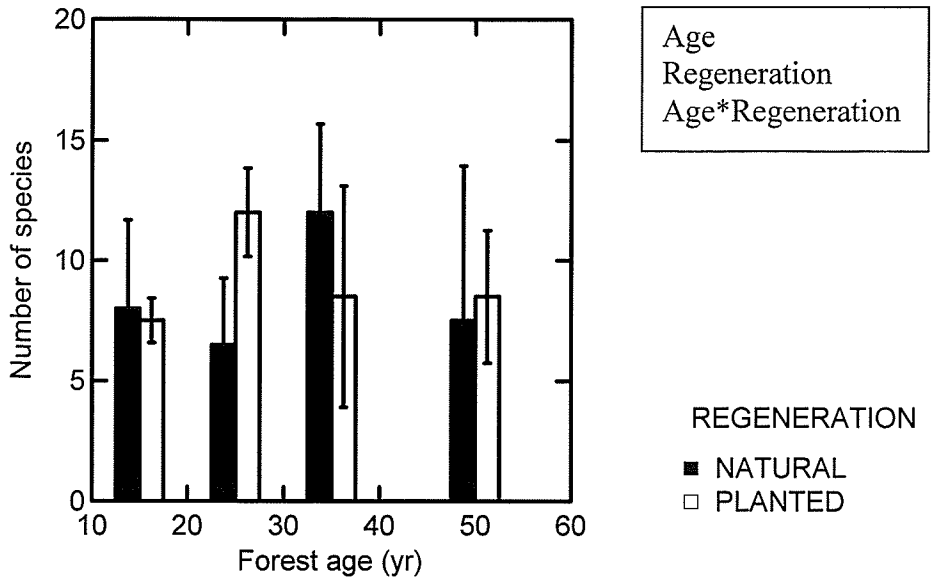


Figure 3.2.4 Total number of butterfly species caught in the 2004 collection year; patterns associated with forest age and regeneration type.

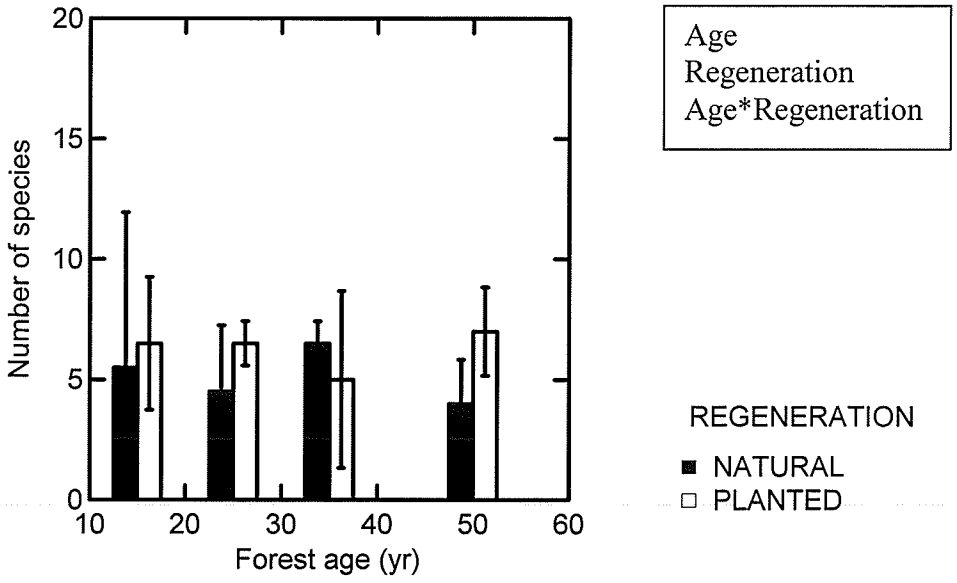


Figure 3.2.5 Total number of host plant specialist species caught in the 2003 collection year; patterns associated with forest age and regeneration type.

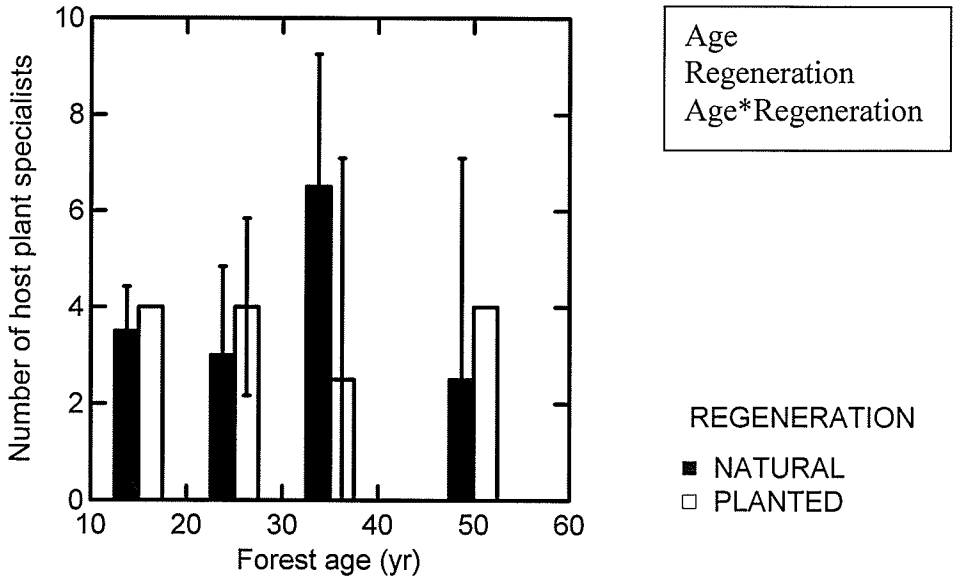


Figure 3.2.6 Total number of host plant specialist species caught in the 2004 collection year; patterns associated with forest age and regeneration type.

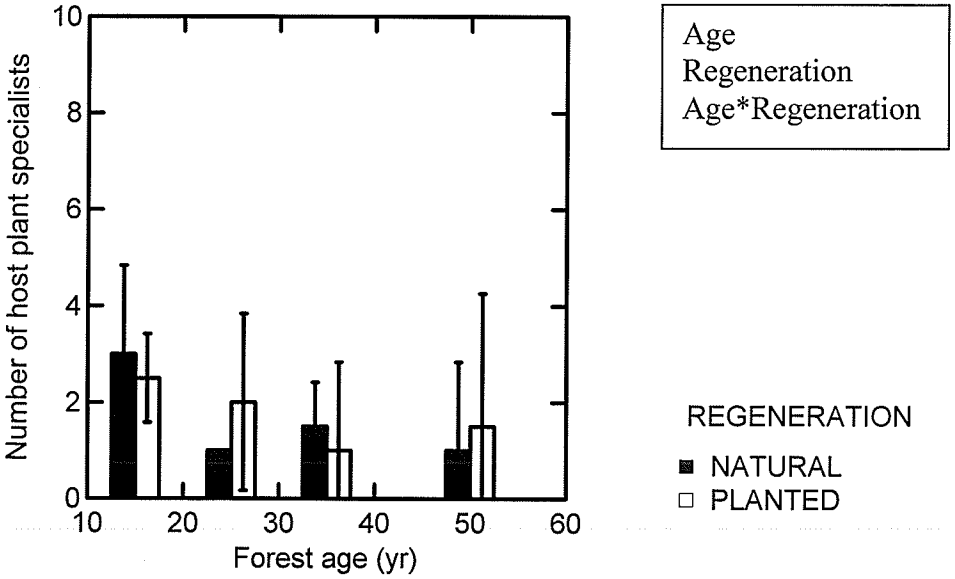


Figure 3.2.7 Alpha diversity of the butterfly assemblage of the 2003 collection year; patterns associated with forest age and regeneration type.

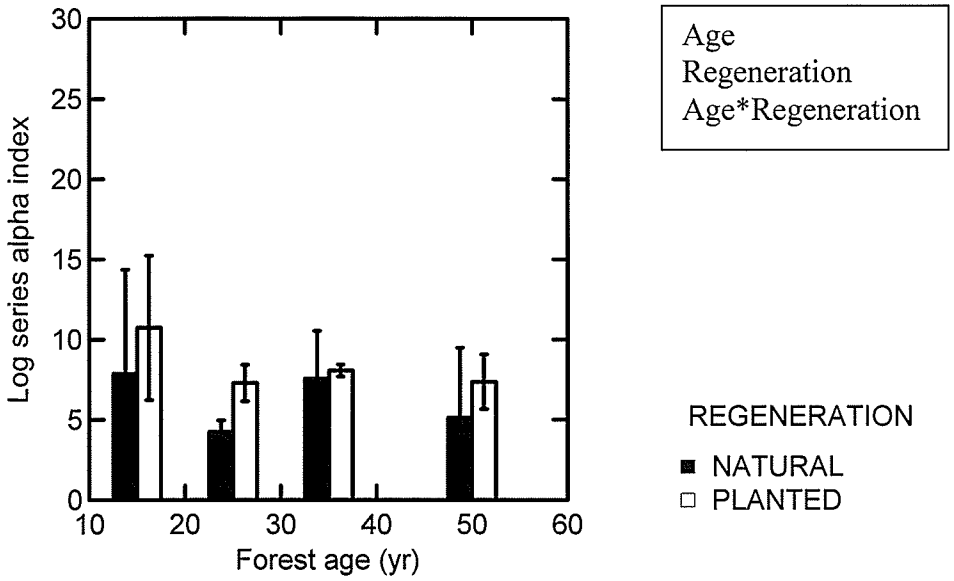


Figure 3.2.8 Alpha diversity of the butterfly assemblage of the 2004 collection year; patterns associated with forest age and regeneration type.

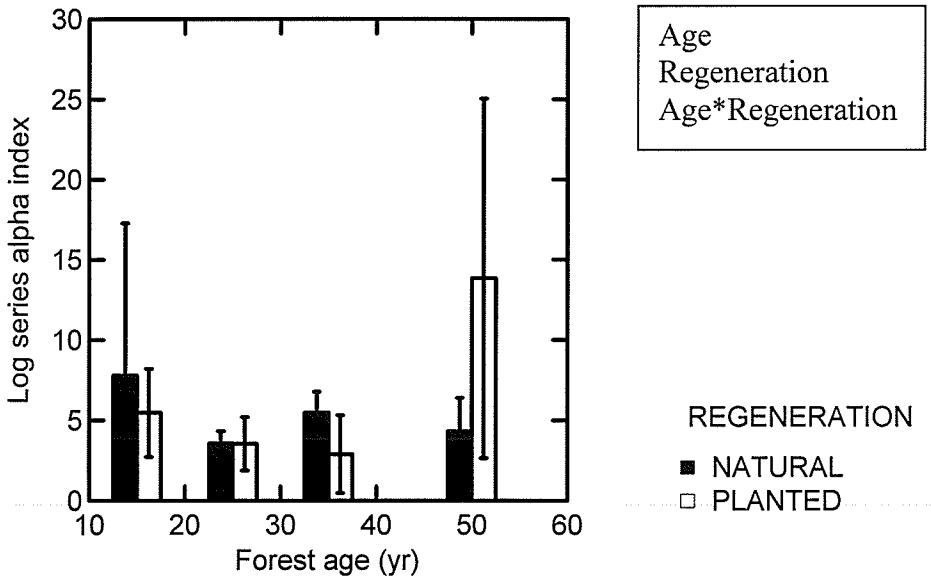


Figure 3.2.9 Species dominance of the butterfly assemblage of 2003 collection year; patterns associated with forest age and regeneration type.

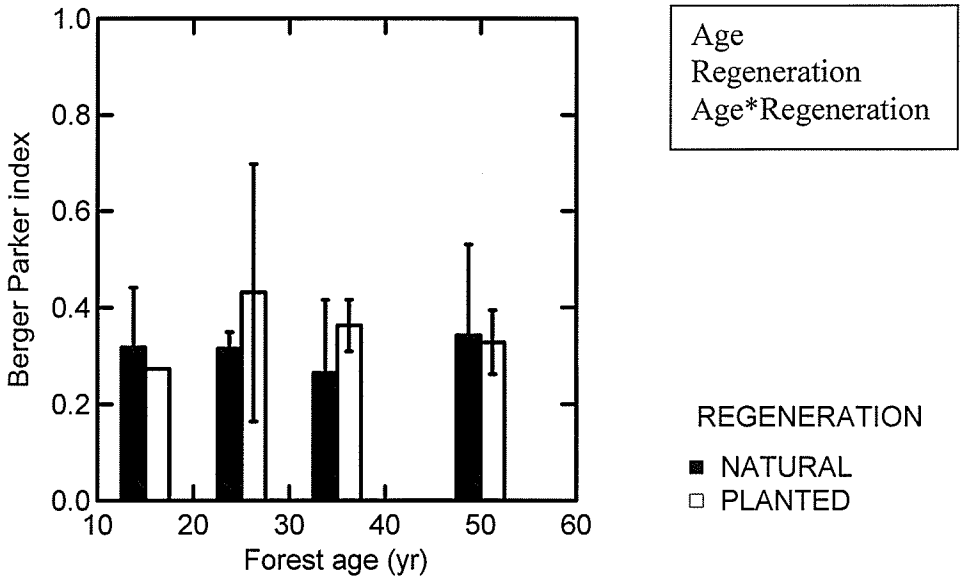


Figure 3.2.10 Species dominance of the butterfly assemblage of the 2004 collection year; patterns associated with forest age and regeneration type.

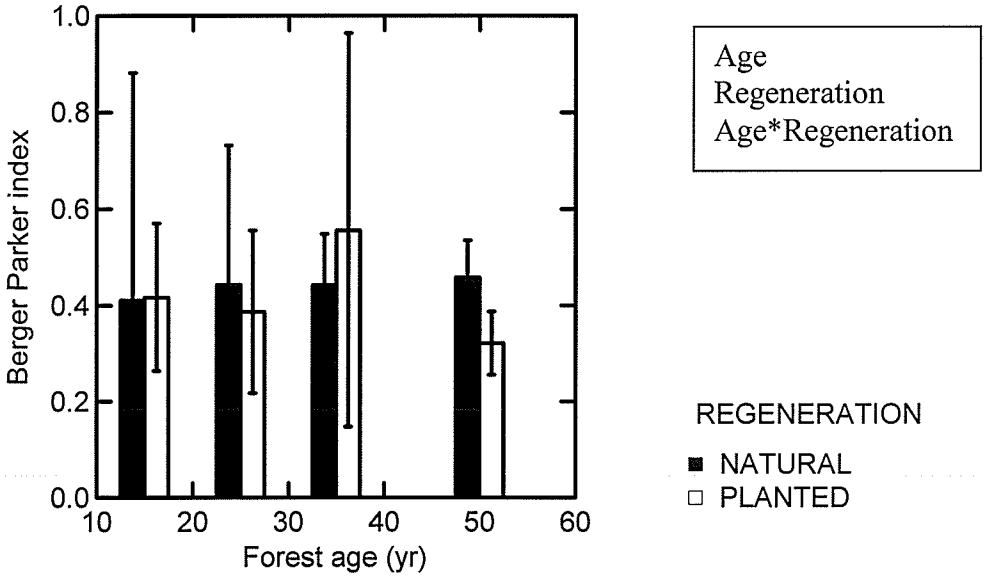


Figure 3.2.11 Species evenness of the butterfly assemblage of 2003 collection year; patterns associated with forest age and regeneration type.

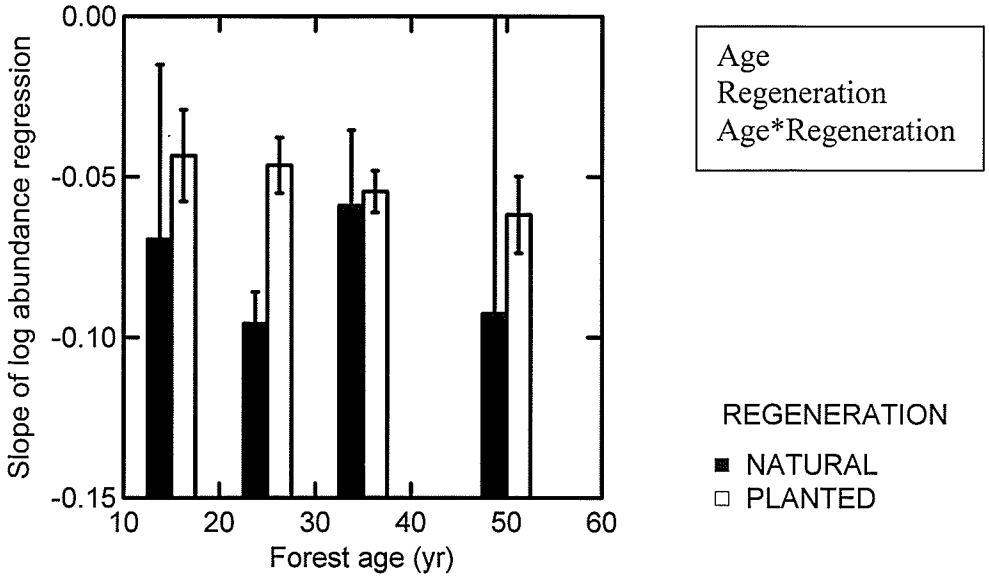


Figure 3.2.12 Species evenness of the butterfly assemblage of the 2004 collection year; patterns associated with forest age and regeneration type.

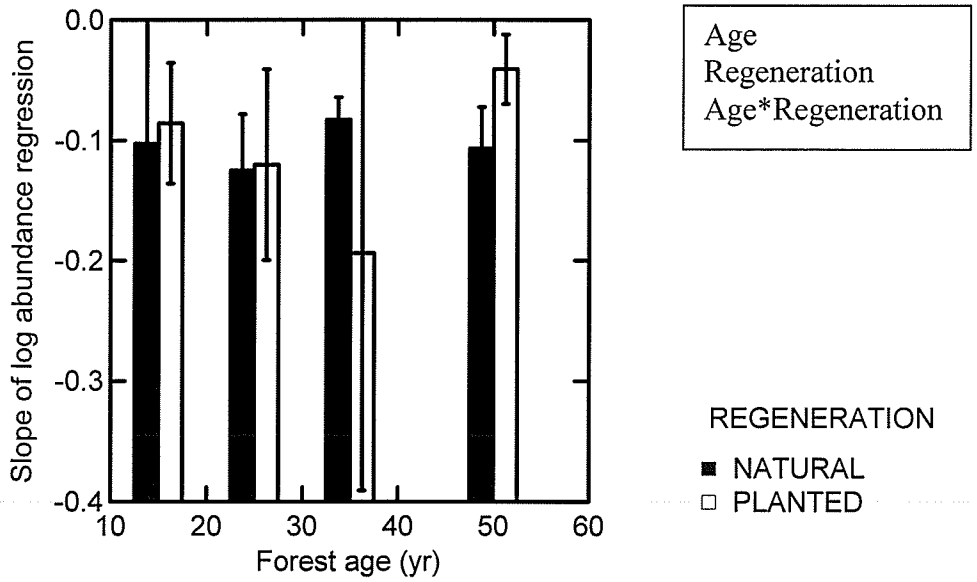


Figure 3.2.13 Kendall's index of beta diversity of the butterfly assemblages of 2003 collection year; patterns associated with forest age and regeneration type.

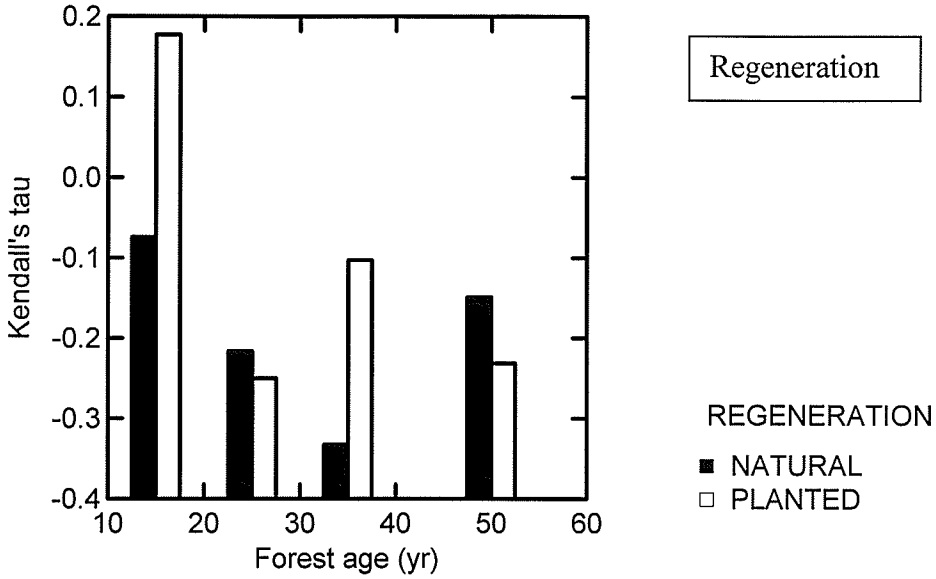


Figure 3.2.14 Kendall's index of beta diversity of the butterfly assemblages of the 2004 collection year; patterns associated with forest age and regeneration type.

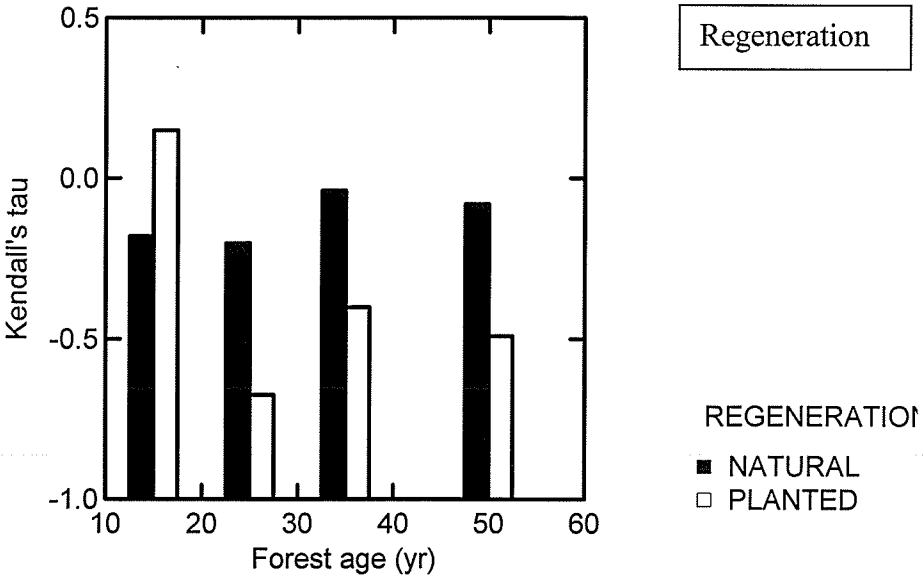


Figure 3.2.15 Jaccard's index of beta diversity of the butterfly assemblages of 2003 collection year; patterns associated with forest age and regeneration type.

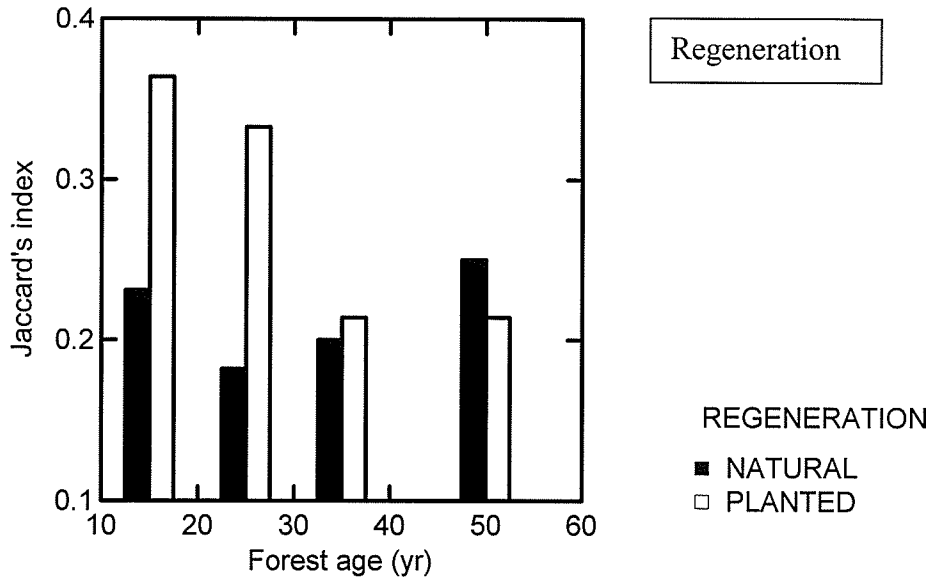
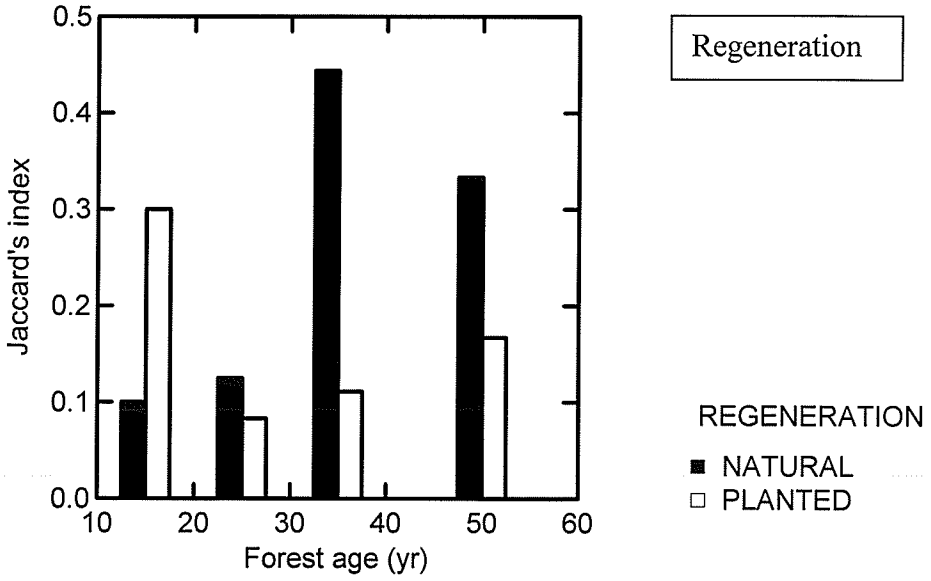


Figure 3.2.16 Jaccard's index of beta diversity of the butterfly assemblages of the 2004 collection year; patterns associated with forest age and regeneration type.



3.3 Effect of forest management on the diversity and composition of carabid beetle (Coleoptera: Carabidae) assemblages in jack pine (*Pinus banksiana*) forests in southeastern Manitoba

Abstract

The health of biological communities may be affected by forest management practices including reforestation strategies. The response of the carabid beetle assemblage to stand level changes associated with regeneration type and with forest age was examined. Carabid beetles were sampled with continuous pitfall trapping in planted and naturally regenerating forests of 15, 25, 35, and 50 years of age. Total catch, species richness, alpha diversity, species evenness and species dominance measures were examined for the influence of forest age and regeneration type and beta diversity between replicates was compared. Assemblage composition was evaluated with ordination analysis. Various habitat characteristics were measured in a parallel study and the relationship between carabid beetle assemblages and environmental characteristics was examined. Results were compared to those of a similar study in the same sites 10 years ago. The main findings were the following:

- The total number of individuals caught tended to increase with forest age; however, this was only significant in 2003. This measure was strongly influenced by the most common species, *Synuchus impunctatus*, and year to year differences in catch of this species contributed to the different trends in beetle catch in each year.
- Alpha diversity decreased with forest age, but only significantly so in 2003. The trend of decreasing alpha diversity with increasing forest age occurred as a result of both decreasing numbers of species and decreasing species evenness in older forests. Trends in alpha diversity in each year were strongly influenced by the

population patterns of the two most common species, *S. impunctatus* and *Pterostichus pensylvanicus*.

- Alpha diversity in planted sites exceeded that of naturally regenerating sites in one of two study years. This result was strongly influenced by 15-year-old plantations; these sites had a number of uncommon species, primarily open habitat and generalist species, in their assemblages.
- Carabid assemblages in 15-year-old sites were the most distinct, containing a number of species characteristic of open areas; these communities were associated lower canopy density. As forests aged and canopy closure increased, the number of open habitat species decreased and the number of forest species increased in the assemblage.
- In sites older than 15 years, understory features influenced the assemblage; sites with high shrub cover had carabid communities distinct from those with lower shrub cover.
- Assemblages of 15-year-old planted and naturally regenerated sites differed. Carabid assemblages in these planted sites contained more carabid beetle species, both open habitat and generalist species. A higher cover of grass litter was associated with the beetle assemblages of planted sites, distinguishing them from those regenerating naturally.
- The original chronosequence study design predicted the current study results, validating the use of chronosequence studies when examining carabid assemblages in forests.

INTRODUCTION

Disturbance is an integral part of healthy boreal forest ecosystem functioning (Barnes et al. 1998). Constituent flora and fauna of these forests are well adapted to regular natural disturbance, particularly by fire (Esseen et al. 1997). The degree to which forest management emulates the key features of natural disturbance and regeneration will potentially determine the long-term health of the biotic community (Haila et al. 1994). The analysis of biological communities, including biodiversity measurement, can serve as a tool to assess the success of forest management strategies; the measurement of the diversity of certain insect taxa to assess ecosystem health is well documented (Niemelä et al. 1993; Niemelä 1997).

Carabid beetles meet many of the selection criteria for an indicator group for assessing ecosystem health. They are widely distributed and ubiquitous; they have a stable taxonomy that is well described; the ecological requirements of many carabid species are known; they are easily and effectively sampled; and in certain circumstances they show a predictable response to changing environmental conditions (Beaudry et al. 1997; Raino and Niemelä 2003).

Carabid beetles are frequently used as ecological indicators in boreal forest studies. In this region, they have been used primarily to study the effects of stand clearing disturbance and subsequent forest succession on carabid assemblages (e.g. Holliday 1992; Niemelä et al. 1993; Niemelä et al. 1994; Koivula et al. 2002). The carabid assemblage has demonstrated a relatively consistent response to these ecosystem changes. Carabids have also been employed, albeit less often, to study the effects of various management strategies on boreal forest health. Management practices evaluated

include the influence of regeneration strategies (Lafrenière 1994), forest thinning (Koivula 2002), competition control (Duchesne et al. 1999), and post-harvest burning (Beaudry et al. 1997). When used to evaluate ecosystem effects of this magnitude, the carabid assemblage often responds to these interventions.

When carabid beetles have been employed to evaluate ecosystem change occurring as a result of forest succession, a chronosequence or age-class-based design has been used. In this method, space is substituted for time, and the influence of successional effects on the carabid community is inferred from these results. This method has proven reliable in floral communities of old fields; when chronosequence sites were revisited, the basic patterns of successional change were generally predicted by the initial results (Debussche et al. 1996; Foster and Tilman 2000). The reliability of chronosequence designs to determine successional change in the carabid beetle assemblage has not been evaluated; therefore it is essential to assess the validity of this strategy.

A chronosequence study of the influence of forest management on the carabid beetle assemblage was conducted in the Sandilands Provincial Forest in southeastern Manitoba from 1991 – 1994. It is now approximately 10 years since this study took place. The current project reassesses the carabid beetle community in the same sites and examines changes in insect diversity over the intervening period. It also assesses how well temporal changes were predicted by the previous age-class-based experimental design.

The specific objectives of this study are as follows:

- To determine whether alpha diversity of the carabid community differs between planted and naturally regenerated jack pine stands of a similar age.

- To determine whether alpha diversity of the carabid community is influenced by forest age.
- To determine whether beta diversity of carabid beetle assemblage differs between planted and naturally regenerated stands.
- To compare the carabid beetle community occurring in planted jack pine stands to those occurring in naturally regenerated stands of a similar age.
- To investigate relationships between carabid assemblages and habitat variables that may explain differences in these assemblages.
- To evaluate how well the original chronosequence study design predicted the current study results.

MATERIALS AND METHODS

This study was conducted in the Sandilands Provincial Forest, situated in southeastern Manitoba. A full description of regional characteristics can be found in Chapter 3.1.

Sixteen sites were established, eight in forests regenerating naturally after fire and eight in planted forests. Two replicates representing each of four different forest ages in each regeneration type were used; the approximate ages of these forests were 15, 25, 35 and 50 years. The sites were originally selected in 1991, and at the time of selection, the forests were approximately 5, 15, 25 and 40 years of age. Full details regarding site history, site selection and site characteristics are provided in Chapter 3.1; specific site locations can be found in Table 3.1.1 and Figure 3.1.1. In 1991 and 1992, Lafrenière

(1994) investigated the influence of regeneration type and forest age on carabid communities in these same sites.

The sites used for the original studies were located and re-established. The study sites were 100 X 100 m, and were located in forest stands that were a minimum of two hectares in size. Sites were located at least 20 m away from any major discontinuity such as a roadway or trail. All sites were dominated by jack pine, with a minimum composition of 75% of the tree stems being jack pine. In addition, they were all located in well-drained upland regions.

Sites were given code names corresponding to regeneration type (B or PL), year of origin, and replicate (A or B). For example, B87A is the first replicate of a site that is regenerating naturally after an ecosystem-altering fire in 1987. Similarly, PL52B is the second replicate of a site that that was planted in 1952. Replicate letters were assigned for convenience only, they do not imply a blocked study design.

Field Methods

Environmental characteristics

Site characteristics including flora were thoroughly investigated and the methods and results of this sampling are presented in Chapter 3.1. Temperature and precipitation data were acquired and are presented in Chapter 3.2.

Carabid beetle sampling

Carabid beetles were sampled continuously at each site using pitfall traps of a similar design to those of Lafrenière (1994). Within each site, 16 traps were arranged in a

square four by four grid centred within the site, as illustrated in Figure 3.1.2. Traps were set approximately 20 m apart to reduce inter-trap interference. Each pitfall trap consisted of two nested 450 ml plastic containers recessed into the ground until the rim of the upper cup was flush with the soil surface. In this nested system the lower cup was not removed from the ground, while the top cup was removed to obtain the carabid samples; this reduced disruption to the ground surface surrounding the trap. Initially, a salt water preservative was used in each pitfall trap. Because of animal disturbance, 1:1 propylene glycol and water preservative was substituted for salt water approximately half way through the first field season. Due to continuing animal disturbance, toward the end of the 2003 season a 4 % formaldehyde solution was substituted as a preservative, and this preservative was also used in the spring of 2004. Further trap disruption by animals necessitated a switch to dry trapping for the second half of the 2004 field season. Changes in preservative regime were instituted in the same week in each site to eliminate bias in carabid catch. When preservatives were used, traps were filled to approximately a 4 cm depth of liquid, and a few drops of detergent were added to reduce surface tension. In 2003, traps were covered with a 30 X 30 cm wooden lid of a three to five millimetre thickness, held off the ground by 7.5 cm steel nails. The lid helped to reduce trap flooding, as well as to prevent excessive debris from collecting in the trap. Small rodents nested in pitfall traps toward the end of the 2003 collection season, so 15 X 15 cm lids were used in 2004. In sites where disturbance by larger animals continued after the switch to dry trapping, wire mesh covers were placed over the traps. These covers were approximately 1.5 X 1.5 m in size, with a mesh grid size of about 8 cm X 8 cm.

Pitfall trap catch was retrieved at weekly intervals. Samples from each trap were removed to separate glass vials, preserved in 70% ethanol, and taken to the laboratory for later sorting and identification of the carabid beetles. The preservative in each trap was changed when it became discoloured or fetid. Any substrate disturbed by animal digging was repaired during the weekly trap servicing. Traps operated from 26 May to 4 October 2003, and from to 30 September 2004.

Carabid beetles were identified to species using keys available in Lindroth (1961-1969) and JB Wallis Museum specimens. Names were standardized to follow the taxonomy of Bousquet and Larochelle (1993). Carabids that could not be conclusively identified by the author were identified by Dr. Yves Bousquet, Agriculture Canada. Voucher specimens are deposited at the JB Wallis Museum, Winnipeg Manitoba and Canadian National Collection, Ottawa Ontario. Species authorities are found in Appendix 8.

To explore changes in the carabid beetle assemblage, the collected species were classified according to their usual habitat: open habitat or field species, those usually collected in open habitats such as meadows or newly disturbed sites; forest species, those most abundant in mature forests; and generalists, those species found in both habitat types. Classification was based upon habitat descriptions compiled by Larochelle and Larivière (2003). A list of species by habitat association is found in Table 3.3.1.

Statistical Analysis

The number of individuals caught was used as a general indicator of carabid beetle activity. The total number of species (species richness), and the log series alpha

index were used to assess alpha diversity of the carabid assemblage. Calculations of log series alpha are described in Chapter 3.2. Species dominance was evaluated with the Berger Parker Index and species evenness was determined by calculating the regression slope of the log abundance of the constituent species. Details of these techniques may be found in Chapter 3.2.

The effect of regeneration type, forest age, and the interaction of the two, on the each of the above site level activity and diversity parameters was conducted using analysis of variance. A repeated measures analysis was used to evaluate the influence of field season bias on each of these measures. In addition, to evaluate the effect of the interaction of regeneration type and regeneration type * age, a repeated measures general linear model hypothesis test was performed.

Data was tested for normality prior to analysis by graphing residuals from a general linear model estimate against the estimated values, and assessing for the appropriate distribution pattern in the scattergram. When a heterogeneous distribution of residuals was noted, data was appropriately transformed and analyzed in that form.

Jaccard's index (C_J) and Kendall's τ correlation coefficient were used to measure beta diversity of the carabid community in each of the replicate pairs. A full description of these methods may be found in Chapter 3.1.

Beta diversity measures were compared using a paired t-test. In order to evaluate the influence of collection year on beta diversity measures, a repeated measures model was used. Because there is no independent variable in this model, this tests functions as a multiple year version of a paired t-test.

All these analyses were performed using SYSTAT 10.2 (SYSTAT 2002). For all analysis, an alpha value of ≤ 0.05 was considered significant.

Multivariate modeling techniques were used to evaluate the carabid beetle assemblages of the test sites and to examine the influence of forest age and regeneration type, and of habitat characteristics on these communities. Principle Components Analysis (PCA) and Redundancy Analysis (RDA) were selected for these evaluations as they best represented the raw data. Unless otherwise specified, for all analyses, all carabid species collected and all study sites were used. In the Redundancy Analyses, the ordination was first constrained by the treatment independent variables forest age (Ages 15, 25, 35 and 50) and regeneration type (Natural and Planted), which were all coded as nominal variables. Second, the same species and site data were analysed by ordination constrained by measured environmental variables. For both constrained analyses, Monte Carlo simulation was used (499 permutations); in the second model only the environmental variables found to be significant ($p \leq 0.05$) were included in the model as they were considered to have the strongest influence on the carabid community. Further details of the use of these techniques are found in Chapter 3.1.

Comparable carabid beetle data for the same study sites was available for the years 1991 –1994. The previously described activity and diversity measures were determined for each of these study years. The results of both studies were compared using repeated measures analysis of variance. For this analysis, site B76B, which was not established until the current study, was removed. For a comparison of community composition between the two studies, each of the two current study years was compared with the previous study year that most resembled it in terms of average collection season

temperature. For these ordinations, the current study sites were used as supplementary variables.

RESULTS

Environment

Full details of the analysis of canopy closure, light attenuation, overstory characteristics, ground cover, coarse woody debris and understory vegetation are found in Chapter 3.1. Acquired temperature and precipitation data are found in Chapter 3.2.

Carabid Beetles

A total of 64 species of carabid beetle were caught over the course of the study. A total of 1816 carabid beetles representing 38 species were caught in 2003, and 3781 beetles of 59 different species were caught in 2004. Mean catch of the most common species for each year is found in Table 3.3.2. A complete list of the carabid beetles collected over the two years can be found in Appendix 8.

Synuchus impunctatus and *Pterostichus pensylvanicus* were the two most commonly collected species in both years. In 2003, these two species made up 53% of the entire catch; *S. impunctatus* accounted for 31% while *P. pensylvanicus* comprised 22% of the catch. In 2004 these two species made up 79% of the entire catch; *S. impunctatus* representing 46% and *P. pensylvanicus* 33%. These two forest generalists generally dominated the sites regardless of forest age.

Aside from *S. impunctatus* and *P. pensylvanicus*, certain species tended to characterize the assemblage of sites of different age groups. The generalist *Carabus*

taedatus, the open habitat species *Harpalus lewisi* and the forest species *Dicaelus sculptilis* were relatively common in the 15-year-old sites, depending on the study year. In addition, a number of uncommon species occurred in these sites, many of them open habitat species including *Harpalus* and *Amara* spp. *Syntomus americanus* occurred most commonly in the 25-year-old sites and this species, in addition to the forest species *Calathus ingratus* (in 2003 only) and *D. sculptilis* were commonly caught in these sites. The species representative of the 35-year-old sites varied from year to year. A high number of *Agonum retractum* were caught in the planted sites, especially in PL64B, in 2003. In this year the catch of *A. retractum* exceeded that of *S. impunctatus* and *P. pensylvanicus* in these sites; however the catch of this species was much lower in 2004. In 2003, *C. ingratus* was relatively common, while in 2004 *D. sculptilis* and *C. taedatus* were. In the 50-year-old sites, *D. sculptilis* was commonly caught in both study years and *C. ingratus* was common in 2003 while *Sphaeroderus stenostomus lecontei* was common in 2004. *Agonum retractum* was commonly caught, but localized to a specific site, B46A.

Carabid catch and site diversity

In 2003, there was a significant effect of forest age on the $\log_e$ total of individuals caught, but not of regeneration type or the interaction of the two (Table 3.3.3). In 2004, none of these factors had a significant influence on the log total of the number of beetles caught. The number of beetles collected in 2003 increased with forest age, with the peak in number of individuals caught occurring in 35-year-old sites in the planted replicates, and in the 50-year-old sites in the naturally regenerating stands (Figure 3.3.1). This trend to increasing numbers of beetles with forest age is not clearly repeated in 2004, although

as with 2003, the greatest number of beetles was caught in 50-year-old naturally regenerating sites (Figure 3.3.2). A significant interaction of collection year and forest age was evident (Table 3.3.4). This occurred as a result of the increased catch of beetles in young forests in the second collection year. There was no significant interaction of regeneration type and age*regeneration type ($F_{8,14} = 0.782$, $p > 0.05$).

Because of the high degree of dominance of the two most commonly collected species, the catch of *S. impunctatus* and *P. pensylvanicus* were analysed separately. In 2003 there was no effect of regeneration type, forest age or the interaction of the two factors on the catch of *S. impunctatus*; however in 2004 there was a significant effect of the interaction of age and regeneration type (Table 3.3.3). In addition, there was a significant interaction of collection year and forest age, primarily due to the influence of increasing catch in younger sites in 2004 (Table 3.3.4). The proportion of *S. impunctatus* increased from 30% to 74% of the catch in 15-year-old sites. In comparison the proportional catch of this species in the 50-year-old sites was similar from year to year. In 2003 a general trend to increasing catch of this species with increasing forest age was evident, although higher numbers of this species in 35- and 50-year-old forests were strongly related to one regeneration type or another (Figure 3.3.3). In 2004, this species became more dominant in the younger sites and was most common in the 15-year-old sites (Figure 3.3.4).

No significant influence of regeneration type, age or the interaction of the two on the catch of *P. pensylvanicus* was found in either of the two study years (Table 3.3.3); however, the interaction of collection year and forest age approached significance (Table 3.3.4). This species tended to increase with forest age in both study years (Figures 3.3.5

and 3.3.6). The proportion of the age-specific catch of *P. pensylvanicus* increased the most in the 50-year-old sites (from 28 to 48%) but decreased in the 15-year-old sites (from 14 to 7%). This species was seldom caught in 15-year-old plantations.

There was no significant effect of regeneration type, forest age or the interaction of the two factors on the number of species collected in either of the two study years, nor was there when the two years were combined (Table 3.3.3). Neither was there a significant interaction of collection year with forest age, regeneration type or age*regeneration type (Table 3.3.4). There was no significant interaction of regeneration type and regeneration type*age ($F_{8,14} = 0.767$, $p > 0.05$). The total number of species collected generally decreased with forest age (Figures 3.3.7 and 3.3.8). The 15-year-old planted and the 25-year-old natural sites had the highest number of species of their respective regeneration type.

There was a significant influence of age, regeneration type and the interaction of the two on the log series alpha index of species diversity in 2003, however, none of these factors were significant in 2004 (Table 3.3.3). There was a significant interaction of collection year and forest age (Table 3.3.4). This occurred because of the high level of alpha diversity in the young planted sites in 2003; diversity in the following year was more similar between forests of differing ages. The interaction of regeneration type and age*regeneration type approached significance ($F_{8,14} = 2.525$, $p =$ approx. 0.06). The 15-year-old planted sites had a strong influence on the results in 2003 (Figure 3.3.9). There was a reduction in species diversity in the young forests in 2004, especially in the young planted sites (Figure 3.3.10). A general trend to decreasing alpha diversity with forest age

is seen in both study years and this trend is generally similar to that seen in species richness.

In 2003, there was no significant influence of regeneration type or the interaction of age and regeneration type on the Berger Parker index of species dominance, however the influence of forest age approached significance (Table 3.3.3). In 2004, there was a significant effect of age but neither regeneration type nor the interaction of age and regeneration type was significant. There was a significant effect of collection year and of the interaction of collection year and forest age on the Berger Parker index (Table 3.3.4). There was no significant interaction of regeneration type and age*regeneration type ($F_{8,14} = 0.460$, $p > 0.05$). In 2003, a high level of species dominance was seen in 35-year old forests, while in 2004 a high degree of species dominance was found in 15-year old forests. In 2003 species dominance increased with forest age until the 35-years, however decreased in the 50-year-old sites (Figure 3.3.11). These sites showed a similar level of evenness to the youngest forests. The pattern differed in 2004, where in the youngest forests a very high level of species dominance was found and there was a general trend to decreasing species dominance with forest age in 25- to 50-year-old forests (Figure 3.3.12).

The evenness measure of the regression slope of the log abundance of the species present in each site was not statistically different from year to year; therefore the two years were combined for this analysis (Table 3.3.4). There was a significant effect of age on this measure but neither regeneration type nor the interaction of regeneration type and forest age were significant (Table 3.3.3). There was no significant interaction of regeneration type and age*regeneration type ($F_{8,14} = 0.540$, $p > 0.05$). Species evenness

decreased with forest age to a low in the 50-year-old sites in both study years (Figures 3.3.13 and 3.3.14).

Beta diversity

The Jaccard's index was not significantly different in the two collection years (Table 3.3.4), therefore the analyses of the two years were combined. There was no significant effect of regeneration type on Jaccard's index over the two years ($F_{1,3} = 2.203$, $p > 0.05$). According to this index, with the exception of the planted sites in 2004, beta diversity tended to be lowest in the 35-year-old stands. The temporal pattern of beta diversity in naturally regenerating sites was similar in both study years; replicate similarity was greater in the 35-year-old sites than in younger or older sites (Figures 3.3.15 and 3.3.16). However, the temporal pattern for the planted replicates differed from year to year; most notably the beta diversity of the 50-year-old planted replicates was lower in 2004. A greater degree of similarity was found in the planted replicates than the naturally regenerating ones at all age groups except the 35-year-old replicates.

Kendall's τ was not significantly influenced by regeneration type in either of the study years (2003: $t = -0.40$, $df = 3$, $p > 0.05$; 2004: $t = -1.44$; $df = 3$, $p > 0.05$) and the two collection years were significantly different from each other (Table 3.3.4). In 2003, the beta diversity in planted and naturally regenerating sites displayed opposite trends (Figure 3.3.17). In the naturally regenerating sites, replicate similarity was greatest in the 15-year-old forests and declined with forest age, while in the planted replicates, the opposite trend occurred. In 2004, 15-year-old replicates of both regeneration types were very similar, decreasing in similarity with forest age in naturally regenerating sites

(Figure 3.3.18). Because 35- and 50-year-old naturally regenerating replicates tended to show a greater degree of beta diversity than either planted or younger sites in both of the collection years, this phenomenon was explored further. Sites were categorized into two age groups, 15- and 25-year-old ("young") sites and 35- and 5-year-old ("old") sites, and a repeated measures analysis was conducted on these groups. Over the two years, there was a significant interaction of regeneration type and age ($F_{1,2} = 59.405$, $p < 0.05$) and a near-significant effect of regeneration type ($F_{1,2} = 15.869$, p = approx. 0.06).

Uncommon species

For the purposes of this analysis, the species making up less than 0.5% of the total catch when the two years were combined were considered rare or uncommon. The number of uncommon species were analysed with analysis of variance. There was no significant influence of regeneration type, forest age or the interaction of the two on the number of uncommon species. The number of uncommon species was greatest in 15-year-old planted sites in both study years (Figures 3.3.19 and 3.3.20).

Habitat specialists

In both years, the number of forest species was significantly affected by forest age, but not by regeneration type or the interaction of the two factors (Table 3.3.3). In 2003, there was a clear trend to increasing numbers of forest specialists with forest age; little difference in the number of forest species was noted between regeneration types (Figure 3.3.21). In 2004, a generally similar pattern was found, however, there were slightly fewer species in 50- than in 35-year-old forests (Figure 3.3.22). Similar numbers

of forest species were found in naturally regenerating sites of 25, 35 and 50 years while slightly fewer were collected in the 15-year-old sites.

The number of field species collected was not significantly influenced by regeneration type, however, was close to being significantly influenced by forest age in 2003 (Table 3.3.3). None of the factors were significant in 2004. There was a decrease in the number of field species associated with forest age although this trend was more evident in 2003 (Figures 3.3.23 and 3.3.24). In 2004, a number of species more typical of open habitats were found in the 50-year-old sites. In both study years the number of field species was greater in 15-year-old planted sites compared to the naturally regenerating replicates of the same age.

The number of habitat generalists was not significantly influenced by any of the experimental design factors. The number of these species tended to be the least in the 50-year-old sites, although this trend was more evident in 2003 (Figures 3.3.25 and 3.3.26).

Community composition

2003

The Principal Components Analysis of the carabid beetle species collected in 2003 produced an ordination where 60.6% of the variation was explained on the first two ordination axes, 40.3% on axis one and 20.3% on axis two. The sites were loosely distributed along an age gradient, with the youngest sites influencing axis one the most (Figure 3.3.27). In this ordination diagram, the youngest sites, with the exception of B87A, tended to form the most distinctive, age-related grouping. These sites were associated with the occurrence of open habitat species such as *Amara* spp. and *H. lewisi*

(Table 3.3.1). Forest species such as *P. pensylvanicus*, *C. ingratus* and *S. lecontei* as well as *Scaphinotus bilobus* and *S. impunctatus* (Table 3.3.1) were found in association with the closed forest sites. Sites with high catches of the locally occurring species *A. retractum* tended to group together, away from the remainder of the sites.

Redundancy Analysis of the 2003 carabid species, constrained by forest age and regeneration type as environmental variables, produced an ordination where the cumulative amount of variation accounted for by the first two axes was 33.5%, however axis one (26.1%) accounted for most of this variation (Figure 3.3.28). Although all of the variables are included in the diagram, the only statistically significant one was Age 15. The sites were generally arranged along axis one according to forest age. As in the Principal Components Analysis, the 15-year-old forests were the most distinct age related group and weighed strongly on axis one. Open habitat carabid species were associated with the youngest sites, while closed forest species generally related to the older sites. The distribution of sites along axis two was most influenced by the mid-aged stands and regeneration type. The location of the Age 25, 35 and planted centroids along the negative end of axis two was influenced by species such as *Badister obtusus* and *Poecilus lucublandus* that only appeared in mid-aged plantations in 2003, *C. taedatus,* a species found more commonly in mid-aged stands and in planted sites, and by *S. americanus* a species more common in mid-aged sites. In addition, *A. retractum*, a species prevalent in 2003 in specific locations, was common in mid-aged plantations.

Redundancy Analysis of 2003 carabid species data with the measured environmental variables produced an ordination where three factors were significant in explaining species and site distribution: light attenuation to 20 centimetres, per cent cover

of shrubs and per cent cover of grass litter (Figure 3.3.29). The total variation accounted for by the environment data in this ordination was 47.7%, 34.4% on axis one and 13.3% on axis two. In this ordination, the youngest sites generally separated from the remaining sites along axis one. The degree of light attenuation was closely associated with this axis. In sites older than 15 years, those with high shrub cover had distinct carabid beetle communities from those with lower shrub cover. Fifteen-year-old planted sites had different assemblages from their naturally regenerating counterparts; this was associated with per cent grass cover.

The presence of *A. retractum*, a commonly caught species in 2003, was strongly related to sites with higher shrub cover such as PL64B and B46A. To illustrate the influence of *A. retractum* on the ordination, this species was removed and Figure 3.3.30 was the result. In this ordination 46.9% of the variation was explained on the first two axes, 28.9% on axis one and 18.1% on axis two. In this ordination, only tree height was a significant environmental variable. Axis one separated the sites along a successional gradient in this case influenced by tree height rather than light admittance. Axis two was unconstrained, contributing to the high variance explained in the ordination. The sites having a large catch of *A. retractum*, B46A and PL64B, became less distinct with the removal of this species from the diagram.

2004

Principal Components Analysis of the 2004 collection data produced an ordination where 48.7% of the species variation was explained on the first two ordination axes; 33.3% on axis one and 15.4% on axis two. The associated ordination diagram

(Figure 3.3.31) for the 2004 carabid community produced a generally similar distribution of sites and species to that for the 2003 data. One notable exception was the shift of S. *impunctatus* to a central location in the 2004 diagram relating to the increasing prevalence of this species in younger sites in the second study year. The decreased influence of *A. retractum* is also evident in the 2004 ordination diagram. For example, PL64B became less distinct in 2004 compared to 2003 as the catch of this species decreased.

Redundancy Analysis of the 2004 carabid beetle collection constrained by forest age and regeneration type produced an ordination where a total of 30.6% of the variation in species data was accounted for on the first two axes, 24% of this on axis one (Figure 3.3.32). As in the 2003 ordination, only Age 15 was significant. Axis one related to a successional gradient and the 15-year-old sites weighed strongly on this axis. In 2004, the two 15-year-old planted sites had an especially strong influence on axis one. This appears to be due to the large number of uncommon species which were collected in these sites in this year. There was a strong influence of Age 25 on axis two. This was due to the influence of B76B, another site where a number of uncommon species were caught in 2004. The 35- and 50-year old sites were more closely oriented in species space in 2004 than in the previous year. This may be a result of the reduction in catch of *A. retractum*, a species tending to influence B46A and PL64B quite strongly in 2003.

Redundancy Analysis of the 2004 carabid catch constrained by the measured environmental variables produced an ordination in which 38.5% of the total variation was explained along the first two ordination axes (Figure 3.3.33). Of this, 28.3% was accounted for by axis one and 10.3% by axis two. The significant environmental

variables were canopy closure, per cent cover of deciduous litter, and per cent cover of grass litter. Both canopy closure and per cent cover of grass litter had a strong influence on axis one and both were associated with forest succession. Younger sites and species characteristic of open habitats were associated with one end of this axis. At the opposite end of axis one, increasing canopy closure was associated with sites and species characteristic of closed canopy forests. Deciduous litter was associated with axis two; the two shrub-rich sites, PL64B and B46A, were associated with this variable. This variable corresponded to shrub cover in the 2003 Redundancy Analysis. As in 2003, 15-year-old planted sites had different assemblages from their naturally regenerating counterparts and this was again associated with per cent grass cover.

Uncommon species

Figure 3.3.34 depicts the ordination of the combined catch of the 2003 and 2004 seasons, log arithmetically transformed and standardized. This had the effect of highlighting the less commonly occurring species, distinguishing sites with more uncommon species in their assemblages over the two collection years. The 15-year-old planted sites were especially distinct in this diagram. The less common species occurring in these sites included open habitat species such as *Cymindis borealis* and several *Amara* and *Harpalus* species (Table 3.3.1), these species tended to occur in the young planted sites in both collection years. In addition, B76B contained a number of less common species, notably those more often associated with more moist areas, such as *Chlaenius niger*, *Blethisa multipunctata aurata* and *Agonum trigeminum* (Table 3.3.1). These hygrophilous species were present in the assemblage in the 2004 collection year only.

Community composition shifts from year to year

Figure 3.3.35 depicts the Principal Components Analysis of the community composition of the sites in 2003 and in 2004. A shift of the sites in species space was evident between the two years of the current study as a result of the influence of *S. impunctatus*, and perhaps *P. pensylvanicus*, on the assemblage. A degree of convergence in the sites is evident, relating to the increasing proportion of the common species in the site assemblages.

A Comparison of the Current Study with 1991 – 1994 Collection Data

Activity and diversity

These repeated measures analyses were influenced by aging of the sites over the 10 years between studies. Five-year-old sites were represented only by the first study, and 50-year-old sites by the second study and this influenced the following results. A summary of the mean of each of the diversity measures over the course of the initial four collection years is presented in Table 3.3.5.

There was no significant influence of collection period (study one vs. two) on the log transformed total individuals caught (Table 3.3.6), however, the interaction of collection period and forest age was significant. This occurred because of the high carabid catch in five-year-old sites of the first study. When all six collection years were combined there was a significant influence of forest age on the number of beetles caught and this trend was also evident in the first study but not in the second. Figure 3.3.36 depicts the standardized number of individuals for each of the study sites, for each study year, plotted against their actual age at the time of collection. A trend to greater numbers

of beetles collected in the very youngest (five year old) and the older (40 to 50 year old) forests was evident.

There was no significant effect of collection period on species richness (Table 3.3.6). There was a significant effect of forest age on species richness when all study years were combined as well as within the initial study years, however not in the current study. A trend to a decreasing number of species between the five-year-old sites and the older sites is evident (Figure 3.3.37). Species richness tended to be higher in the five- and 15-year-old planted sites than the naturally regenerating sites of the same age, however, species richness values tend to converge by 25 years. At each forest stage, with the exception perhaps of the oldest forests and the 15-year-old plantations, values for planted sites tended to cluster as did those for naturally regenerating sites, suggesting a relatively consistent response between the two studies.

There was no significant influence of collection period on the log series alpha index (Table 3.3.6). The interaction of collection period and forest age was significant however; again this occurred as a result of the influence of the five-year-old sites of the first study. When all study years were combined, there was a significant effect of forest age, and the interaction of regeneration type and forest age was close to significant, but regeneration type was not. When each of the two studies was considered separately, the significant effect of forest age was also apparent. A trend to higher diversity in younger (5- – 15-year-old) planted sites than their naturally regenerating counterparts was evident (Figure 3.3.38). Diversity tended to peak later in naturally regenerating forests. At each forest stage, with the exception perhaps of the oldest forests, standardized diversity

values of planted sites tended to cluster as did naturally regenerating sites, suggesting a relatively consistent diversity response between the two studies.

No significant difference between studies was noted for the Berger Parker index of species dominance (Table 3.3.6). Over all of the six study years there was no influence of regeneration type, forest age or the interaction of the two, nor was there when the first four study years were evaluated separately, however an age effect was found in the current study as outlined in a previous section. These findings are illustrated in Figure 3.3.39, where a similar index regardless of forest age is noted. A similar degree of dispersion of site values from the previous and the current study was noted.

A near significant influence of collection period was noted for the log species abundance regression slope. Forest age had a significant influence on this measure when all six collection years were combined and was close to significant when the first four study years were evaluated, however not when the last two years were (previously described). A trend to decreasing evenness was noted with increasing forest age (Figure 3.3.40). A similar dispersion of site values was noted, especially in the 15- and 25- year old sites, illustrating the similarities between study years.

There was no significant influence of collection period on beta diversity, as measured by Jaccard's index (Table 3.3.7). Nor was there a significant influence of regeneration type when all six collection years were combined or when each of the collection periods was examined separately. Overall, younger replicates tended to be the most similar and beta diversity increased with increasing forest age (Figure 3.3.41).

Beta diversity as measure by Kendall's τ was not significantly different from study to study, nor was it significant when all collection years were combined or when

each collection period was evaluated separately (Table 3.3.7). Kendall's τ followed a similar pattern to the Jaccard's Index when all sites were plotted together (Figure 3.3.42).

Community composition

Figure 3.3.43 depicts the 1991 and 2003 carabid communities in each of the sites in 1991 species space. Figure 3.3.44 depicts 1992 and 2004 sites in a similar manner. Five year old sites were characterized by open habitat species such as *Harpalus* and *Amara* spp., while older sites tended to be inhabited by forest species such as *P. pensylvanicus*, *C. ingratus* and *S. impunctatus*, *D. sculptilis* and *S. lecontei* (not illustrated). A successional gradient related to forest age at the time of sampling was evident in both year pairs. The greatest amount of carabid community turnover was seen between five- and 15-year-old forests, while progressively less turnover was evident as the forests aged. A greater degree of turnover in the oldest sites was found in 1992-2004 than 1991-2003. However, this trend appeared to occur as a result of the two common species *P. pensylvanicus* and *S. impunctatus*; large catches of these species in 2004 influenced the trajectory of some sites more than others e.g. PL52A. A convergence of the carabid community with forest age was particularly evident in these diagrams. Sites of particular ages, especially in older age groups, were relatively similar in composition regardless of study period. To further clarify this, for the above year combinations, sites that were 15 or 25 years old at the time of their respective study were examined and Figures 3.3.45 and 3.3.46 show the results. Although there is some scattering and overlap of sites, 15- and 25-year-old sites tended to be distinct in the 1991 and 2003 year pairing (Figure 3.3.45). Moreover, 25-year-old sites from the current study clustered within the

range of 25-year-old sites from the previous study. These trends were less apparent in the 1992 and 2004 pairing (Figure 3.3.46).

DISCUSSION

There are a number of limitations to pitfall trapping for carabid beetles. However, alternative methods, such as hand collection, heat extraction and litter-washing, demand greater resources and would limit the breadth of carabid beetle sampling in this study. Although pitfall trapping provides a measure of carabid activity rather than carabid abundance in a habitat, continuous pitfall trapping over the entire activity period of the beetles has been found to be a relatively reliable method of sampling (Baars 1979). A comparison of carabid species between habitats would be reasonable in that trapping efficiency is expected to be similar from site to site for a particular species and therefore would provide a measure of the relative abundance of that species in a site (Richardson and Holliday 1982).

Although changing trap components such as roof size and the type of preservative was not ideal, it was deemed preferable to the loss of traps or the reduction in trap catch occurring as a result of animal disturbance. As the trapping technique was identical in all sites, changes in trap design would not affect the comparison of the carabid community between sites. Changes in trap design are of greater concern when comparing results between studies. Although formalin has been found to attract carabid beetles, so has ethylene glycol, the preservative used extensively in the initial investigation (Adis 1976 in Adis 1979). Regardless, Lafrenière (1994) found no significant difference in trap catch between those filled with ethylene glycol and those without preservative. In addition, roof

size has been found not to affect pitfall trap catch (Work et al. 2002). Therefore, it is reasonable to compare carabid catch between the two studies using the same sites.

Components of the Carabid Beetle Community and their Response to Environment Change (forest succession and weather)

The weather in the two study years was quite different (Table 3.2.2). The collection season of 2003 was generally hot and dry while 2004 tended to be cool and wet. These differences would be expected to influence the carabid beetle community as reduced catch of some carabid species is found in dry conditions (Epstein and Kulman 1990), and indeed the carabid beetle assemblage differed between collection years. Commonly collected species in 2003 were *S. impunctatus*, *P. pensylvanicus*, *A. retractum* and *C. ingratus*. Twenty six species of carabid beetle occurred rarely in that year. Over double the number of beetles were caught in the 2004 collection year and the catch of the most commonly collected species in 2004, *S. impunctatus* and *P. pensylvanicus* and *D. sculptilis*, was two to three times that of the previous year. In contrast, catch of *A. retractum* and *C. ingratus* was a third or less than the previous year. In addition, double the number of uncommon species was caught in 2004 compared to the previous year.

Common species

Synuchus impunctatus

Catch of *S. impunctatus* not only increased overall in 2004, but the distribution of this species changed as well. *S. impunctatus* was described by Lindroth (1966) as a species of open areas and light forests, being found under leaves or shrubs. Since that

description, *S. impunctatus* has been associated with both newly disturbed and mature forest (Epstein and Kulman 1990; Niemelä et al. 1993; Duchesne et al. 1999; Pearce et al. 2003), although in Manitoba it is often found in mature stands (Holliday 1991; Lafrenière 1994; Wytrykush 2001). The recorded diet of this species includes Lepidoptera larvae and seeds (Larochelle and Larivière 2003) which may explain its ability to inhabit different forest stages in different locations or situations. Granivorous species are often more prevalent in newly disturbed forests where they have an abundant food source (Šustek 1981; Spence et al. 1997). Lepidopteran larvae would be expected to be plentiful in older boreal forests as the abundance of moths tends to increase with forest age (Elliott 1997), providing a food source for this species in older forests. Assuming that *S. impunctatus* is preferentially a forest species in Manitoba, the year to year variation of the patterns of catch may be explained by the weather patterns. Carabid species that typically dwell in forests are often eurythermic (Thiele 1977). In forests, they would generally encounter moister conditions than those usual in open areas, and temperature fluctuations would be buffered. In 2004 conditions were cool and damp throughout the Sandilands region; therefore it is possible that open sites became more favourable habitat for this species. It is conceivable that *S. impunctatus* could disperse into these young sites, as there was mature forest near these stands. This species is wing dimorphic (Lindroth 1966), and they have been recorded to re-colonize an area in one year or less (Niemelä et al. 1993).

In addition to an altered distribution pattern, the catch of *S. impunctatus* increased in all forest age classes. Dry conditions are known to reduce the catch of at least some carabid species (Epstein and Kulman 1990), therefore the relatively hot and dry

conditions in 2003 may have influenced the relative abundance of this and other species. It is also possible that this species undergoes some sort of cyclical population pattern and is more prevalent in some years as other authors have found year to year differences in relative abundance as well, with or without overt weather changes (Lafrenière 1994; Beaudry et al. 1997; Wytrykush 2001). Lafrenière (1994) found a similar pattern between warm and cool summers, albeit not as substantial as that found in the current study.

Pterostichus pensylvanicus

Pterostichus pensylvanicus is typically described as a forest species (Lindroth 1966; Goulet 1974; Niemelä et al. 1992a). Females of *P. pensylvanicus* oviposit under litter, preferring wetter substrates; both desiccation and high temperatures increase egg mortality (Goulet 1974). Therefore they would be expected to thrive more effectively in older forests where these conditions are more likely to be met. This is especially likely in the upland forests of the Sandilands area, as soils in this region are very well drained and tend to be dry. Year to year difference in *P. pensylvanicus* catch could be expected to have occurred as a result of weather related differences. Snow fall accumulations over the winter of 2003/2004 greatly exceeded that of the previous winter (Table 3.2.1) and this may have enhanced overwinter survival of this species. In addition, the hot, dry condition of the 2003 collection season may have led to higher mortality or reduced activity and this may have influenced the catch of this species. Opposite conditions in 2004 may have facilitated greater survival or activity levels. Similarly, in the initial study period, there was also increase in the relative abundance of this species in a cold, wet summer (1992) following a hot dry one (1991) (Lafrenière 1994). Differences in predator activity from

year to year may have influenced the catch of this and other species in addition to year to year changes.

Calathus ingratus

Calathus ingratus is a forest species, commonly caught in mature conifer forests in Manitoba (Holliday 1991; Lafrenière 1994). It has been associated with moist ground and with deciduous litter, a ground cover which retains moisture better than conifer litter (Uetz 1979; Niemelä and Spence 1994). This species was rarely caught in 15-year-old forests, and was most commonly collected in 35- and 50-year-old forests. Catch of *C. ingratus* decreased from 2003 to 2004. This species reproduces in the summer, and overwinters either in the larval or adult stage (Bousquet and Pilon 1977). As the summer of 2003 was hot and dry, perhaps egg or larval stages of this species were adversely affected leading to a reduction of catch in the following year. Regardless of mechanism, this pattern is likely weather related as this was the same pattern found in 1991 and 1992 (Lafrenière 1994), two years of generally similar overall weather to 2003 and 2004.

Agonum retractum

Agonum retractum is a species commonly associated with deciduous forest and broad-leaf litter (Lindroth 1966; Spence and Niemelä 1994; Pearce et al. 2003; Larochelle and Larivière 2003). This species was collected relatively commonly in this study; it was the third most commonly caught species in 2003 and the fifth most commonly caught in 2004. However, catch of this species was highly localized. It was prevalent in sites, such as B46A and PL64B, with a well developed layer of broad-leaf

shrubs, a representation of deciduous trees within the overstory and an abundance of deciduous litter. Catch of this species decreased from 2003 when there were 340 individuals caught, to 2004 when 81 were, perhaps in response to weather related differences. Individuals of this species overwinter as adults (Larochelle and Larivière 2003) so they would be exposed to the same climate related pressures as *C. ingratus*.

Dicaelus sculptilis

Dicaelus sculptilis is a forest species, known primarily from deciduous forests (Richardson and Holliday 1982; Epstein and Kulman 1990; Holliday 1991) although some authors report it from conifer stands as well (Larochelle and Larivière 2003). Lafrenière (1994) did collect this species, albeit in relatively low numbers, in both of his collection years therefore this finding is not unprecedented. Catch of this species was generally higher in older forests. This species was more commonly caught in 2004 than 2003, although sites where it was more commonly collected in 2003 were also those in which it was more commonly collected in 2004, suggesting that this species increased in activity or relative abundance in situ. The greater number of this species collected in 2004 may be a result of the weather related influences previously described for other species, however, there was no similar pattern in 1991 and 1992 (Lafrenière 1994). An increase in catch in the 1993 and 1994 collection season suggests that this variation may be driven by factors other than weather.

Uncommon species

The number of uncommon species in 2004 was double that of 2003. Three distinct categories of uncommon species were identified: those that are normally found in open habitats, such as most of the *Amara* and *Harpalus* spp.; species preferring moister sites such as many of the *Bembidion* and *Chlaenius* spp.; and those which are actually rare, either in general or in this region specifically, such as *S. bilobus*, *Amara schwarzi*, *Chlaenius platyderus* and *Bembidion* new sp. (Lindroth 1961-1969; Larochelle and Larivière 2003; Y. Bousquet, personal communication). Of the uncommon species caught, 12 were species that are primarily associated with moister conditions and these species were only caught in 2004. This accounted for much of the difference in the number of uncommon species present between collection years.

Habitat specialists

The age and regeneration trends in the habitat specialist groups were generally similar from year to year, however differences related to forest age were less pronounced in 2004. In 2004, more forest species were found in the youngest sites, especially those regenerating after fire. In these sites, there was also an increase in generalists as compared to 2003. These differences may be due in part to an overall increase in carabid catch, however considering the increases were evident in the forest species and generalist groups and not the open habitat specialists, it may suggest that conditions were substantially different in these sites in 2004. As the 15-year-old naturally regenerating sites had the most open area, the microclimatic conditions within these sites would be

most influenced by climatic differences, perhaps making conditions within these sites more suitable for a number of species, especially those more typically inhabiting forests.

Community Composition

The carabid assemblage as a whole

Carabid beetle assemblages in the 15-year-old sites were the most distinct in all ordinations. A number of species requiring open conditions were found in these sites. A strong reduction in the number of these field species was noted in older sites, in conjunction with increasing canopy density. Concomitantly, an increase in the number of forest species occurred with increasing forest age. These changes were more gradual than those of open habitat species, suggesting a steady re-establishment of forest specialists. These findings indicate that the degree of canopy closure was a primary influence driving changes in the carabid assemblage. A shift in the carabid beetle community, including the recovery of forest specialists and a loss of open habitat species, has been associated with canopy closure by a number of other authors (e.g. Niemelä et al. 1993; Koivula et al. 2002).

Less expected was the influence of understory components on the carabid beetle assemblage. Certain carabid species were characteristic of sites with high shrub or deciduous litter cover. However, this distribution was strongly affected by the presence of *A. retractum*, a species restricted to closed canopy sites with high shrub cover. In comparison, many mature forest species such as *P. pensylvanicus*, *S. bilobus*, *S. lecontei*, *Harpalus fulvilabris* and *C. ingratus* were strongly associated with sites with lower shrub or deciduous litter and grass litter cover. This distribution however, was strongly

influenced by the forest species *P. pensylvanicus*. Many carabid beetle species have very specific thermal and moisture requirements (Thiele 1977) and others respond to the abundance of broadleaf litter (Koivula et al. 1999). Thus the influence of understory characteristics on the carabid beetle assemblage would be expected to occur as a result of the influence of these structural components on microclimate and on litter structure (Niemelä et al. 1996). It appears that structural complexity in the understory exerts a greater influence on the carabid community than forest age does, once canopy closure occurs. Per cent cover of grass litter, was significant in the Redundancy Analyses but rather than being a significant driving variable, may represent a successional gradient, as grass litter tended to decrease sequentially with forest age.

There were more open habitat and generalist species in 15-year-old planted sites than in their naturally regenerating counterparts. As the Redundancy Analyses suggest (Figures 3.3.29 and 3.3.33), this may have occurred because of differences in grass litter, or its antecedent, grass. Many open habitat carabid species are granivores and grass seed is a common food source for them (Niemelä 1993). Therefore, food availability may play a role in the higher number of these species in the young planted sites. It is also conceivable that the structural complexity provided by the grass litter influences the high number of field and generalist species in these sites. Structurally complex litter may influence ground biota by buffering temperature and moisture fluctuations, as well as offering protection from predation (Uetz 1979), thereby enhancing survival in these sites. Alternatively, it is possible that the carabid assemblage was responding to environmental differences not directly measured by the sampling techniques, and that grass litter cover is serving as a proxy measure.

Sites that had especially distinct carabid assemblages overall were B46A and PL64B, while that of B87A differed substantially from the rest of the 15-year-old sites (e.g. Figures 3.3.27 and 3.3.30). Notably, these sites were also distinctive in terms of their understory vegetation. Thus both the understory plant community and the carabid community may indicate sites that are especially unusual structurally

Uncommon species

Uncommon species were not equally distributed. The number of uncommon species was highest in 15-year-old plantations and in the site B76B (Figure 3.3.34). Uncommon species of the 15-year-old planted sites were primarily those associated with open habitat conditions and the reasons for high number of open habitat species in these sites has previously been discussed.

In addition to a number of open habitat species collected, there were several species preferring moist conditions and some rare species caught in B76B over the two study years. This site did not appear particularly unusual in terms of relief, soil development or soil moisture, nor in terms of understory development so the presence of a greater number of these species is difficult to explain in terms of site characteristics. It is evident that the presence of uncommon or unique species can be site specific.

Carabid Activity and Diversity

The total number of individuals caught in each study year was strongly influenced by the two most common species, *S. impunctatus* and *P. pensylvanicus* and this caused the difference in trends between the 2003 and 2004 collection seasons in addition to the

trends associated with forest age. Similarly this phenomenon influenced the site level diversity findings from year to year, as the increased dominance of *S. impunctatus* in the young sites decreased alpha diversity. This can be seen in both the log series alpha and Berger Parker indices and accounts for the significant interaction between collection year and forest age for both of these measures. Because of these strong effects of climate variation on the composition and diversity of the carabid assemblage, drawing conclusions about the state of the forest ecosystem from one year of carabid beetle collection could be risky.

Regardless of the year to year variation, however, there was an identifiable trend of decreasing alpha diversity with increasing forest age. This occurred as a result of both decreasing numbers of species (species richness) and decreasing species evenness in older forests. In younger forests the carabid beetle assemblage tends to be composed of both open habitat and forest generalist species (Niemelä et al. 1993; Niemelä et al. 1994; Koivula et al. 2002). Canopy closure is typically the critical feature driving species diversity in forest environments (Haila et al. 1994; Haila 1994). With increasing canopy closure there is a reduction of open habitat species and a recovery of forest specialists within the assemblage (Niemelä et al. 1993; Koivula and Niemelä 2002; Koivula et al. 2002). An assemblage comprised of a small number of dominant species and a large number of uncommon ones is commonly found in habitats, such as forests, where few factors influence the ecology (Thiele 1977; Magurran 1988). The boreal forest is a relatively harsh environment and only a few carabid species may be well adapted to thrive in these conditions (Niemelä 1993). Increasing dominance of a few species with

canopy closure has been found in other conifer forests (Day and Carthy 1988; Niemelä 1993).

Habitat heterogeneity would be expected to influence the number of species present in a site so it is surprising that alpha diversity is greater in the 15-year-old planted sites than in naturally regenerating forests of the same age. The naturally regenerating sites had a greater degree of canopy variability therefore should offer a greater variety in habitat and microclimate conditions, including a greater abundance of open areas than the planted sites. Although overall stand morphology may be more heterogeneous in the naturally regenerating forests than in the planted ones, at a finer scale the reverse may be true. In young planted sites a greater variety of conditions may be available within a few metres than in naturally regenerating sites. Residual micro-topography created by disc trenching in these sites would be expected to have created a variety of soil moisture conditions, while a variety of light conditions would be available within a few metres as a result of the tree spacing dictated by planting. Therefore, heterogeneity at the micro-site level may influence the beetle community by providing access to required conditions or resources (Niemelä et al. 1992b; Niemelä et al. 1996). In addition, the understory has a strong influence on microclimate and litter structure and thus may be an important factor in determining local diversity (Niemelä et al. 1996). Although not significantly different, species richness of summer ground vegetation, shrubs and moss were greater in the 15-year-old planted sites than in the naturally regenerating ones, therefore, differences in the understory composition may have influenced species diversity in these sites as well.

Kendall's τ was strongly influenced by collection year and this was as a result of the high catch of *S. impunctatus* as well as the altered distribution pattern of this species

in 2004. Because this measure considers the relative abundance of species in an assemblage it was highly sensitive to these year to year changes. In comparison, Jaccard's index was statistically comparable and showed some of the same general trends from year to year. In both study years beta diversity in older naturally regenerating sites exceeded that of planted sites, this was especially apparent from the Kendall's diversity index. This was due to differences in catch of a number of the more common species between replicates. This was especially well illustrated by differences between the two 50-year-old natural replicates. In B46A, the catch of *A. retractum* was high in both collection years, and catch of this species was essentially restricted to this replicate. The catch of *P. pensylvanicus* and *C. ingratus* in B46A was three or more times that of B52B in both years. In contrast, individuals of *D. sculptilis* and *H. fulvilabris* were rare or absent in B46A, but relatively common in B52B over the two years. In comparison species distribution was more similar between the 50-year-old planted replicates. Because this measure considers relative abundance it was more sensitive to the distribution differences of carabid species between replicates than the Jaccard's index.

Predicting Carabid Community Succession with Chronosequence Studies

The summary measures from the initial four study year generally predicted the overall trends evident in the current study. The degree to which they did so varied from measure to measure and tended to vary with forest age. The total number of individuals was well predicted, especially in the 15- and 25-year old sites which were directly predictable from the chronosequence. Species richness and alpha diversity trends associated with forest age were generally well predicted, although results for 25- and 35-

year-old sites were better predicted. In addition, the higher species diversity in planted 15-year-old forests was generally well predicted. Species evenness results showed more variability overall than the previous results, although the trend to decreasing species evenness with forest age was evident. This measure may be more influenced by year to year variability in the carabid community than the other measures.

Changes in the carabid assemblage occurring with forest succession were generally well predicted by the original study. This is not surprising as there are few carabid beetle species thriving in jack pine forests and those that do so form a large part of the ground beetle assemblage. Therefore despite initial differences between carabid communities in different sites, there is a great degree of convergence in the carabid community as the forest ages.

CONCLUSIONS

Canopy density is the main variable influencing the carabid assemblage; however, understory characteristics are also important in determining the assemblage composition. Regeneration type does influence the carabid assemblage, however, this was only clearly evident in 15-year-old forests. Diversity measures show trends in the carabid community associated with forest age, however influences of regeneration type on the carabid assemblage are best illustrated with multivariate modeling techniques. The original chronosequence study design predicted the current study results, validating the use of chronosequence studies when examining carabid assemblages in forests.

SUMMARY

For each of the main community components analysed, a summary of the main findings follows.

- The log total number of beetles caught increased with forest age in 2003; there was no significant effect of regeneration type or the interaction of age and regeneration type. In 2004 neither age, regeneration type nor their interaction significantly influenced the number of carabid beetles caught.
- Species richness was not significantly affected by forest age, regeneration type or the interaction of the two in either study year. It tended to decrease with forest age.
- In 2003, alpha diversity was influenced by forest age, regeneration type and the interaction of the two. Species diversity tended to decrease with forest age and tend to be highest in 15-year-old planted sites. There were no significant effects in 2004.
- Species dominance was not significantly affected by forest age, regeneration type or the interaction of the two in 2003. In 2004 species dominance decreased with forest age; this was as a result of a high catch of *Synuchus impunctatus* in the 15-year-old sites. Neither regeneration type nor the interaction of age and regeneration type significantly influenced species dominance in 2004.
- There was a near-significant affect of forest age on species evenness; species evenness tended to decrease with age in both years. There was no significant affect of regeneration type or the interaction of age and regeneration type.

- Beta diversity was not significantly influenced by regeneration type over the two years when the original experimental design was used in the analysis. However, there was a significant interaction between age and regeneration type, and a near-significant effect of regeneration type when the measures were re-classified; beta diversity in older naturally regenerating forests exceeded that of planted and younger forests with the Kendall's tau measure of beta diversity.
- Carabid assemblages in 15-year-old sites were the most distinct, containing a number of species characteristic of open areas; these communities were associated with lower canopy density. As forests aged, the number of open habitat species decreased and the number of forest species increased in the assemblage.
- In sites older than 15 years, understory features influenced the assemblage; sites with high shrub cover had distinct carabid communities from those with lower shrub cover.
- Planted and naturally regenerated sites differed in the 15-year-old age class. Carabid assemblages in these planted sites contained more beetle species, both field species and habitat generalists. A higher cover of grass litter distinguished the young planted sites from those regenerating naturally.
- When results of diversity measures were compared with the original study, similar patterns were found;
    - There was a significant influence of forest age, but not of regeneration type or the interaction of age and regeneration type on the number of beetles caught. This result was influenced by the 5-year-old sites of the

original study, however, beetle catch generally increased with forest age from 15 years on.

- There was a significant effect of forest age, but not regeneration type or the interaction of the two on species richness. Species richness tended to decrease with forest age.
- There was a significant influence of forest age, but not of regeneration type or the interaction of age and regeneration type on alpha diversity. This result was influenced by the 5-year-old sites of the original study, however. Alpha diversity decreased with forest age; it tended to be higher in 5- and 15-year-old planted stands.
- Over the two study periods, species dominance was not influenced by forest age or regeneration type or the interaction of the two.
- Species evenness was not significantly influence by regeneration type or the interaction of age and regeneration type. Species evenness tended to decrease with forest age over the two studies.
- There was no significant influence of regeneration type on beta diversity when both studies were combined. Overall, younger replicates tended to be the most similar, and beta diversity increased with forest age.
- When the carabid assemblages between studies were compared, a similar successional gradient related to forest age at the time of sampling was evident.

- Therefore, the original chronosequence study design generally predicted the current study results.

Table 3.3.1 Habitat associations of carabid species collected

Field species	Forest species	Generalists
Agonum cupreum	*Agonum retractum*	*Agonum thoreyi* (H)
Agonum gratiosum	*Calathus ingratus*	*Agonum trigeminum* (H)
Agonum placidum	*Calosoma frigidum*	*Anisodactylus sanctaecrucis*
Amara cupreolata	*Dicaelus sculptilis upiodes*	*Badister obtusus*
Amara farcta	*Dromius piceus*	*Blethsia multipunctata aurata* (H)
Amara impuncticollis	*Harpalus fulvilabris*	*Bradycellus lugubris*
Amara laevipennis	*Platynus decentis*	*Carabus serratus*
Amara latior	*Pterostichus novus*	*Carabus taedatus*
Amara obesa	*Pterostichus pensylvanicus*	*Cymindis neglectus*
Amara schwarzi	*Scaphinotus bilobus*	*Harpalus opacipennis*
Amara sinuosa	*Scaphinotus elevatus*	*Harpalus pensylvanicus*
Anisodactylus harrisii (H)	*Sphaeroderus stenostomus lecontei*	*Harpalus solitaris*
Anisodactylus merula		*Notiophilus semistriatus*
Bembidion mimus (H)		*Pterostichus adstrictus*
Bembidion quadramaculatum (H)		*Pterostichus femoralis*
Bembidion versicolor (H)		*Pterostichus melanarius*
Calosoma calidum		*Pterostichus mutus*
Chlaenius niger (H)		*Synuchus impunctatus*
Chlaenius pensylvanicus (H)		
Chlaenius platyderus		
Chlaenius sericeus sericeus (H)		
Chlaenius tomentosus tomentosus		
Cymindis borealis		
Cymindis cribicollis		
Harpalus herbivagus		
Harpalus laticeps		
Harpalus lewisii		
Harpalus nigritarsus		
Harpalus plenalis		
Harpalus somnulentus		
Pasimachus elongatus		
Poecilus lucublandus lucublandus		
Pterostichus commutabilis		
Syntomus americanus		

H = Hygrophilic

Species habitat associations derived from Larochelle and Larivière (2003)

Table 3.3.2 Commonly collected carabid beetle species

	Species	Regeneration type	Mean catch ± SE 15 years	25 years	35 years	50 years
2003	*Synuchus impunctatus*	Natural	13 ± 9.5	28 ± 15.5	21 ± 1.5	70 ± 46.5
		Planted	9 ± 6.5	33 ± 2.0	63 ± 20.0	45 ± 2.0
	Pterostichus pensylvanicus	Natural	9 ± 7.5	28 ± 1.0	24 ± 22.5	60 ± 37.0
		Planted	1 ± 0.0	15 ± 6.5	32 ± 19.5	37 ± 1.5
	Agonum retractum	Natural	0	1 ± 0.5	1 ± 0.5	57 ± 57.0
		Planted	0	10 ± 6.5	100 ± 78.5	3 ± 3.0
	Calathus ingratus	Natural	1 ± 0.5	13 ± 11.0	13 ± 13.0	8 ± 6.5
		Planted	1 ± 0.0	0 ± 0.0	6 ± 2.0	22 ± 8.5
	Harpalus fulvilabris	Natural	2 ± 1.5	6 ± 3.0	6 ± 3.5	6 ± 4.5
		Planted	1 ± 0.5	3 ± 1.5	10 ± 3.0	5 ± 2.5
	Dicaelus sculptilis	Natural	2 ± 1.5	8 ± 1.0	5 ± 0.0	5 ± 5.0
		Planted	2 ± 1.5	3 ± 3.0	4 ± 4.0	7 ± 6.5
	Carabus taedatus	Natural	3 ± 1.0	2 ± 0.0	6 ± 4.5	1 ± 0.5
		Planted	5 ± 3.0	7 ± 1.0	8 ± 7.0	2 ± 2.0
	Syntomus americanus	Natural	1 ± 0.5	6 ± 5.5	2 ± 0.5	1 ± 0.5
		Planted	5 ± 4.0	7 ± 0.0	2 ± 2.0	1 ± 0.5
	Sphaeroderus lecontei	Natural	0	0	3 ± 0.0	3 ± 2.0
		Planted	0	0	3 ± 0.5	3 ± 1.0
2004	*Synuchus impunctatus*	Natural	127 ± 22.0	125 ± 29.5	30 ± 14.0	158 ± 42.0
		Planted	196 ± 14.0	46 ± 32.0	122 ± 49.0	70 ± 20.0
	Pterostichus pensylvanicus	Natural	29 ± 18.0	79 ± 30.5	69 ± 61.5	186 ± 100.5
		Planted	1 ± 1.0	60 ± 41.5	72 ± 43.0	135 ± 1.5
	Dicaelus sculptilis	Natural	8 ± 7.0	9 ± 1.0	10 ± 2.0	5 ± 4.5
		Planted	7 ± 5.0	2 ± 1.0	15 ± 14.0	17 ± 15.5
	Sphaeroderus lecontei	Natural	1 ± 1.0	7 ± 2.5	8 ± 1.0	12 ± 5.0
		Planted	1 ± 0.5	3 ± 1.0	6 ± 0.5	13 ± 0.5

Species	Regeneration type	Mean catch ± SE 15 years	25 years	35 years	50 years
Syntomus americanus	Natural	4 ± 4.0	8 ± 5.0	4 ± 1.0	5 ± 4.5
	Planted	8 ± 5.5	14 ± 4.0	1 ± 1.0	1 ± 0.5
Agonum retractum	Natural	2 ± 1.5	0	1 ± 0.0	22 ± 21.0
	Planted	0	2 ± 2.0	13 ± 8.0	1 ± 0.0
Carabus taedatus	Natural	6 ± 0.0	3 ± 1.5	3 ± 1.5	0
	Planted	9 ± 0.5	5 ± 2.5	14 ± 14.0	2 ± 1.5
Harpalus fulvilabris	Natural	2 ± 1.0	5 ± 2.5	3 ± 2.0	6 ± 5.5
	Planted	2 ± 2.0	3 ± 1.5	8 ± 1.0	3 ± 0.5
Calathus ingratus	Natural	1 ± 0.5	2 ± 1.5	1 ± 1.0	6 ± 3.5
	Planted	1 ± 1.0	0	2 ± 1.0	9 ± 0.0

Table 3.3.3 Analysis of variance results for activity and diversity measures for carabid beetle assemblages in 2003 and 2004

			2003		2004		Repeated measures between subjects	
Measure	Effect	df	F-ratio	P	F-ratio	P	F-ratio	P
Log total individuals	Age	3	4.501	0.04	1.377	0.32	2.44	0.14
	Regeneration	1	0.861	0.38	0.003	0.96	0.33	0.58
	Age*Regeneration	3	0.996	0.44	1.901	0.21	1.68	0.25
	Error	8						
Pterostichus pensylvanicus	Age	3	2.195	0.17	3.088	0.09	2.88	0.10
	Regeneration	1	0.565	0.47	0.477	0.51	0.51	0.50
	Age*Regeneration	3	0.295	0.83	0.109	0.95	0.15	0.93
	Error	8						
Synuchus impunctatus	Age	3	2.107	0.18	3.224	0.08	1.69	0.25
	Regeneration	1	0.129	0.73	0.004	0.95	0.02	0.89
	Age*Regeneration	3	1.067	0.42	4.930	0.03	5.61	0.02
	Error	8						
Number of species	Age	3	0.390	0.76	0.970	0.45	0.71	0.57
	Regeneration	1	1.400	0.27	0.392	0.55	0.02	0.91
	Age*Regeneration	3	0.886	0.49	1.108	0.40	1.47	0.30
	Error	8						
Log series α	Age	3	23.466	0.00	0.513	0.68	6.39	0.02
	Regeneration	1	5.547	0.05	0.195	0.67	0.60	0.46
	Age*Regeneration	3	8.281	0.01	0.559	0.66	3.29	0.08
	Error	8						
Berger Parker	Age	3	3.439	0.07	5.720	0.02	3.87	0.06
	Regeneration	1	0.765	0.41	0.162	0.70	0.05	0.84
	Age*Regeneration	3	0.323	0.81	0.805	0.53	0.74	0.56
	Error	8						
Slope	Age	3	10.833	0.00	1.631	0.26	4.09	0.05
	Regeneration	1	0.439	0.53	0.131	0.73	0.00	1.00
	Age*Regeneration	3	0.949	0.46	0.547	0.66	0.76	0.55
	Error	8						
Rare species	Age	3	1.387	0.32	2.375	0.15	–	–
	Regeneration	1	3.459	0.10	0.809	0.39	–	–
	Age*Regeneration	3	0.685	0.59	2.712	0.12	–	–
	Error	8						

			2003		2004		Repeated measures between subjects	
Measure	Effect	df	F-ratio	P	F-ratio	P	F-ratio	P
Forest species	Age	3	6.500	0.02	7.667	0.01	–	–
	Regeneration	1	0.167	0.69	1.333	0.28	–	–
	Age*Regeneration	3	0.500	0.69	0.667	0.60	–	–
	Error	8						
Field species	Age	3	3.376	0.07	1.694	0.24	–	–
	Regeneration	1	1.032	0.34	0.053	0.82	–	–
	Age*Regeneration	3	0.301	0.82	1.663	0.25	–	–
	Error	8						
Generalist species	Age	3	2.727	0.11	0.774	0.54	–	–
	Regeneration	1	0.727	0.42	0.925	0.36	–	–
	Age*Regeneration	3	1.576	0.27	0.119	0.95	–	–
	Error	8						

Table 3.3.4 Repeated measures analyses results for summary measures of the carabid assemblages in 2003 and 2004

Measure	Effect	df	F-ratio	P
Log total individuals	Year	1	42.232	0.00
	Year*age	3	6.559	0.02
	Year*regeneration	1	1.316	0.28
	Year*age*regeneration	3	0.144	0.95
	Error	8		
Synuchus impunctatus	Year	1	32.117	0.00
	Year*age	3	3.965	0.05
	Year*regeneration	1	0.057	0.82
	Year*age*regeneration	3	2.271	0.16
	Error	8		
Pterostichus pensylvanicus	Year	1	21.416	0.00
	Year*age	3	3.422	0.07
	Year*regeneration	1	0.399	0.55
	Year*age*regeneration	3	0.061	0.98
	Error	8		
Species richness	Year	1	11.565	0.01
	Year*age	3	0.942	0.46
	Year*regeneration	1	2.079	0.19
	Year*age*regeneration	3	0.189	0.90
	Error	8		
Log series α	Year	1	1.766	0.22
	Year*age	3	9.144	0.01
	Year*regeneration	1	4.260	0.07
	Year*age*regeneration	3	1.853	0.22
	Error	8		
Berger Parker	Year	1	15.458	0.00
	Year*age	3	5.488	0.02
	Year*regeneration	1	0.503	0.50
	Year*age*regeneration	3	0.607	0.63
	Error	8		
Slope of log abundance	Year	1	0.436	0.53
	Year*age	3	2.104	0.18
	Year*regeneration	1	0.993	0.35
	Year*age*regeneration	3	0.163	0.92
	Error	8		

Measure	Effect	df	F-ratio	P
Jaccard's index	Year	1	6.794	0.08
	Year*regeneration	1	0.525	0.52
	Error	3		
Kendall's τ	Year	1	52.143	0.01
	Year*regeneration	1	0.833	0.43
	Error	3		

Table 3.3.5 Mean of activity and diversity measures 1991 - 1994

Measure	Regeneration type	Mean index ± SE 40 years	25 years	15 years	5 years
Log total	Natural	2.11 ± 0.10	1.68 ± 0.07	1.68	2.53 ± 0.1
	Planted	2.14 ± 0.15	1.76 ± 0.24	1.80 ± 0.25	2.28 ± 0.1
Number of species	Natural	11.38 ± 0.38	10.75 ± 0.75	10.50	14.88 ± 2.6
	Planted	10.13 ± 1.38	10.00 ± 1.50	12.75 ± 1.75	18.75 ± 2.0
Log series alpha	Natural	3.12 ± 0.47	4.38 ± 0.06	4.37	3.27 ± 0.9
	Planted	2.66 ± 0.02	3.40 ± 0.04	4.98 ± 0.62	5.29 ± 0.5
Berger Parker	Natural	0.51 ± 0.07	0.39 ± 0.03	0.38	0.51 ± 0.1
	Planted	0.43 ± 0.01	0.49 ± 0.06	0.39 ± 0.10	0.38 ± 0.0
Slope of log abundance	Natural	-0.18 ± 0.00	-0.16 ± 0.02	-0.19	-0.17 ± 0.0
	Planted	-0.21 ± 0.01	-0.17 ± 0.00	-0.13 ± 0.00	-0.11 ± 0.0
Jaccard's index	Natural	0.39 ± 0.07	0.34 ± 0.16	–	0.46 ± 0.07
	Planted	0.45 ± 0.02	0.34 ± 0.09	0.45 0.11	0.54 ± 0.07
Kendall's τ	Natural	0.16 ± 0.10	-0.06 ± 0.18	–	0.32 ± 0.10
	Planted	0.37 ± 0.10	0.13 ± 0.12	0.07 ± 0.15	0.30 ± 0.11

Table 3.3.6 Repeated measures results for summary measures for oringinal and current study combined, original study and current study

	Within subjects				Between subjects		
Effect	df	F-ratio	P		df	F-ratio	P
Log total							
Overall							
Year	5	5.348	0.00				
Year*Age	15	4.292	0.00	Age	3	5.978	0.02
Year*Regenerationeration	5	0.477	0.79	Regeneration	1	0.809	0.78
Year*Age*Regeneration	15	0.801	0.67	Age*Regeneration	3	0.702	0.58
Error	35			Error	7		
First 4 years							
Year	3	1.856	0.17				
Year*Age	9	1.555	0.19	Age	3	8.099	0.01
Year*Regeneration	3	0.768	0.52	Regeneration	1	0.000	1.00
Year*Age*Regeneration	9	0.862	0.57	Age*Regeneration	3	0.523	0.68
Error	21			Error	7		
Last 2 years							
Year	1	33.268	0.00				
Year*Age	3	5.639	0.03	Age	3	2.153	0.18
Year*Regeneration	1	1.092	0.33	Regeneration	1	0.324	0.59
Year*Age*Regeneration	3	0.096	0.96	Age*Regeneration	3	1.287	0.35
Error	7			Error	7		
Between 1st and 2nd study							
Year	1	1.624	0.24				
Year*Age	3	5.752	0.03				
Year*Regeneration	1	0.160	0.70				
Year*Age*Regeneration	3	0.912	0.48				
Error	7						
Species richness							
Overall							
Year	5	6.346	0.00				
Year*Age	15	1.598	0.12	Age	3	4.721	0.04
Year*Regeneration	5	0.726	0.61	Regeneration	1	0.845	0.39
Year*Age*Regeneration	15	0.506	0.92	Age*Regeneration	3	1.312	0.34
Error	35			Error	7		
First 4 years							
Year	3	9.013	0.00				
Year*Age	9	1.720	0.15	Age	3	6.624	0.02
Year*Regeneration	3	0.930	0.44	Regeneration	1	0.704	0.43
Year*Age*Regeneration	9	0.843	0.59	Age*Regeneration	3	1.081	0.42
Error	21			Error	7		

	Within subjects				Between subjects		
Effect	df	F-ratio	P		df	F-ratio	P
Last 2 years							
Year	1	8.217	0.02				
Year*Age	3	0.599	0.64	Age	3	0.415	0.75
Year*Regeneration	1	1.127	0.32	Regeneration	1	0.465	0.52
Year*Age*Regeneration	3	0.058	0.98	Age*Regeneration	3	0.984	0.45
Error	7			Error	7		
Between 1st and 2nd study							
Year	1	0.054	0.82				
Year*Age	3	2.333	0.16				
Year*Regeneration	1	0.000	0.98				
Year*Age*Regeneration	3	0.357	0.79				
Error	7						
Log series α							
Overall							
Year	5	6.107	0.00				
Year*Age	15	3.762	0.00	Age	3	5.296	0.03
Year*Regeneration	5	2.691	0.04	Regeneration	1	0.971	0.36
Year*Age*Regeneration	15	1.077	0.41	Age*Regeneration	3	4.317	0.05
Error	35			Error	7		
First 4 years							
Year	3	9.018	0.00				
Year*Age	9	2.157	0.07	Age	3	4.450	0.05
Year*Regeneration	3	3.007	0.05	Regeneration	1	0.677	0.44
Year*Age*Regeneration	9	1.254	0.32	Age*Regeneration	3	3.719	0.07
Error	21			Error	7		
Last 2 years							
Year	1	1.033	0.34				
Year*Age	3	8.346	0.01	Age	3	6.058	0.02
Year*Regeneration	1	4.151	0.08	Regeneration	1	0.913	0.37
Year*Age*Regeneration	3	1.337	0.34	Age*Regeneration	3	3.010	0.10
Error	7			Error	7		
Between 1st and 2nd study							
Year	1	0.989	0.35				
Year*Age	3	4.812	0.04				
Year*Regeneration	1	0.143	0.72				
Year*Age*Regeneration	3	0.201	0.98				
Error	7						

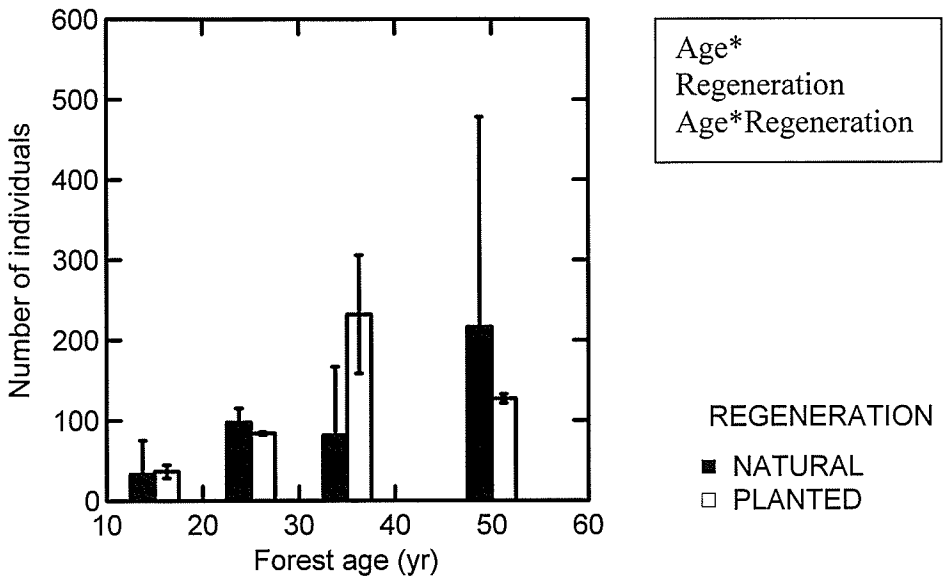
	Within subjects				Between subjects		
Effect	df	F-ratio	P		df	F-ratio	P
Berger Parker Index							
Overall							
Year	5	3.298	0.02				
Year*Age	15	1.762	0.08	Age	3	1.005	0.45
Year*Regeneration	5	0.470	0.80	Regeneration	1	0.096	0.77
Year*Age*Regeneration	15	0.452	0.95	Age*Regeneration	3	0.978	0.46
Error	35			Error	7		
First 4 years							
Year	3	1.475	0.25				
Year*Age	9	1.242	0.32	Age	3	0.329	0.80
Year*Regeneration	3	0.505	0.68	Regeneration	1	0.231	0.65
Year*Age*Regeneration	9	0.406	0.92	Age*Regeneration	3	0.876	0.50
Error	21			Error	7		
Last 2 years							
Year	1	11.810	0.01				
Year*Age	3	4.695	0.04	Age	3	4.975	0.04
Year*Regeneration	1	0.351	0.57	Regeneration	1	0.462	0.52
Year*Age*Regeneration	3	0.440	0.73	Age*Regeneration	3	0.252	0.86
Error	7			Error	7		
Between 1st and 2nd study							
Year	1	0.731	0.42				
Year*Age	3	0.646	0.61				
Year*Regeneration	1	0.487	0.51				
Year*Age*Regeneration	3	0.560	0.66				
Error	7						
Slope							
Overall							
Year	5	9.668	0.00				
Year*Age	15	1.644	0.11	Age	3	8.591	0.01
Year*Regeneration	5	2.893	0.03	Regeneration	1	2.442	0.16
Year*Age*Regeneration	15	1.121	0.37	Age*Regeneration	3	3.903	0.06
Error	35			Error	7		
First 4 years							
Year	3	11.973	0.00				
Year*Age	9	2.547	0.04	Age	3	4.179	0.05
Year*Regeneration	3	5.175	0.01	Regeneration	1	2.962	0.13
Year*Age*Regeneration	9	1.820	0.12	Age*Regeneration	3	3.579	0.07
Error	21			Error	7		

	Within subjects				Between subjects		
Effect	df	F-ratio	P		df	F-ratio	P
Last 2 years							
Year	1	0.375	0.56				
Year*Age	3	1.691	0.26	Age	3	3.547	0.08
Year*Regeneration	1	0.826	0.39	Regeneration	1	0.074	0.79
Year*Age*Regeneration	3	0.146	0.93	Age*Regeneration	3	0.760	0.55
Error	7			Error	7		
Between 1st and 2nd study							
Year	1	9.161	0.06				
Year*Age	3	0.392	0.76				
Year*Regeneration	1	0.350	0.57				
Year*Age*Regeneration	3	0.439	0.73				
Error	7						

Table 3.3.7 Repeated measure results for original and current study combined, original study and current study

Measure	df	F ratio	P
Jaccard's index			
Overall	5	0.799	0.57
First four years	3	1.066	0.43
Last two years	1	6.794	0.08
Between first and second study	1	0.002	0.98
Error	10		
Kendall's tau			
Overall	5	8.381	0.30
First four years	3	0.668	0.22
Last two years	1	52.143	0.44
Between first and second study	1	11.275	0.18
Error	10		

Figure 3.3.1 Total number of carabid beetles caught in the 2003 collection year; patterns associated with forest age and regeneration type.



Significance values: * $p \leq 0.05$, ** $p \leq 0.01$, *** $p \leq 0.005$

Figure 3.3.2 Total number of carabid beetles caught in the 2004 collection year; patterns associated with forest age and regeneration type.

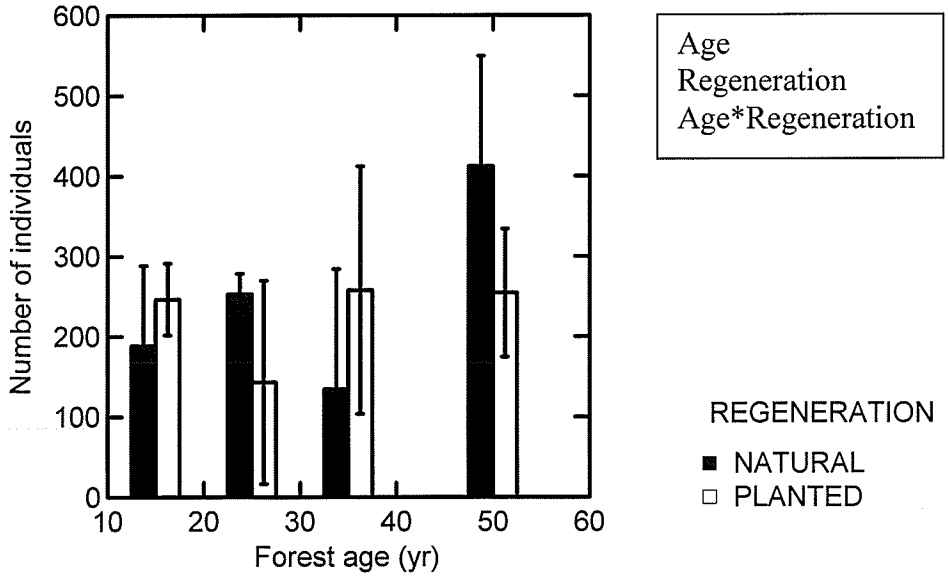


Figure 3.3.3 Total number of *Synuchus impunctatus* caught in the 2003 collection year; patterns associated with forest age and regeneration type.

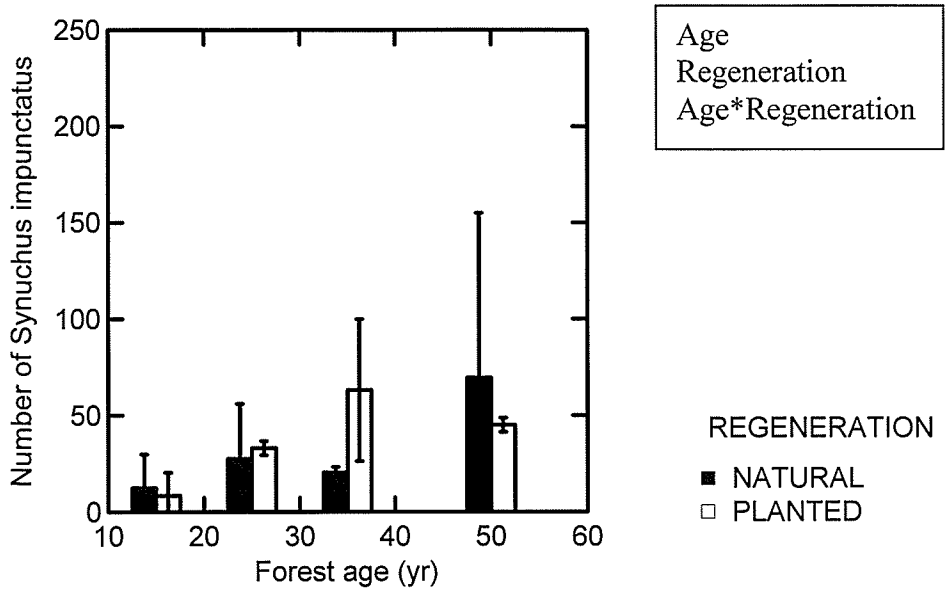


Figure 3.3.4 Total number of *Synuchus impunctatus* caught in the 2004 collection year; patterns associated with forest age and regeneration type.

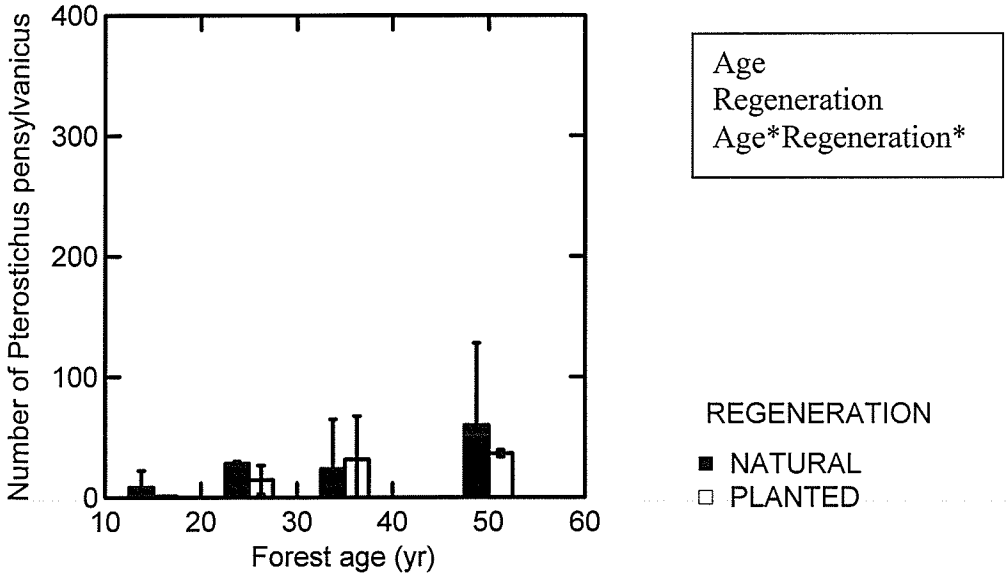


Figure 3.3.5 Total number of *Pterostichus pensylvanicus* caught in the 2003 collection year; patterns associated with forest age and regeneration type.

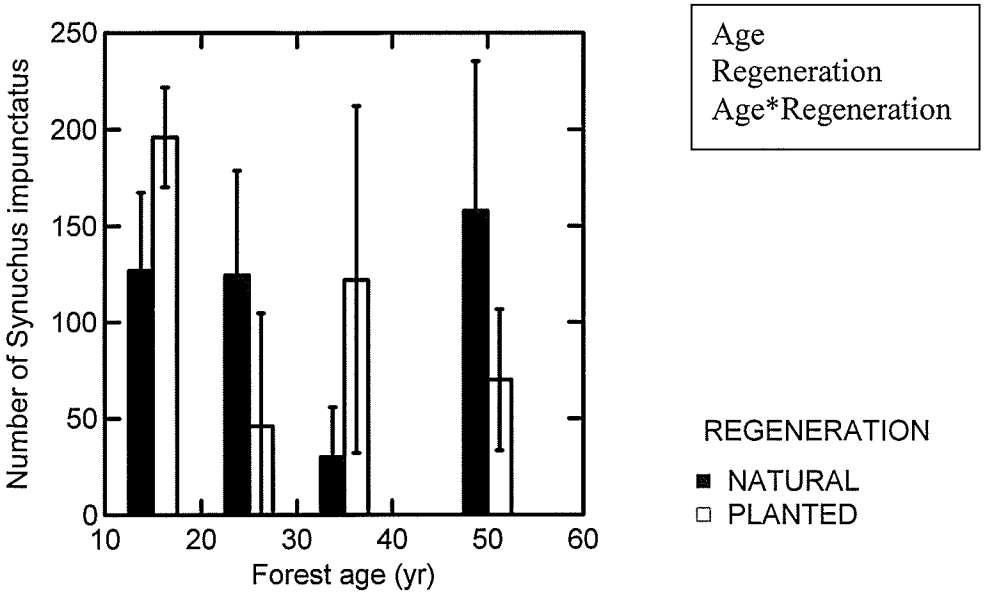


Figure 3.3.6 Total number of *Pterostichus pensylvanicus* caught in the 2004 collection year; patterns associated with forest age and regeneration type.

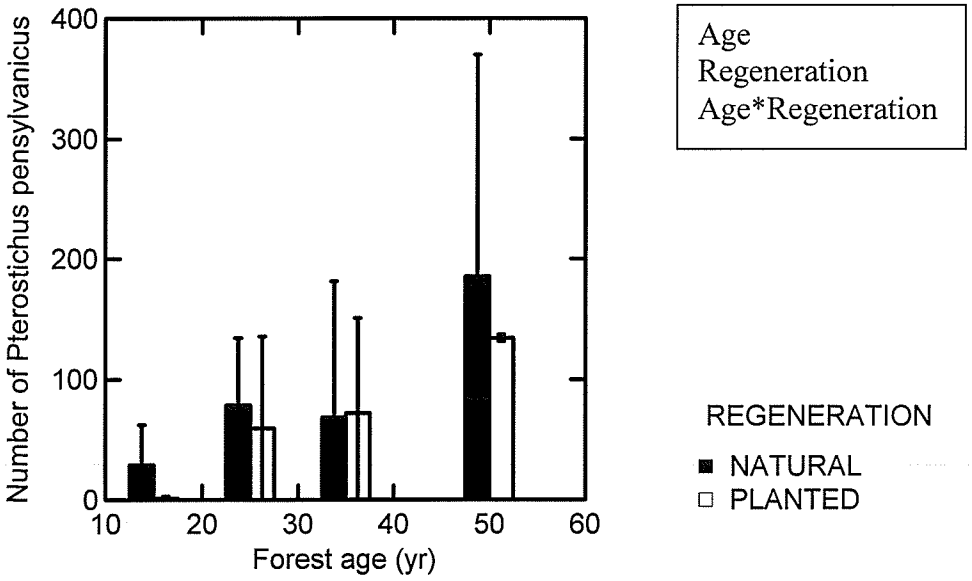


Figure 3.3.7 Total number of carabid beetles species caught in the 2003 collection year; patterns associated with forest age and regeneration type.

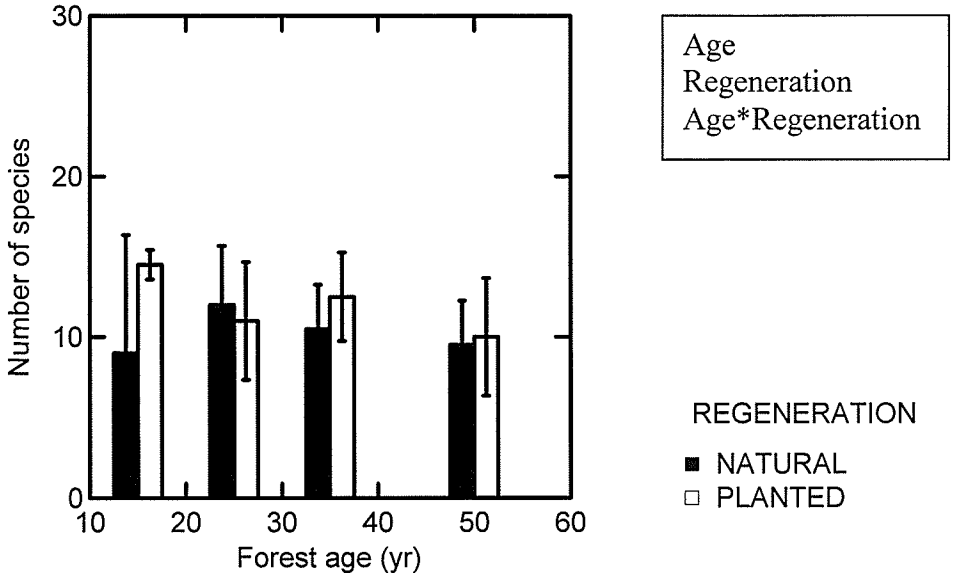


Figure 3.3.8 Total number of carabid beetles species caught in the 2004 collection year; patterns associated with forest age and regeneration type.

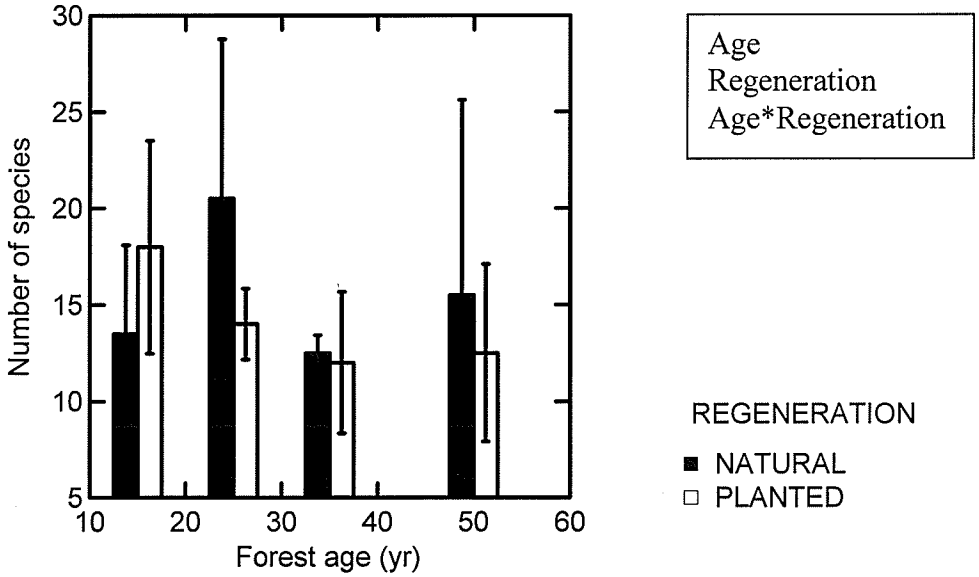


Figure 3.3.9 Alpha diversity of the carabid beetle assemblage of the 2003 collection year; patterns associated with forest age and regeneration type.

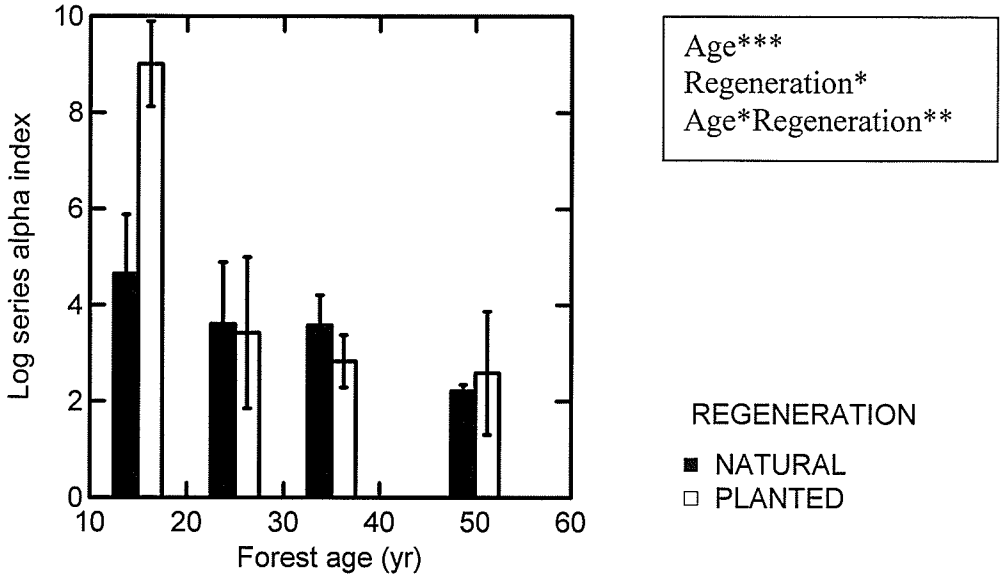


Figure 3.3.10 Alpha diversity of the carabid beetle assemblage of the 2004 collection year; patterns associated with forest age and regeneration type.

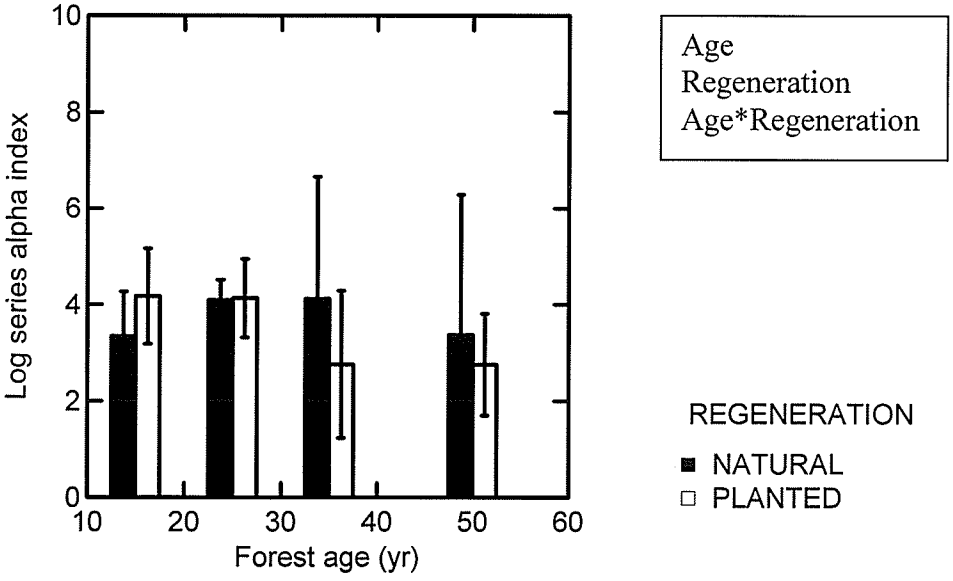


Figure 3.3.11 Species dominance of the carabid beetle assemblage of 2003 collection year; patterns associated with forest age and regeneration type.

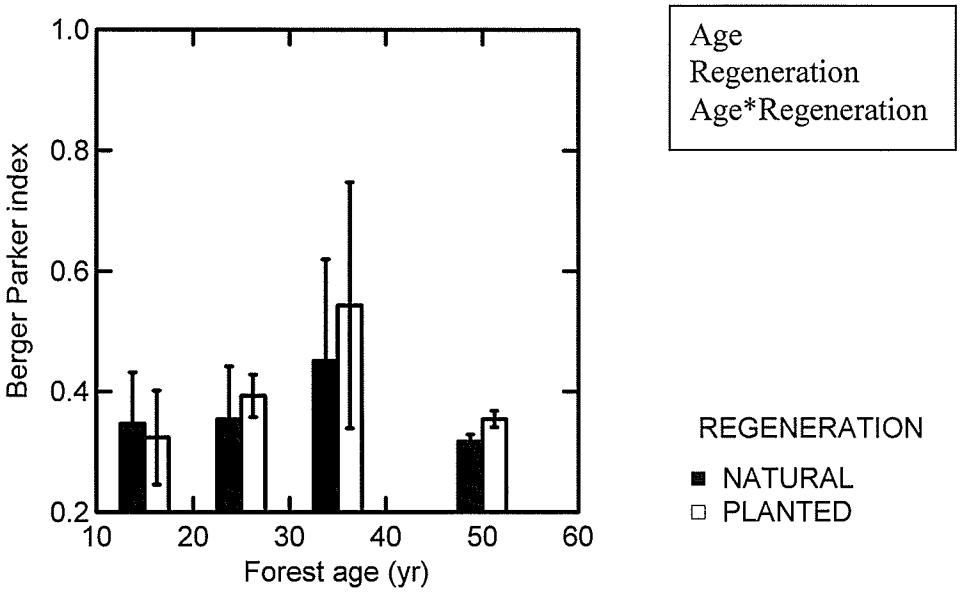


Figure 3.3.12 Species dominance of the carabid beetle assemblage of the 2004 collection year; patterns associated with forest age and regeneration type.

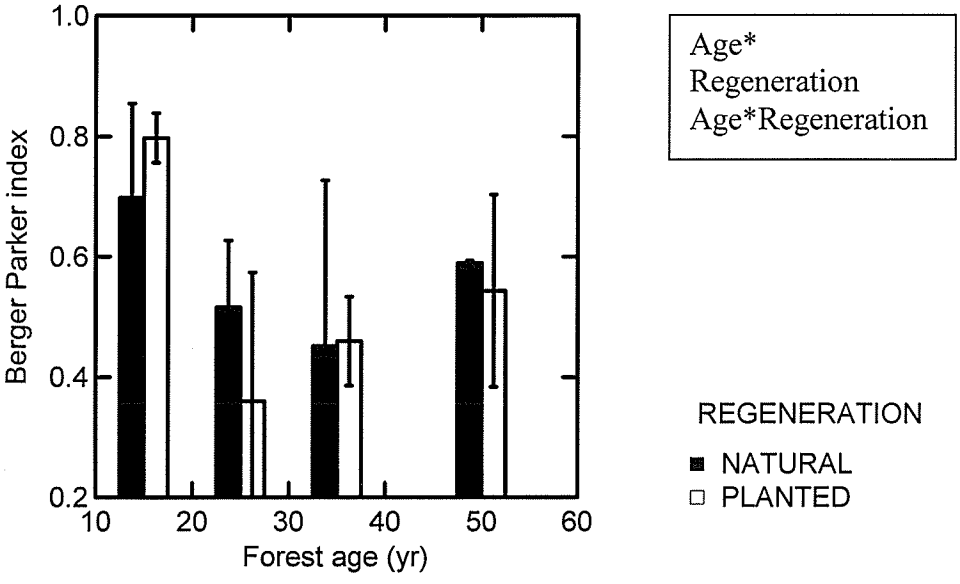


Figure 3.3.13 Species evenness of the carabid beetle assemblage of 2003 collection year; patterns associated with forest age and regeneration type.

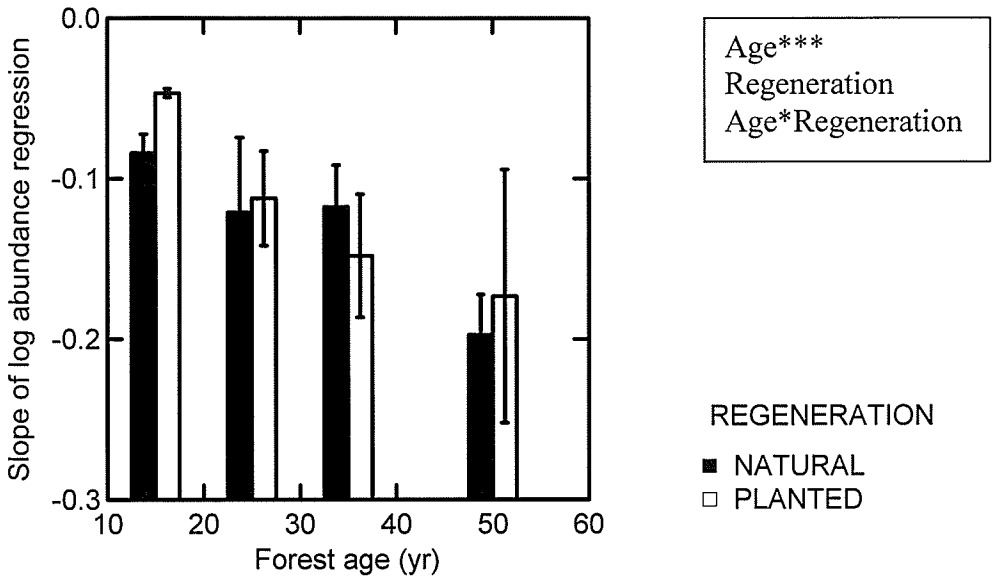


Figure 3.3.14 Species evenness of the carabid beetle assemblage of the 2004 collection year; patterns associated with forest age and regeneration type.

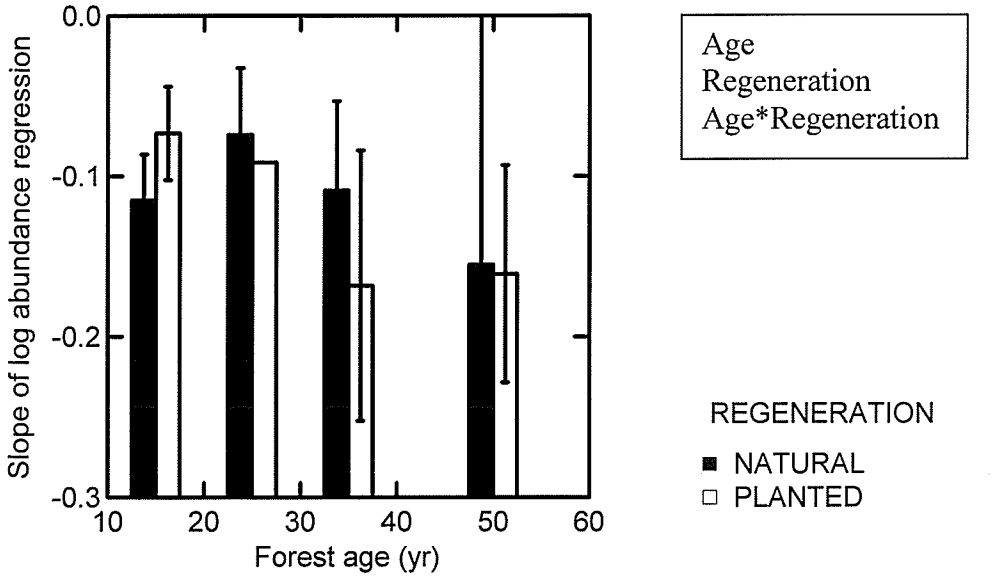


Figure 3.3.15 Jaccard's index of beta diversity of the carabid beetle assemblages of 2003 collection year; patterns associated with forest age and regeneration type.

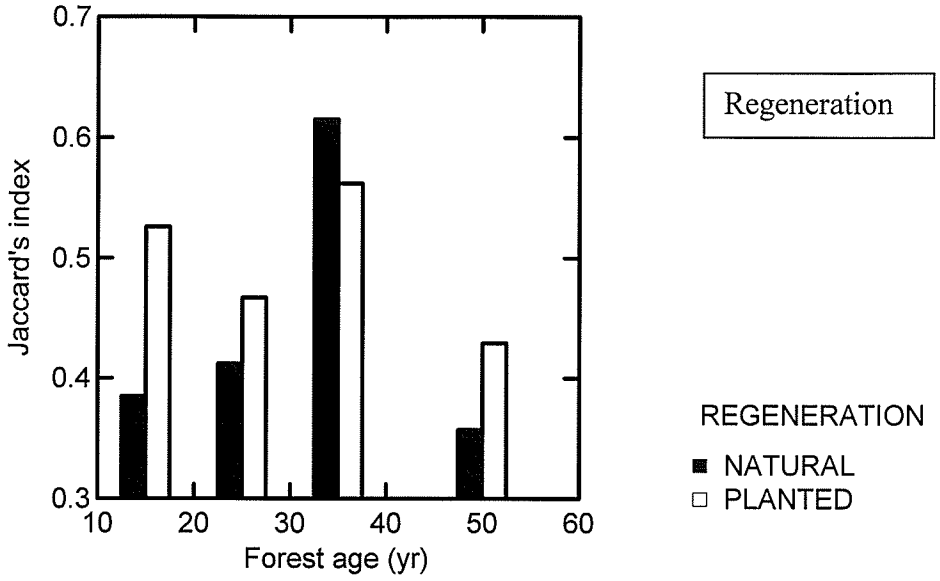


Figure 3.3.16 Jaccard's index of beta diversity of the carabid beetle assemblages of the 2004 collection year; patterns associated with forest age and regeneration type.

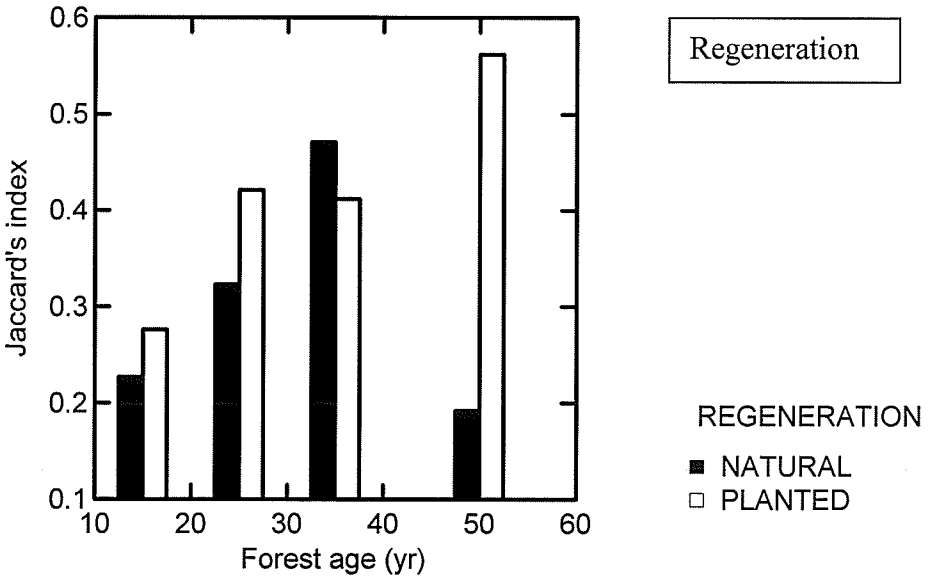


Figure 3.3.17 Kendall's index of beta diversity of the carabid beetle assemblages of the 2003 collection year; patterns associated with forest age and regeneration type.

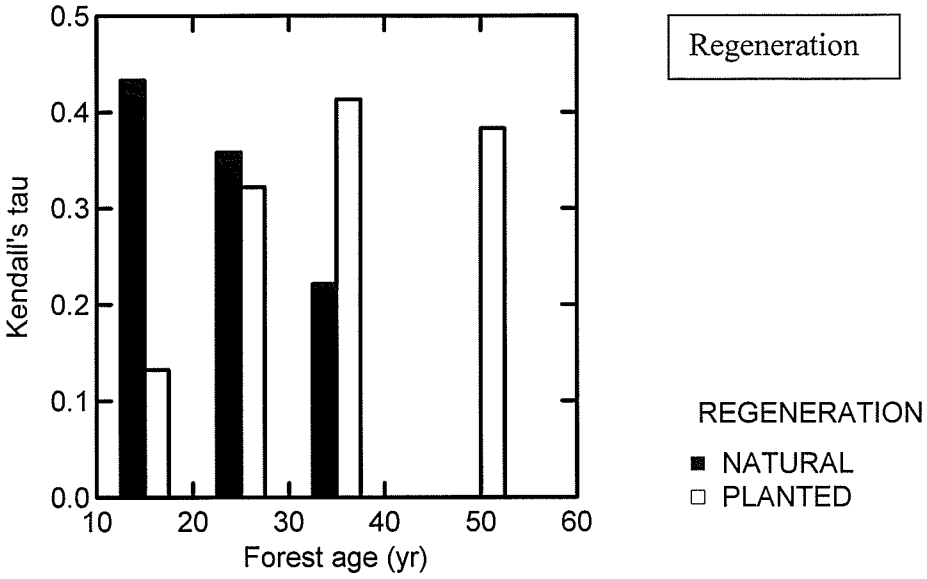


Figure 3.3.18 Kendall's index of beta diversity of the carabid beetle assemblages of the 2004 collection year; patterns associated with forest age and regeneration type.

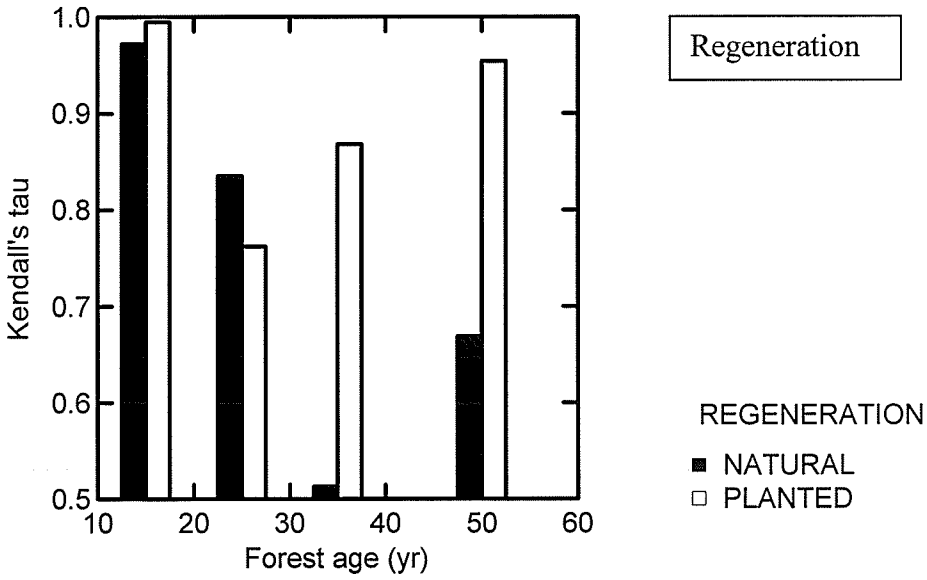


Figure 3.3.19 Total number of uncommon carabid beetle species (<0.05% of the total 2003 and 2004 catch) caught in the 2003 collection year; patterns associated with forest age and regeneration type.

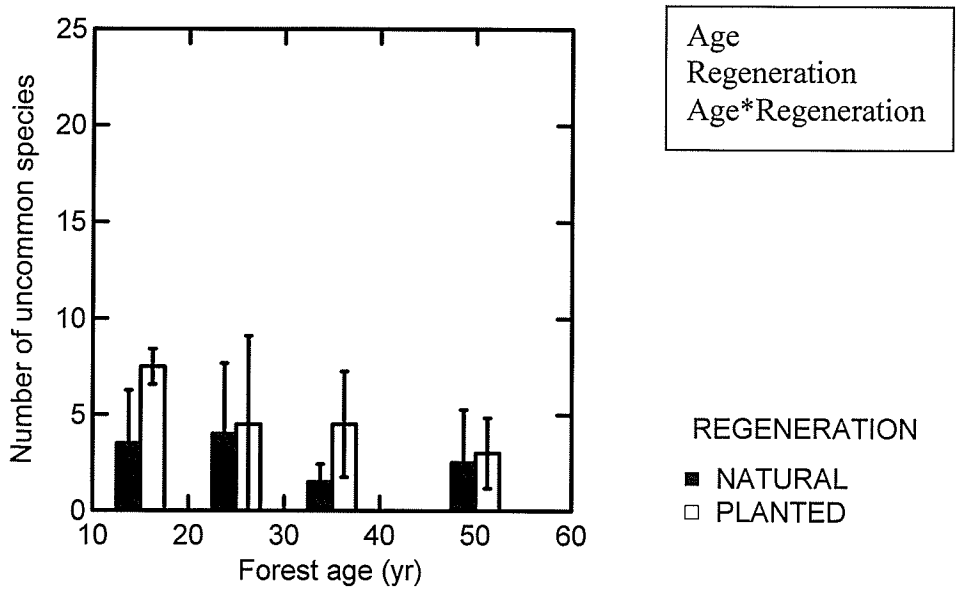


Figure 3.3.20 Total number of uncommon carabid beetle speicies (<0.05% of the total 2003 and 2004 catch) caught in the 2004 collection year; patterns associated with forest age and regeneration type.

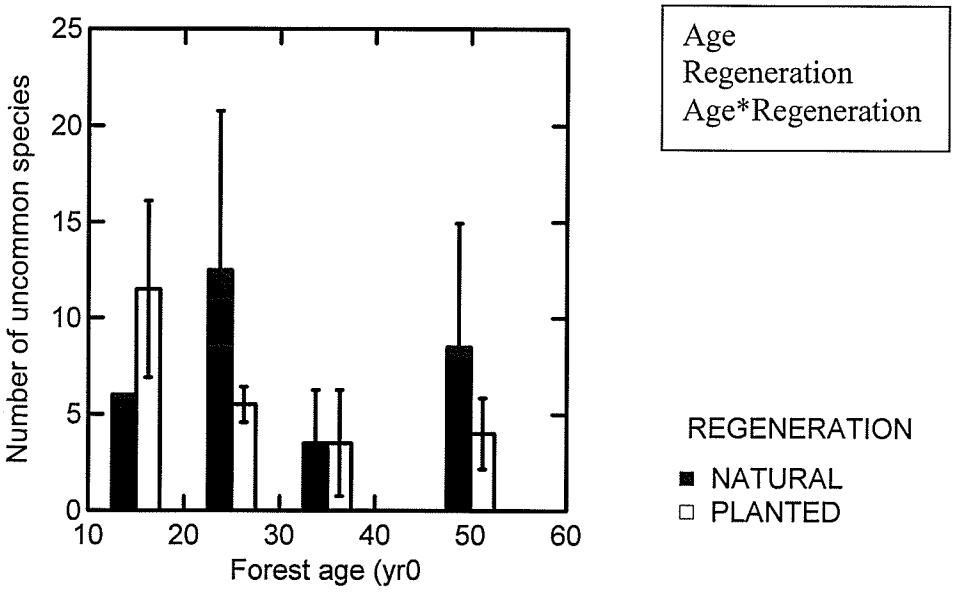


Figure 3.3.21 Total number of forest carabid beetle species caught in the 2003 collection year; patterns associated with forest age and regeneration type.

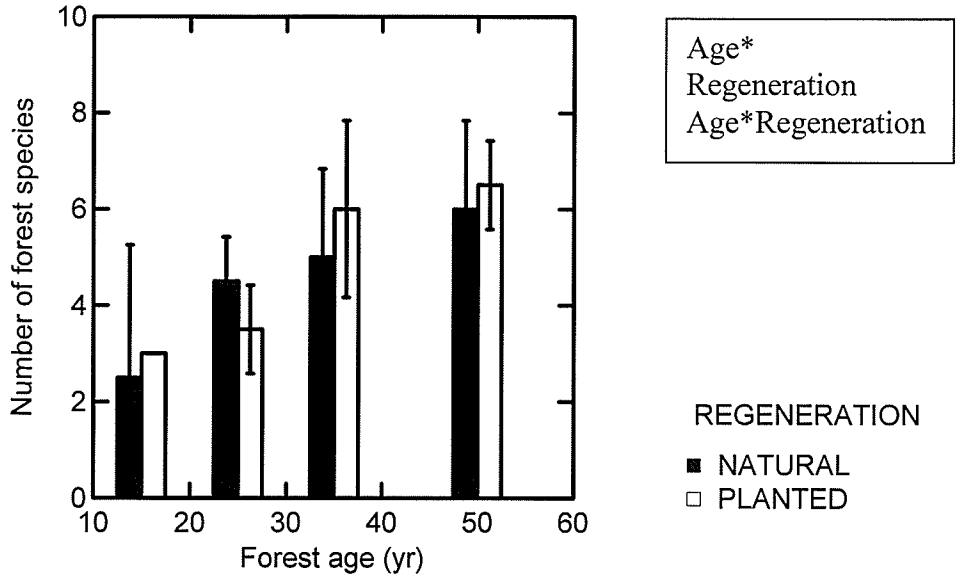


Figure 3.3.22 Total number of forest carabid beetle species caught in the 2004 collection year; patterns associated with forest age and regeneration type.

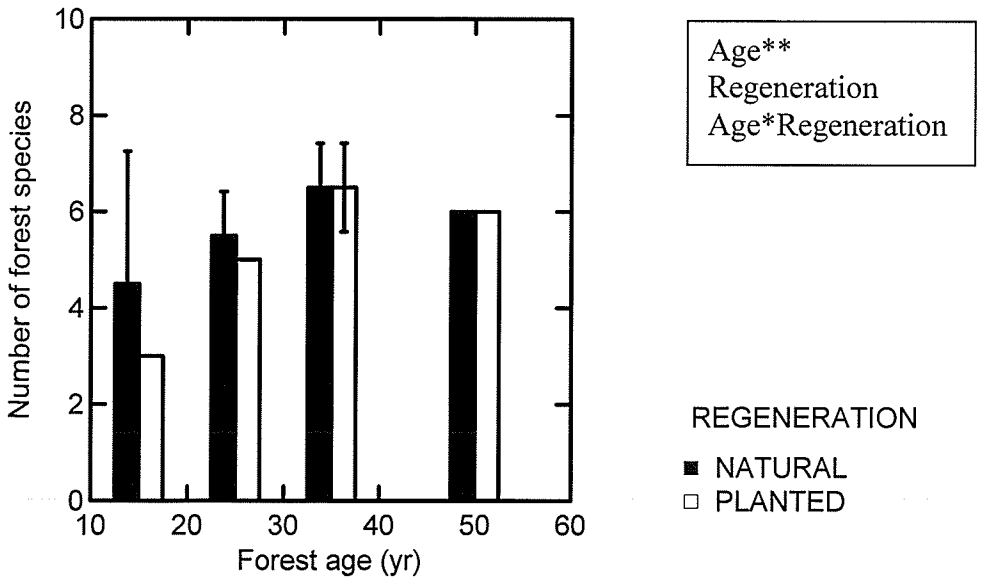


Figure 3.3.23 Total number of open habitat carabid beetle species caught in the 2003 collection year; patterns associated with forest age and regeneration type.

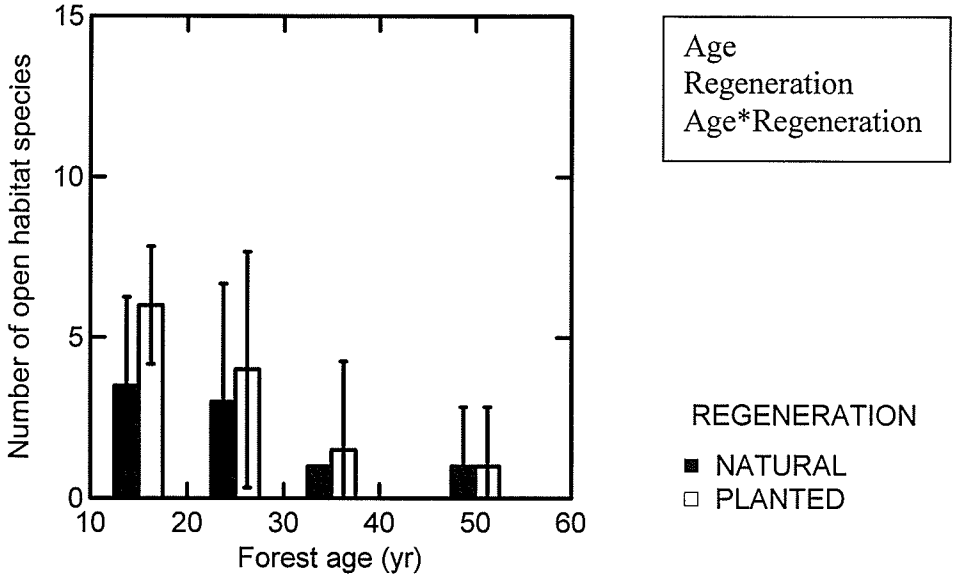


Figure 3.3.24 Total number of open habitat carabid beetle species caught in the 2004 collection year; patterns associated with forest age and regeneration type.

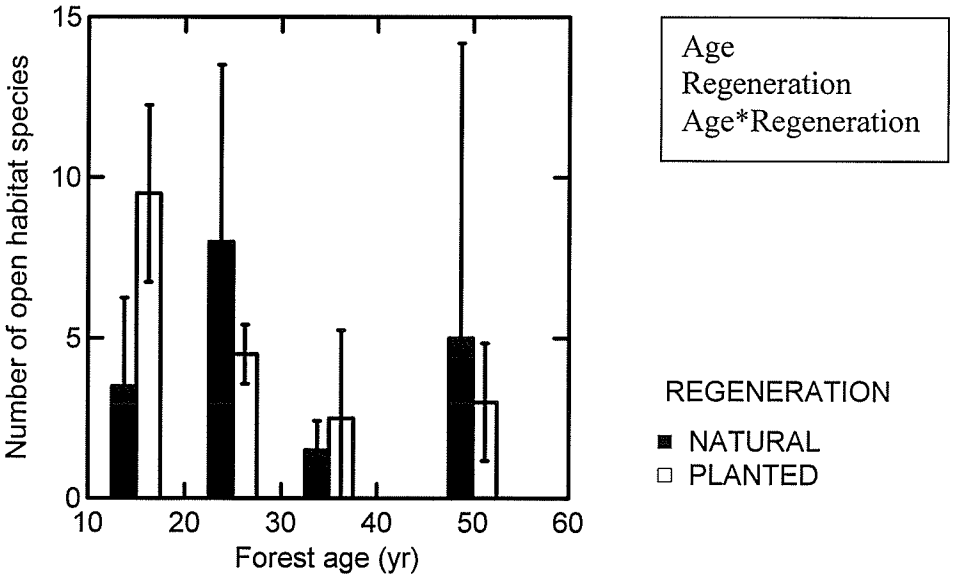


Figure 3.3.25 Total number of generalist carabid beetle species caught in the 2003 collection year; patterns associated with forest age and regeneration type.

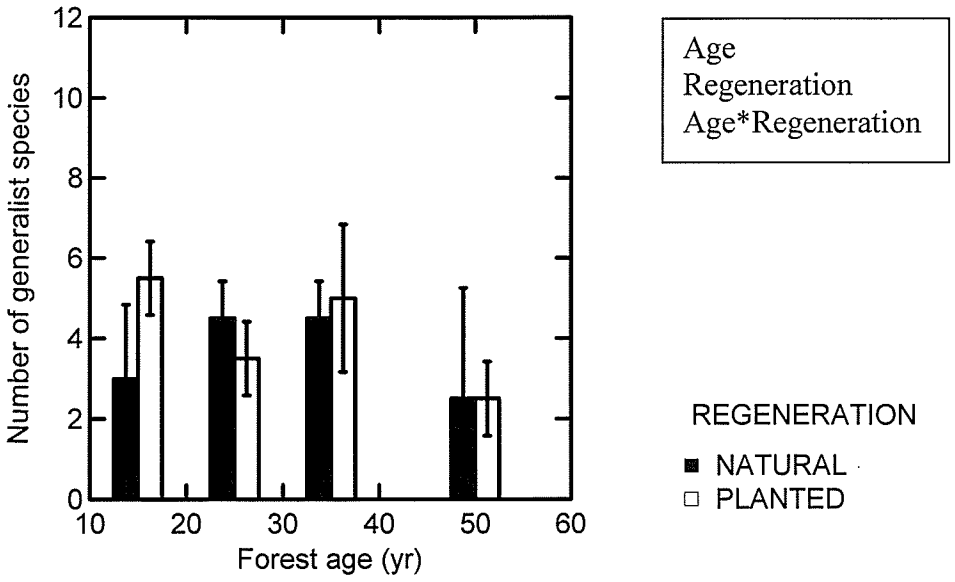


Figure 3.3.26 Total number of generalist carabid beetle species caught in the 2004 collection year; patterns associated with forest age and regeneration type.

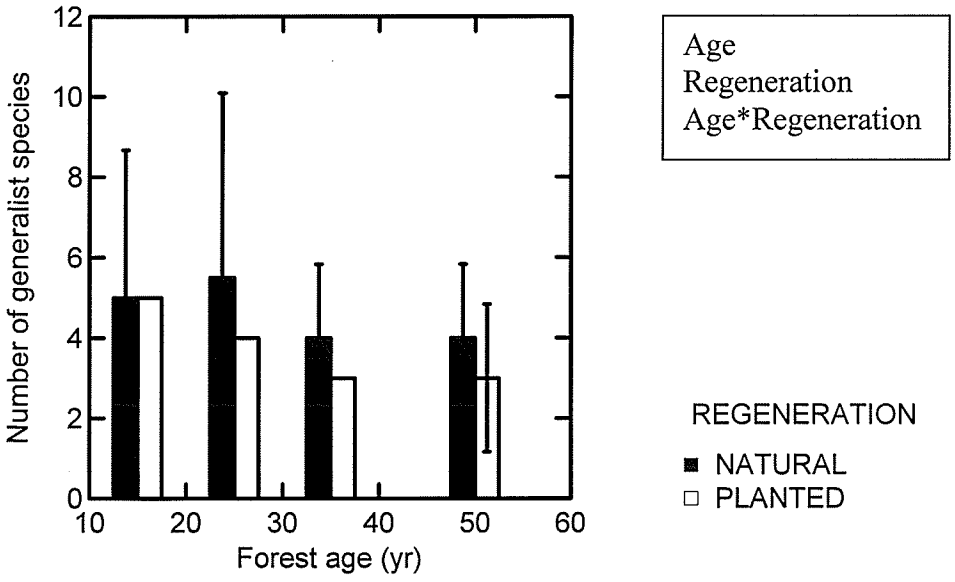
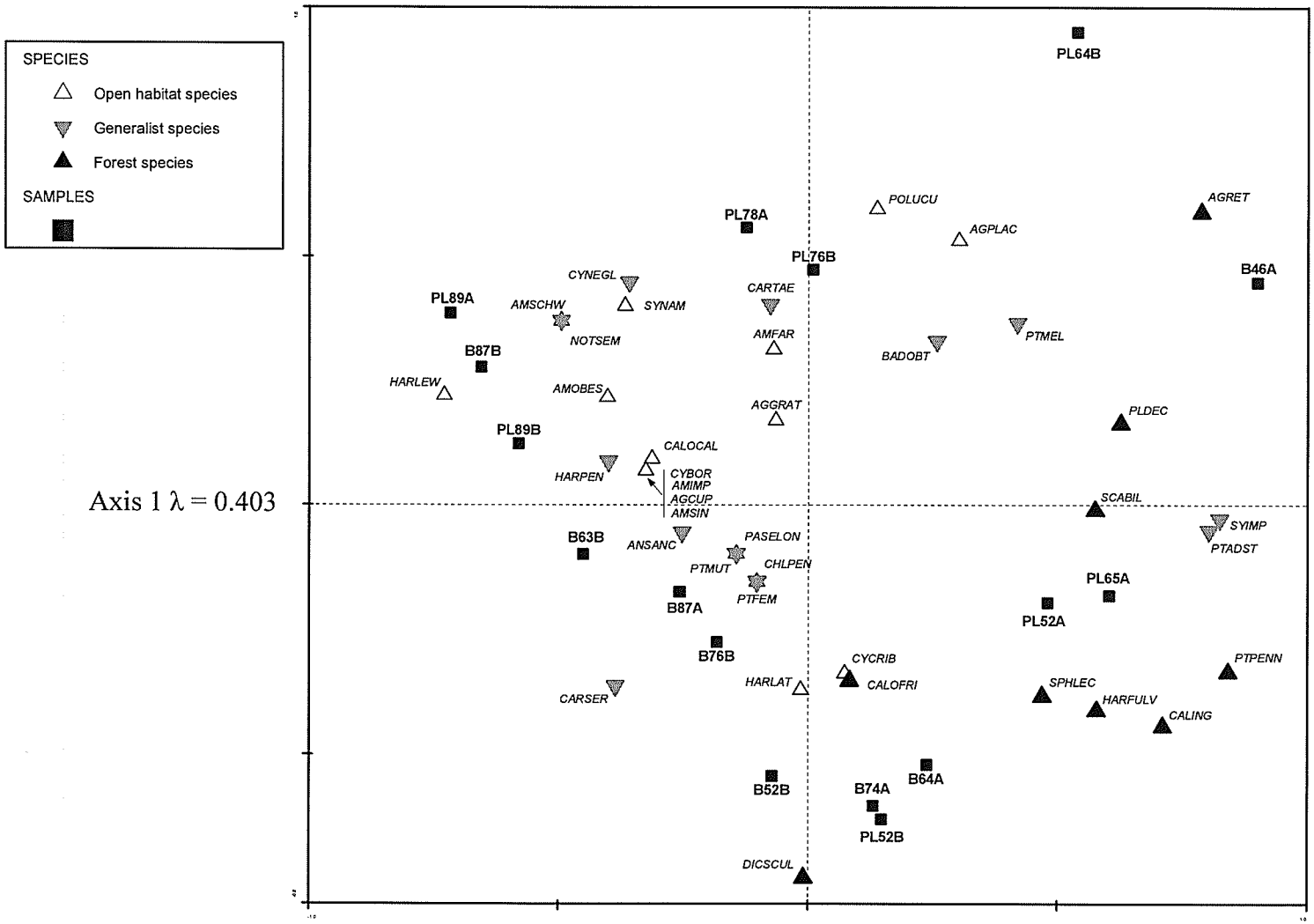


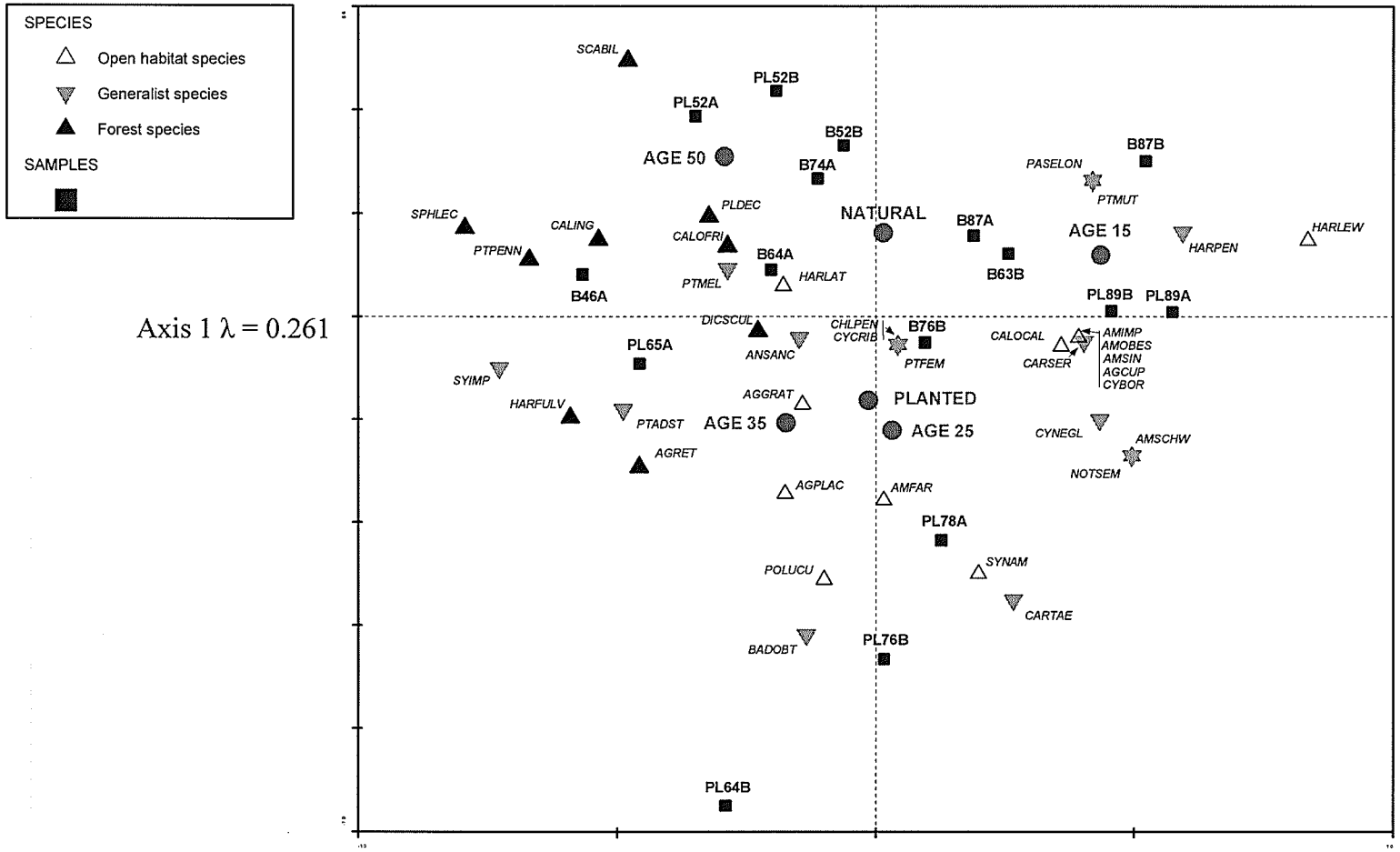
Figure 3.3.27 Principal Components Analysis ordination diagram of 2003 carabid beetle species (Δ) and sites (■). Species codes: AGCUP = *Agonum cupreum*, AGGRAT = *Agonum gratiosum*, AGPLAC = *Agonum placidum*, AGRET = *Agonum retractum*, AMFAR = *Amara farcta*, AMIMP = *Amara impuncticollis*, AMOBES = *Amara obesa*, AMSCHW = *Amara schwarzi*, AMSIN = *Amara sinuosa*, ANSANC = *Anisodactylus sanctaecrucis*, BADOBT = *Badister obtusus*, CALING = *Calathus ingratus*, CALOCAL = *Calosoma calidum*, CALOFRI = *Calosoma frigidum*, CARSER = *Carabus serratus*, CARTAE = *Carabus taedatus agassii*, CHLPEN = *Chlaenius pensylvanicus pensylvanicus*, CYBOR = *Cymindis borealis*, CYCRIB = *Cymindis cribicollis*, CYNEGL = *Cymindis neglecta*, DICSCUL = *Dicaelus sculptilis upiodes*, HARFUL = *Harpalus fulvilabris*, HARLAT = *Harpalus laticeps*, HARLEW = *Harpalus lewisi*, HARPEN = *Harpalus pensylvanicus*, NOTSEM = *Notiophilus semistriatus*, PASELON = *Pasimachus elongatus*, PLDEC = *Platynus decentis*, POLUCU = *Poecilus lucublandus lucublandus,* PTADST = *Pterostichus adstrictus*, PTFEM = *Pterostichus femoralis*, PTMEL = *Pterostichus melanarius*, PTMUT = *Pterostichus mutus*, PTPENN = *Pterostichus pensylvanicus*, SCABIL = *Scaphinotus bilobus*, SPHLEC = *Sphaeroderus stenostomus lecontei*, SYAMER = *Syntomus americanus*, SYIMP = *Synuchus impunctatus*.



Axis 1 λ = 0.403

Axis 2 λ = 0.203

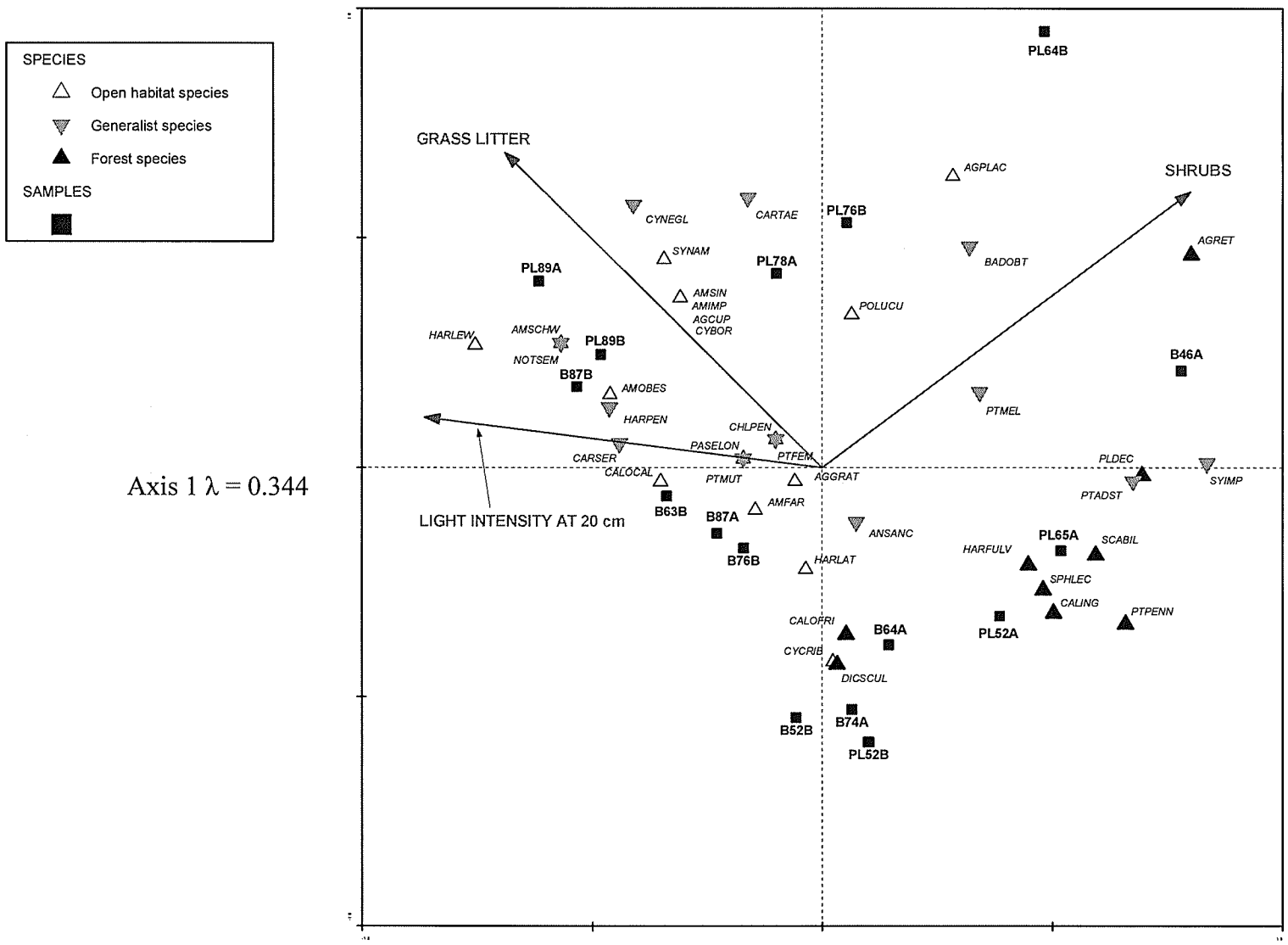
Figure 3.3.28 Redundancy Analysis ordination diagram of 2003 carabid beetle species (Δ) and sites (■) constrained by forest age and regeneration type. Species codes: AGCUP = *Agonum cupreum*, AGGRAT = *Agonum gratiosum*, AGPLAC = *Agonum placidum*, AGRET = *Agonum retractum*, AMFAR = *Amara farcta*, AMIMP = *Amara impuncticollis*, AMOBES = *Amara obesa*, AMSCHW = *Amara schwarzi*, AMSIN = *Amara sinuosa*, ANSANC = *Anisodactylus sanctaecrucis*, BADOBT = *Badister obtusus*, CALING = *Calathus ingratus*, CALOCAL = *Calosoma calidum*, CALOFRI = *Calosoma frigidum*, CARSER = *Carabus serratus*, CARTAE = *Carabus taedatus agassii*, CHLPEN = *Chlaenius pensylvanicus pensylvanicus*, CYBOR = *Cymindis borealis*, CYCRIB = *Cymindis cribicollis*, CYNEGL = *Cymindis neglecta*, DICSCUL = *Dicaelus sculptilis upiodes*, HARFUL = *Harpalus fulvilabris*, HARLAT = *Harpalus laticeps*, HARLEW = *Harpalus lewisi*, HARPEN = *Harpalus pensylvanicus*, NOTSEM = *Notiophilus semistriatus*, PASELON = *Pasimachus elongatus*, PLDEC = *Platynus decentis*, POLUCU = *Poecilus lucublandus lucublandus,* PTADST = *Pterostichus adstrictus*, PTFEM = *Pterostichus femoralis*, PTMEL = *Pterostichus melanarius*, PTMUT = *Pterostichus mutus*, PTPENN = *Pterostichus pensylvanicus*, SCABIL = *Scaphinotus bilobus*, SPHLEC = *Sphaeroderus stenostomus lecontei*, SYAMER = *Syntomus americanus*, SYIMP = *Synuchus impunctatus*.



Axis 1 λ = 0.261

Axis 2 λ = 0.074

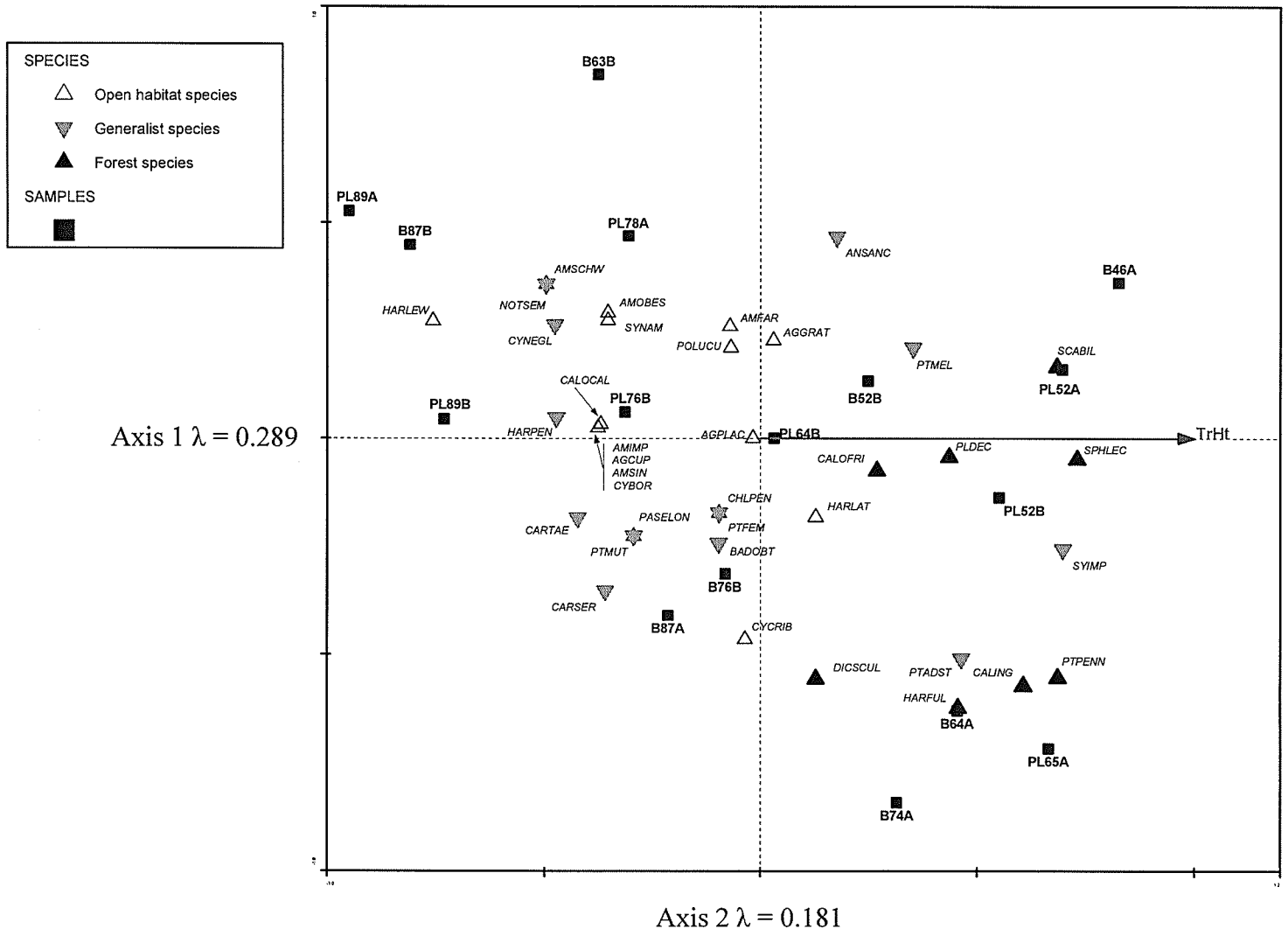
Figure 3.3.29 Redundancy Analysis ordination diagram of 2003 carabid beetle species (Δ) and sites (■) constrained by environment variables. Species codes: AGCUP = *Agonum cupreum*, AGGRAT = *Agonum gratiosum*, AGPLAC = *Agonum placidum*, AGRET = *Agonum retractum*, AMFAR = *Amara farcta*, AMIMP = *Amara impuncticollis*, AMOBES = *Amara obesa*, AMSCHW = *Amara schwarzi*, AMSIN = *Amara sinuosa*, ANSANC = *Anisodactylus sanctaecrucis*, BADOBT = *Badister obtusus*, CALING = *Calathus ingratus*, CALOCAL = *Calosoma calidum*, CALOFRI = *Calosoma frigidum*, CARSER = *Carabus serratus*, CARTAE = *Carabus taedatus agassii*, CHLPEN = *Chlaenius pensylvanicus pensylvanicus*, CYBOR = *Cymindis borealis*, CYCRIB = *Cymindis cribicollis*, CYNEGL = *Cymindis neglecta*, DICSCUL = *Dicaelus sculptilis upiodes*, HARFUL = *Harpalus fulvilabris*, HARLAT = *Harpalus laticeps*, HARLEW = *Harpalus lewisi*, HARPEN = *Harpalus pensylvanicus*, NOTSEM = *Notiophilus semistriatus*, PASELON = *Pasimachus elongatus*, PLDEC = *Platynus decentis*, POLUCU = *Poecilus lucublandus lucublandus,* PTADST = *Pterostichus adstrictus*, PTFEM = *Pterostichus femoralis*, PTMEL = *Pterostichus melanarius*, PTMUT = *Pterostichus mutus*, PTPENN = *Pterostichus pensylvanicus*, SCABIL = *Scaphinotus bilobus*, SPHLEC = *Sphaeroderus stenostomus lecontei*, SYAMER = *Syntomus americanus*, SYIMP = *Synuchus impunctatus*.



Axis 1 λ = 0.344

Axis 2 λ = 0.133

Figure 3.3.30 Redundancy Analysis ordination diagram of 2003 carabid beetle species (Δ) and sites (■) constrained by environment variables. *Agonum retractum* removed from analysis. Species codes: Species codes: AGCUP = *Agonum cupreum*, AGGRAT = *Agonum gratiosum*, AGPLAC = *Agonum placidum*, AMFAR = *Amara farcta*, AMIMP = *Amara impuncticollis*, AMOBES = *Amara obesa*, AMSCHW = *Amara schwarzi*, AMSIN = *Amara sinuosa*, ANSANC = *Anisodactylus sanctaecrucis*, BADOBT = *Badister obtusus*, CALING = *Calathus ingratus*, CALOCAL = *Calosoma calidum*, CALOFRI = *Calosoma frigidum*, CARSER = *Carabus serratus*, CARTAE = *Carabus taedatus agassii*, CHLPEN = *Chlaenius pensylvanicus pensylvanicus*, CYBOR = *Cymindis borealis*, CYCRIB = *Cymindis cribicollis*, CYNEGL = *Cymindis neglecta*, DICSCUL = *Dicaelus sculptilis upiodes*, HARFUL = *Harpalus fulvilabris*, HARLAT = *Harpalus laticeps*, HARLEW = *Harpalus lewisi*, HARPEN = *Harpalus pensylvanicus*, NOTSEM = *Notiophilus semistriatus*, PASELON = *Pasimachus elongatus*, PLDEC = *Platynus decentis*, POLUCU = *Poecilus lucublandus lucublandus,* PTADST = *Pterostichus adstrictus*, PTFEM = *Pterostichus femoralis*, PTMEL = *Pterostichus melanarius*, PTMUT = *Pterostichus mutus*, PTPENN = *Pterostichus pensylvanicus*, SCABIL = *Scaphinotus bilobus*, SPHLEC = *Sphaeroderus stenostomus lecontei*, SYAMER = *Syntomus americanus*, SYIMP = *Synuchus impunctatus*.


SPECIES
Open habitat species
Generalist species
Forest species
SAMPLES
Axis 1 λ = 0.289
Axis 2 λ = 0.181
TrHt
B63B
PL89A
B87B
PL78A
ANSANC
B46A
AMSCHW
NOTSEM
HARLEW
AMOBES
SYNAM
CYNEGL
AMFAR
AGGRAT
POLUCU
PTMEL
SCABIL
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B52B
CALOCAL
PL89B
PL76B
HARPEN
AGPLAC
PL64B
PLDEC
SPHLEC
CALOFRI
AMIMP
AGCUP
AMSIN
CYBOR
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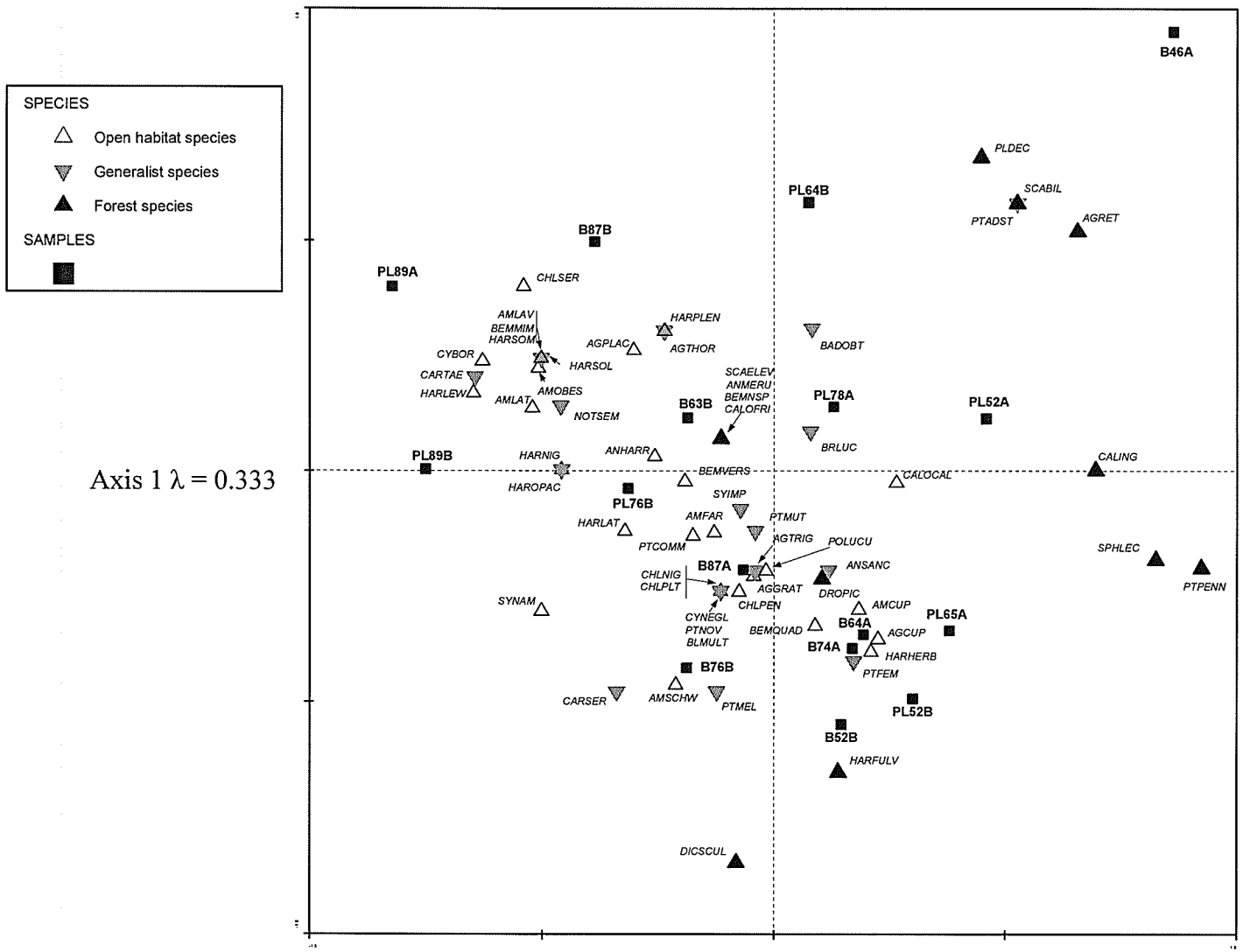
PL65A
B74A

Figure 3.3.31 Principal Components Analysis ordination diagram of 2004 carabid beetle species (Δ) and sites (■). Species codes: AGCUP = *Agonum cupreum*, AGGRAT = *Agonum gratiosum*, AGPLAC = *Agonum placidum*, AGRET = *Agonum retractum*, AGTHOR = *Agonum thoreyi*, AGTRIG = *Agonum trigeminum*, AMCUP = *Amara* cupreolata, AMFAR = *Amara farcta*, AMERLAV = *Amara laevipennis*, AMLAT = *Amara* latior, AMOBES = *Amara obesa*, AMSCHW = *Amara schwarzi*, ANHARR = *Anisodactylus harrisii*, ANMERU = *Anisodactylus merula,* ANSANC = *Anisodactylus sanctaecrucis*, BADOBT = *Badister obtusus*, BEMMIM = *Bembidion mimus*, BEMNSP = *Bembidion* new species, BEMQUAD = *Bembidion quadrimaculatum*, BEMVERS = *Bembidion versicolor*, BLMULT = *Blethisa multipunctata aurata*, BRLUC = *Bradycellus lugubris*, CALING = *Calathus ingratus*, CALOCAL = *Calosoma calidum*, CALOFRI = *Calosoma frigidum*, CARSER = *Carabus serratus*, CARTAE = *Carabus taedatus agassii*, CHLNIG = *Chlaenius niger*, CHLPEN = *Chlaenius pensylvanicus pensylvanicus,* CHLPLT = *Chlaenius platyderus*, CHLSER = *Chlaenius sericeus sericeus*, CYBOR = *Cymindis borealis*, CYNEGL = *Cymindis neglecta*, DICSCUL = *Dicaelus sculptilis upiodes*, DROPIC = *Dromius piceus*, HARFUL = *Harpalus fulvilabris*, HARHERB = *Harpalus herbivagus*, HARLAT = *Harpalus laticeps*, HARLEW = *Harpalus lewisi*, HARNIG = *Harpalus nigritarsus*, HAROPAC = *Harpalus opacipennis*, HARPLEN = *Harpalus plenalis*, HARSOL = *Harpalus solitaris,* HARSOM = *Harpalus somnulentus*, NOTSEM = *Notiophilus semistriatus*, PLDEC = *Platynus decentis*, POLUCU = *Poecilus lucublandus lucublandis,* PTADST = *Pterostichus adstrictus*, PTCOMM = *Pterostichus commutabilis*, PTFEM = *Pterostichus femoralis*, PTMEL = *Pterostichus melanarius*, PTMUT = *Pterostichus mutus*, PTNOV = *Pterostichus novus*, PTPENN = *Pterostichus pensylvanicus*, SCABIL =*Scaphinotus bilobus*, SCAELEV = *Scaphinotus elevatus coloradensis*, SPHLEC = *Sphaeroderus stenostomus lecontei*, SYAMER = *Syntomus americanus*, SYIMP = *Synuchus impunctatus*.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Forest species
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Axis 2 λ = 0.154
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SCABIL
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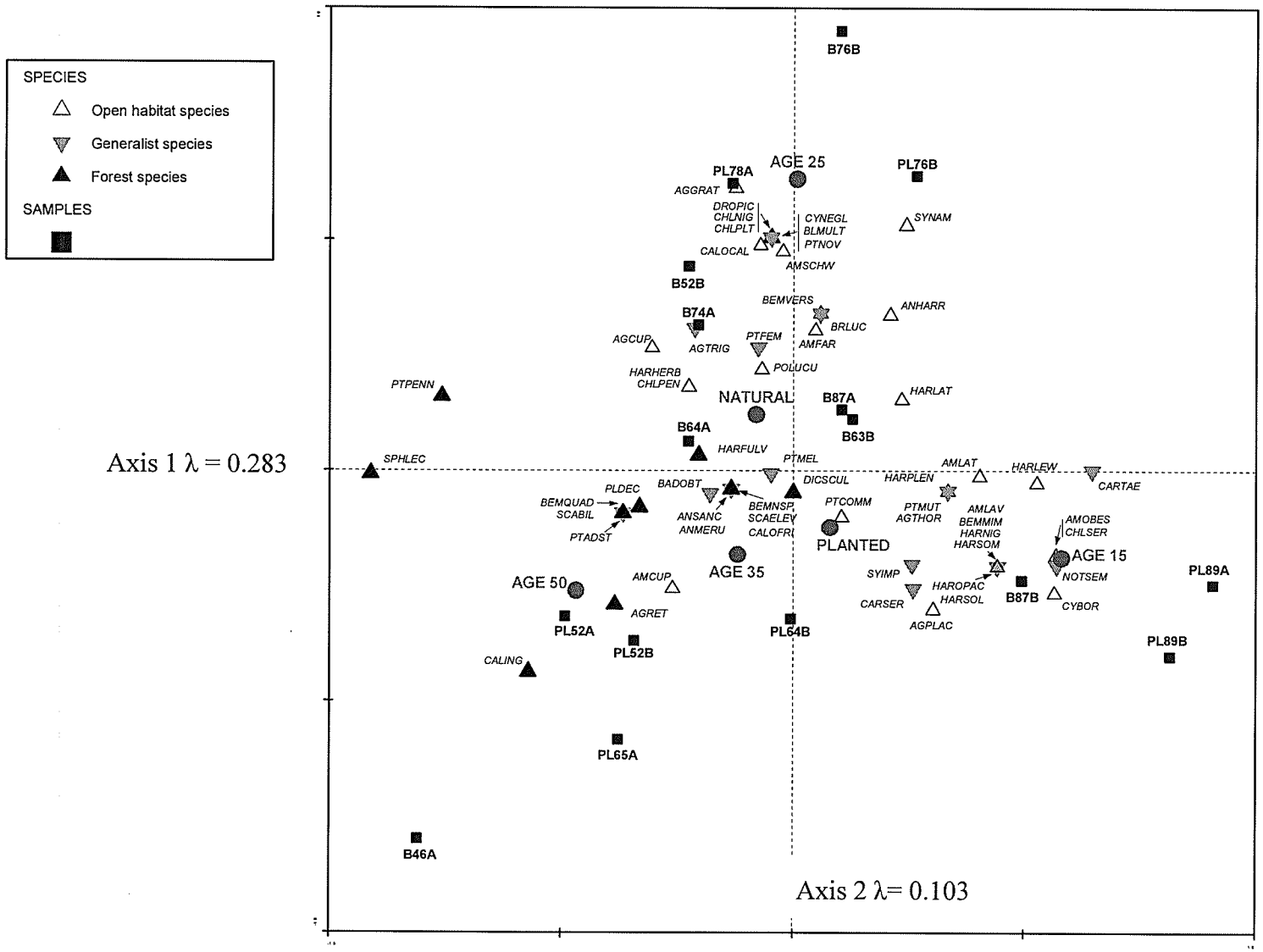
AGRET
B87B
PL89A
CHLSER
AMLAV
BEMMIM
HARSOM
HARPLEN
AGPLAC
AGTHOR
BADOBT
CYBOR
HARSOL
CARTAE
HARLEW
AMOBES
AMLAT
NOTSEM
SCAELEV
ANMERU
BEMNSP
CALOFRI
B63B
PL78A
PL52A
BRLUC
PL89B
HARNIG
ANHARR
BEMVERS
CALOCAL
CALING
HAROPAC
PL76B
SYIMP
AMFAR
PTMUT
HARLAT
AGTRIG
POLUCU
PTCOMM
SPHLEC
B87A
ANSANC
CHLNIG
CHLPLT
AGGRAT
DROPIC
PTPENN
SYNAM
CHLPEN
AMCUP
CYNEGL
PTNOV
BLMULT
BEMQUAD
B64A
PL65A
AGCUP
B74A
HARHERB
PTFEM
B76B
CARSER
AMSCHW
PTMEL
PL52B
B52B
HARFULV
DICSCUL

Figure 3.3.32 Redundancy Analysis ordination diagram of 2004 carabid beetle species (Δ) and sites (■) constrained by forest age and regeneration type. Species codes: AGCUP = *Agonum cupreum*, AGGRAT = *Agonum gratiosum*, AGPLAC = *Agonum placidum*, AGRET = *Agonum retractum*, AGTHOR = *Agonum thoreyi*, AGTRIG = *Agonum trigeminum*, AMCUP = *Amara* cupreolata, AMFAR = *Amara farcta*, AMERLAV = *Amara laevipennis*, AMLAT = *Amara* latior, AMOBES = *Amara obesa*, AMSCHW = *Amara schwarzi*, ANHARR = *Anisodactylus harrisii*, ANMERU = *Anisodactylus merula,* ANSANC = *Anisodactylus sanctaecrucis*, BADOBT = *Badister obtusus*, BEMMIM = *Bembidion mimus*, BEMNSP = *Bembidion* new species, BEMQUAD = *Bembidion quadrimaculatum*, BEMVERS = *Bembidion versicolor*, BLMULT = *Blethisa multipunctata aurata*, BRLUC = *Bradycellus lugubris*, CALING = *Calathus ingratus*, CALOCAL = *Calosoma calidum*, CALOFRI = *Calosoma frigidum*, CARSER = *Carabus serratus*, CARTAE = *Carabus taedatus agassii*, CHLNIG = *Chlaenius niger*, CHLPEN = *Chlaenius pensylvanicus pensylvanicus,* CHLPLT = *Chlaenius platyderus*, CHLSER = *Chlaenius sericeus sericeus*, CYBOR = *Cymindis borealis*, CYNEGL = *Cymindis neglecta*, DICSCUL = *Dicaelus sculptilis upiodes*, DROPIC = *Dromius piceus*, HARFUL = *Harpalus fulvilabris*, HARHERB = *Harpalus herbivagus*, HARLAT = *Harpalus laticeps*, HARLEW = *Harpalus lewisi*, HARNIG = *Harpalus nigritarsus*, HAROPAC = *Harpalus opacipennis*, HARPLEN = *Harpalus plenalis*, HARSOL = *Harpalus solitaris,* HARSOM = *Harpalus somnulentus*, NOTSEM = *Notiophilus semistriatus*, PLDEC = *Platynus decentis*, POLUCU = *Poecilus lucublandus lucublandis,* PTADST = *Pterostichus adstrictus*, PTCOMM = *Pterostichus commutabilis*, PTFEM = *Pterostichus femoralis*, PTMEL = *Pterostichus melanarius*, PTMUT = *Pterostichus mutus*, PTNOV = *Pterostichus novus*, PTPENN = *Pterostichus pensylvanicus*, SCABIL =*Scaphinotus bilobus*, SCAELEV = *Scaphinotus elevatus coloradensis*, SPHLEC = *Sphaeroderus stenostomus lecontei*, SYAMER = *Syntomus americanus*, SYIMP = *Synuchus impunctatus*.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Generalist species
Forest species
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Axis 2 λ= 0.103
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PL78A
AGE 25
PL76B
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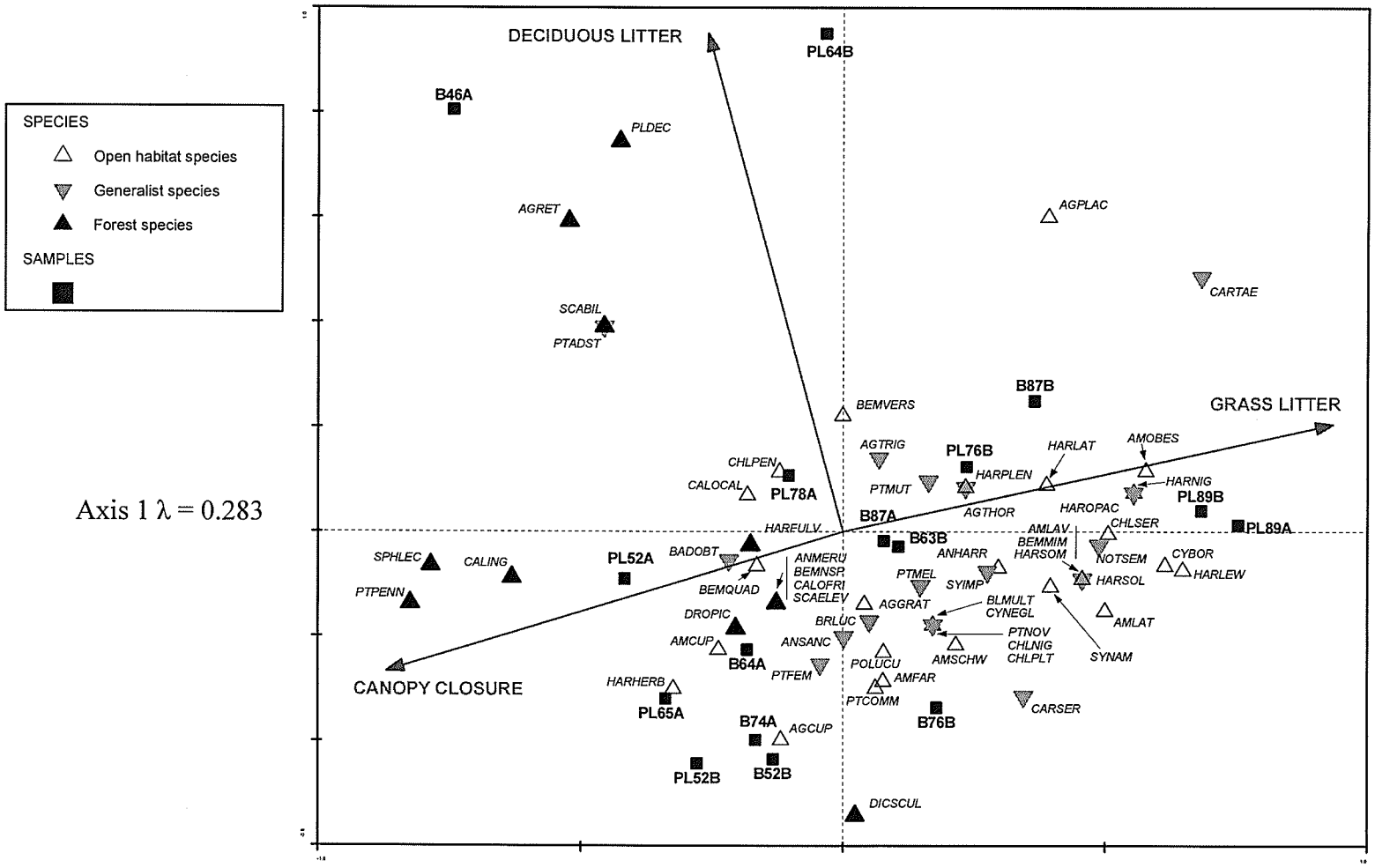
DROPIC
CHLNIG
CHLPLT
CYNEGL
BLMULT
PTNOV
SYNAM
CALOCAL
AMSCHW
B52B
BEMVERS
ANHARR
B74A
BRLUC
AGCUP
PTFEM
AMFAR
AGTRIG
POLUCU
HARHERB
CHLPEN
PTPENN
NATURAL
B87A
HARLAT
B64A
B63B
HARFULV
SPHLEC
PTMEL
AMLAT
HARLEW
CARTAE
HARPLEN
DICSCUL
PLDEC
BADOBT
BEMQUAD
SCABIL
PTCOMM
PTMUT
AGTHOR
AMLAV
BEMMIM
HARNIG
HARSOM
AMOBES
CHLSER
ANSANC
ANMERU
BEMNSP
SCAELEV
CALOFRI
PTADST
PLANTED
AGE 15
AGE 35
SYIMP
NOTSEM
PL89A
AGE 50
AMCUP
HAROPAC
HARSOL
B87B
CYBOR
CARSER
AGPLAC
AGRET
PL52A
PL64B
PL89B
PL52B
CALING
PL65A
B46A

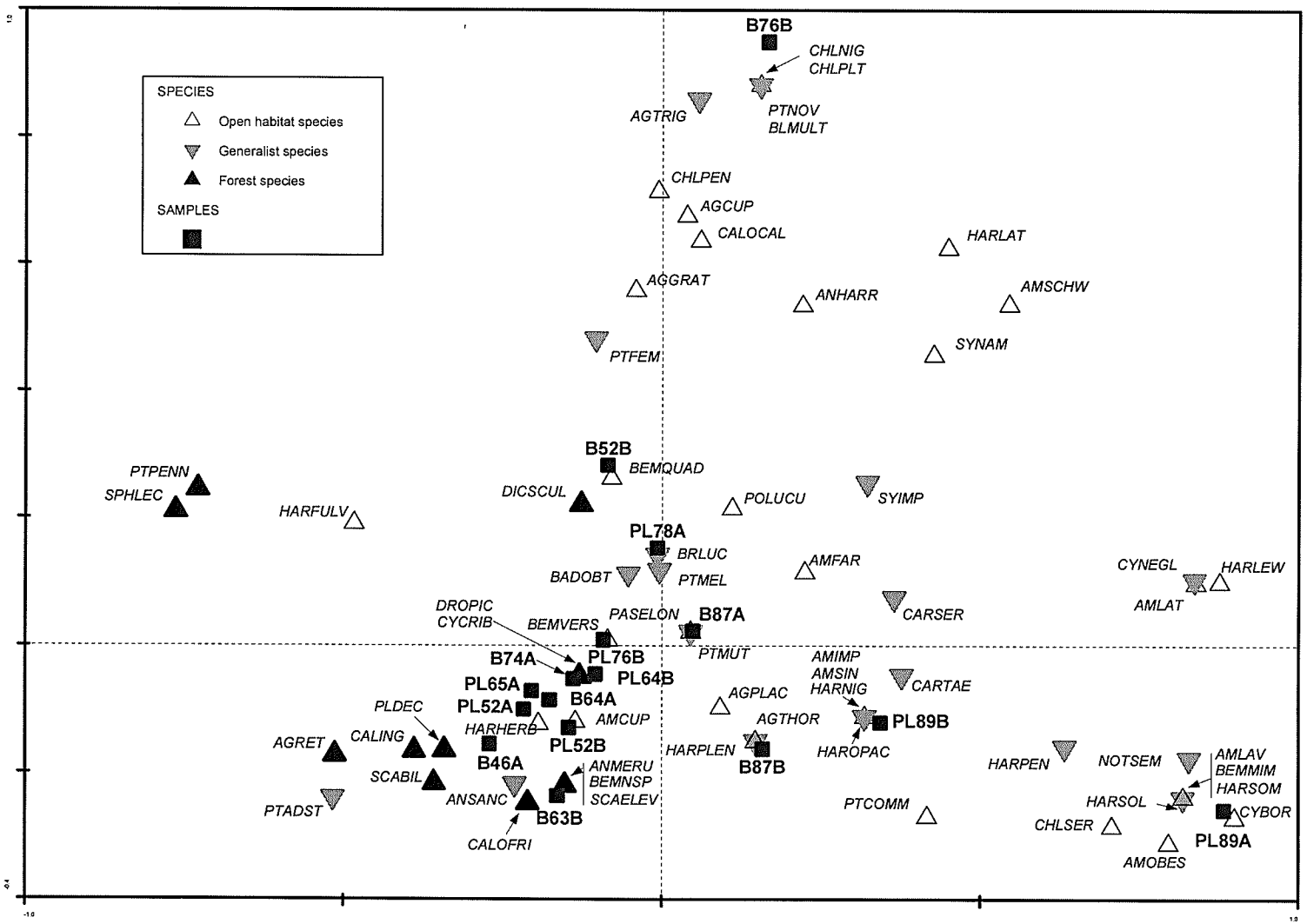
Figure 3.3.33 Redundancy Analysis ordination diagram of 2004 carabid beetle species (Δ) and sites (■) constrained by environment variables. Species codes: AGCUP = *Agonum cupreum*, AGGRAT = *Agonum gratiosum*, AGPLAC = *Agonum placidum*, AGRET = *Agonum retractum*, AGTHOR = *Agonum thoreyi*, AGTRIG = *Agonum trigeminum*, AMCUP = *Amara* cupreolata, AMFAR = *Amara farcta*, AMERLAV = *Amara laevipennis*, AMLAT = *Amara* latior, AMOBES = *Amara obesa*, AMSCHW = *Amara schwarzi*, ANHARR = *Anisodactylus harrisii*, ANMERU = *Anisodactylus merula,* ANSANC = *Anisodactylus sanctaecrucis*, BADOBT = *Badister obtusus*, BEMMIM = *Bembidion mimus*, BEMNSP = *Bembidion* new species, BEMQUAD = *Bembidion quadrimaculatum*, BEMVERS = *Bembidion versicolor*, BLMULT = *Blethisa multipunctata aurata*, BRLUC = *Bradycellus lugubris*, CALING = *Calathus ingratus*, CALOCAL = *Calosoma calidum*, CALOFRI = *Calosoma frigidum*, CARSER = *Carabus serratus*, CARTAE = *Carabus taedatus agassii*, CHLNIG = *Chlaenius niger*, CHLPEN = *Chlaenius pensylvanicus pensylvanicus,* CHLPLT = *Chlaenius platyderus*, CHLSER = *Chlaenius sericeus sericeus*, CYBOR = *Cymindis borealis*, CYNEGL = *Cymindis neglecta*, DICSCUL = *Dicaelus sculptilis upiodes*, DROPIC = *Dromius piceus*, HARFUL = *Harpalus fulvilabris*, HARHERB = *Harpalus herbivagus*, HARLAT = *Harpalus laticeps*, HARLEW = *Harpalus lewisi*, HARNIG = *Harpalus nigritarsus*, HAROPAC = *Harpalus opacipennis*, HARPLEN = *Harpalus plenalis*, HARSOL = *Harpalus solitaris,* HARSOM = *Harpalus somnulentus*, NOTSEM = *Notiophilus semistriatus*, PLDEC = *Platynus decentis*, POLUCU = *Poecilus lucublandus lucublandis,* PTADST = *Pterostichus adstrictus*, PTCOMM = *Pterostichus commutabilis*, PTFEM = *Pterostichus femoralis*, PTMEL = *Pterostichus melanarius*, PTMUT = *Pterostichus mutus*, PTNOV = *Pterostichus novus*, PTPENN = *Pterostichus pensylvanicus*, SCABIL =*Scaphinotus bilobus*, SCAELEV = *Scaphinotus elevatus coloradensis*, SPHLEC = *Sphaeroderus stenostomus lecontei*, SYAMER = *Syntomus americanus*, SYIMP = *Synuchus impunctatus*.



Axis 1 λ = 0.283

Axis 2 λ = 0.103

Figure 3.3.34 Principal Components Analysis ordination diagram of combined 2003 and 2004 carabid beetle species (Δ) and sites (■) with species standardized. Species codes: AGCUP = *Agonum cupreum*, AGGRAT = *Agonum gratiosum*, AGPLAC = *Agonum placidum*, AGRET = *Agonum retractum*, AGTHOR = *Agonum thoreyi*, AGTRIG = *Agonum trigeminum*, AMCUP = *Amara* cupreolata, AMFAR = *Amara farcta*, AMIMP = *Amara impuncticollis*, AMERLAV = *Amara laevipennis*, AMLAT = *Amara* latior, AMOBES = *Amara obesa*, AMSCHW = *Amara schwarzi*, AMSIN = *Amara sinuosa*, ANHARR = *Anisodactylus harrisii*, ANMERU = *Anisodactylus merula,* ANSANC = *Anisodactylus sanctaecrucis*, BADOBT = *Badister obtusus*, BEMMIM = *Bembidion mimus*, BEMNSP = *Bembidion* new species, BEMQUAD = *Bembidion quadrimaculatum*, BEMVERS = *Bembidion versicolor*, BLMULT = *Blethsia multipunctata aurata*, BRLUC = *Bradycellus lugubris*, CALING = *Calathus ingratus*, CALOCAL = *Calosoma calidum*, CALOFRI = *Calosoma frigidum*, CARSER = *Carabus serratus*, CARTAE = *Carabus taedatus agassii*, CHLNIG = *Chlaenius niger*, CHLPEN = *Chlaenius pensylvanicus pensylvanicus,* CHLPLT = *Chlaenius platyderus*, CHLSER = *Chlaenius sericeus sericeus*, CYBOR = *Cymindis borealis*, CYCRIB = *Cymindis cribicollis*, CYNEGL = *Cymindis neglecta*, DICSCUL = *Dicaelus sculptilis upiodes*, DROPIC = *Dromius piceus*, HARFUL = *Harpalus fulvilabris*, HARHERB = *Harpalus herbivagus*, HARLAT = *Harpalus laticeps*, HARLEW = *Harpalus lewisi*, HARNIG = *Harpalus nigritarsus*, HAROPAC = *Harpalus opacipennis*, HARPEN = *Harpalus pensylvanicus*, HARPLEN = *Harpalus plenalis*, HARSOL = *Harpalus solitaris,* HARSOM = *Harpalus somnulentus*, NOTSEM = *Notiophilus semistriatus*, PASELON = *Pasimachus elongatus*, PLDEC = *Platynus decentis*, POLUCU = *Poecilus lucublandus lucublandis,* PTADST = *Pterostichus adstrictus*, PTCOMM = *Pterostichus commutabilis*, PTFEM = *Pterostichus femoralis*, PTMEL = *Pterostichus melanarius*, PTMUT = *Pterostichus mutus*, PTNOV = *Pterostichus novus*, PTPENN = *Pterostichus pensylvanicus*, SCABIL =*Scaphinotus bilobus*, SCAELEV = *Scaphinotus elevatus coloradensis*, SPHLEC = *Sphaeroderus stenostomus lecontei*, SYAMER = *Syntomus americanus*, SYIMP = *Synuchus impunctatus*.


SPECIES
Open habitat species
Generalist species
Forest species
SAMPLES
B76B
CHLNIG
CHLPLT
AGTRIG
PTNOV
BLMULT
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AGCUP
CALOCAL
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AGGRAT
ANHARR
AMSCHW
PTFEM
SYNAM
B52B
BEMQUAD
PTPENN
SPHLEC
DICSCUL
POLUCU
SYIMP
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AMFAR
BADOBT
PTMEL
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AMLAT
DROPIC
CYCRIB
BEMVERS
PASELON
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CARSER
PTMUT
B74A
PL76B
PL64B
AMIMP
AMSIN
HARNIG
CARTAE
PL65A
PL52A
B64A
AGPLAC
PLDEC
AMCUP
AGTHOR
PL89B
HARHERB
AGRET
CALING
PL52B
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HAROPAC
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HARPEN
NOTSEM
AMLAV
BEMMIM
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BEMNSP
SCAELEV
SCABIL
HARSOL
CYBOR
ANSANC
PTCOMM
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B63B
AMOBES
CALOFRI

Figure 3.3.35 2003 and 2004 sites in species space; influence of year to year shifts in the carabid beetle assemblage

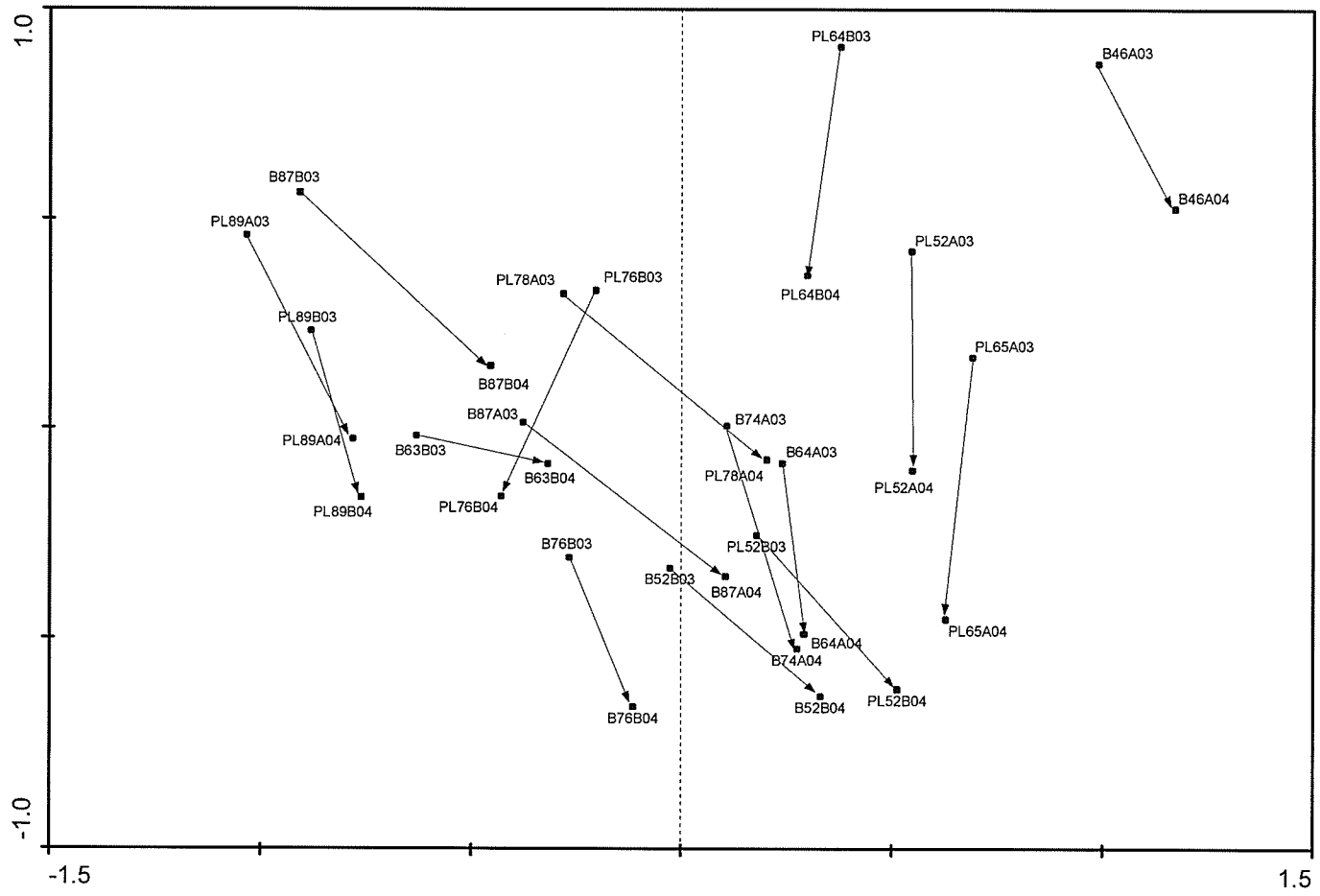


Figure 3.3.36 Standardized number of carabid beetles individuals caught in 1991 – 1994 (open symbols) and 2003 – 2004 (filled symbols) plotted against the actual site age at the time of sampling; patterns related to forest age and regeneration type.

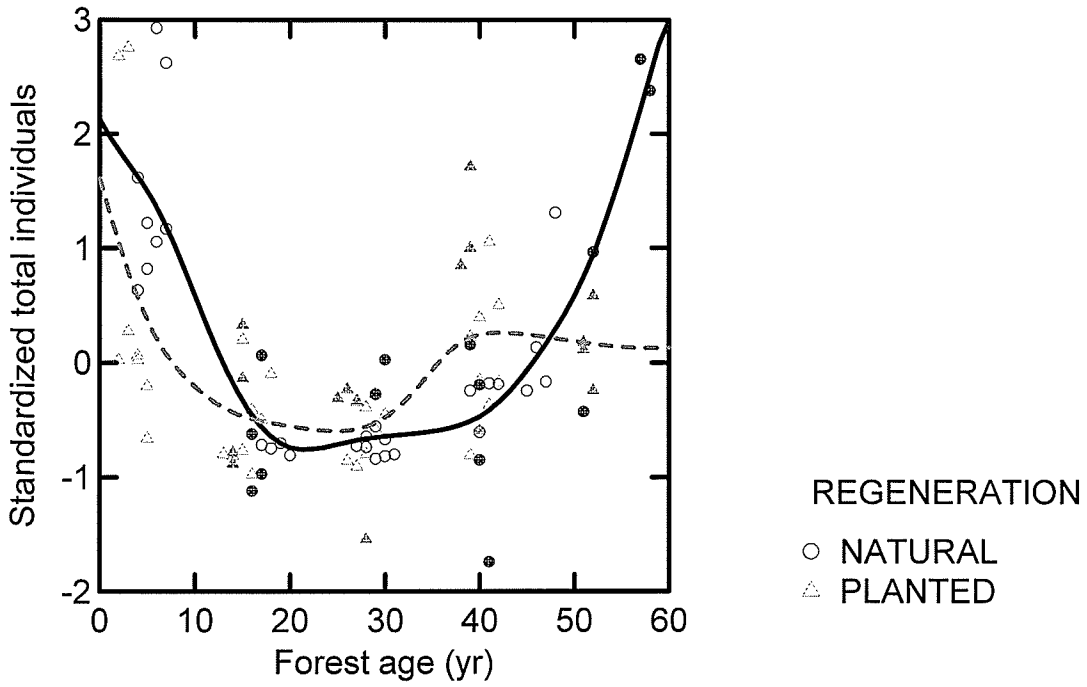


Figure 3.3.37 Standardized number of carabid beetle species caught in 1991 – 1994 (open symbols) and 2003 – 2004 (filled symbols) plotted against the actual site age at the time of sampling; patterns related to forest age and regeneration type.

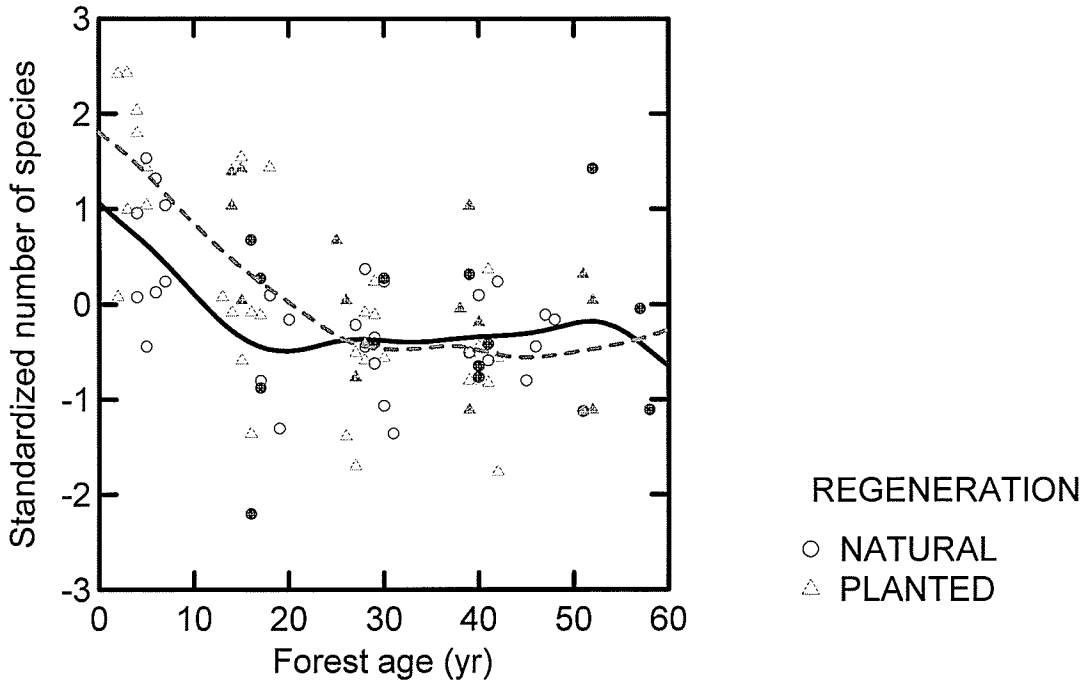


Figure 3.3.38 Standardized alpha diversity of carabid beetle assemblages of 1991 – 1994 (open symbols) and 2003 – 2004 (filled symbols) plotted against the actual site age at the time of sampling; patterns related to forest age and regeneration type.

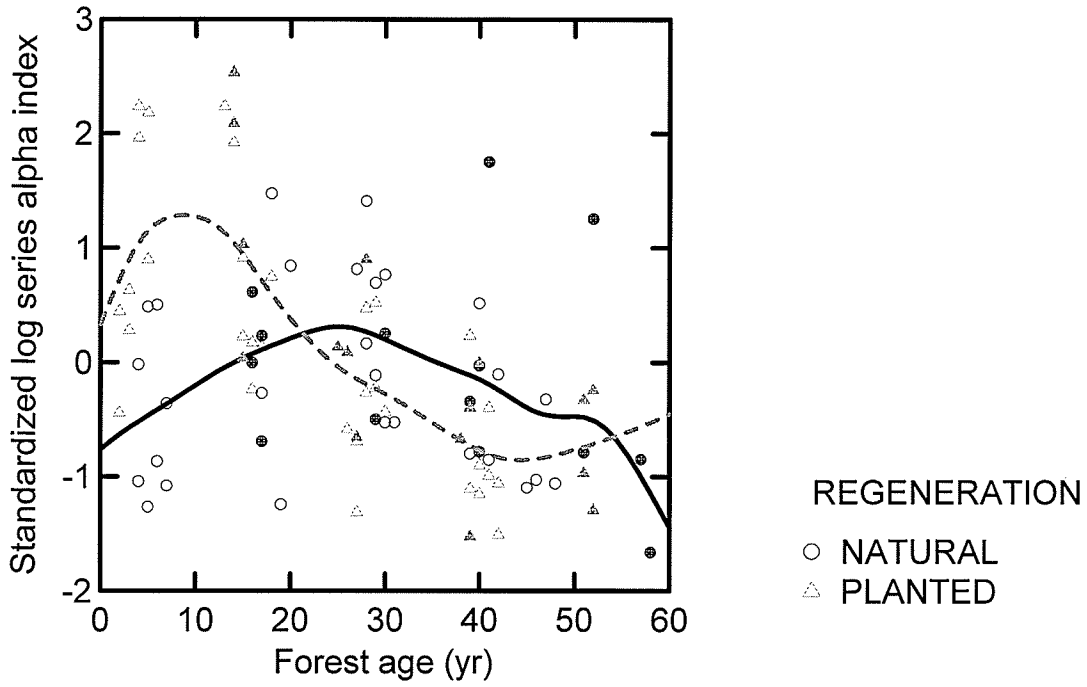


Figure 3.3.39 Standardized species dominance of the carabid beetle assemblages of 1991 – 1994 (open symbols) and 2003 – 2004 (filled symbols) plotted against the actual site age at the time of sampling; patterns related to forest age and regeneration type.

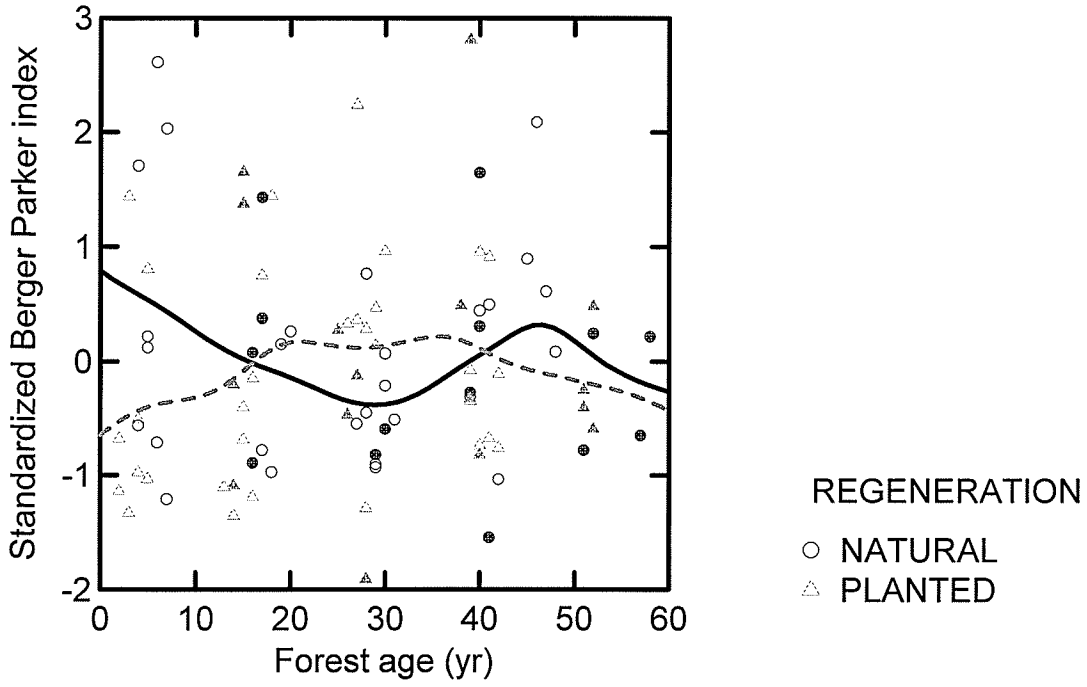


Figure 3.3.40 Standardized species evenness of the carabid beetle assemblages of 1991 – 1994 (open symbols) and 2003 – 2004 (filled symbols) plotted against the actual site age at the time of sampling; patterns related to forest age and regeneration type.

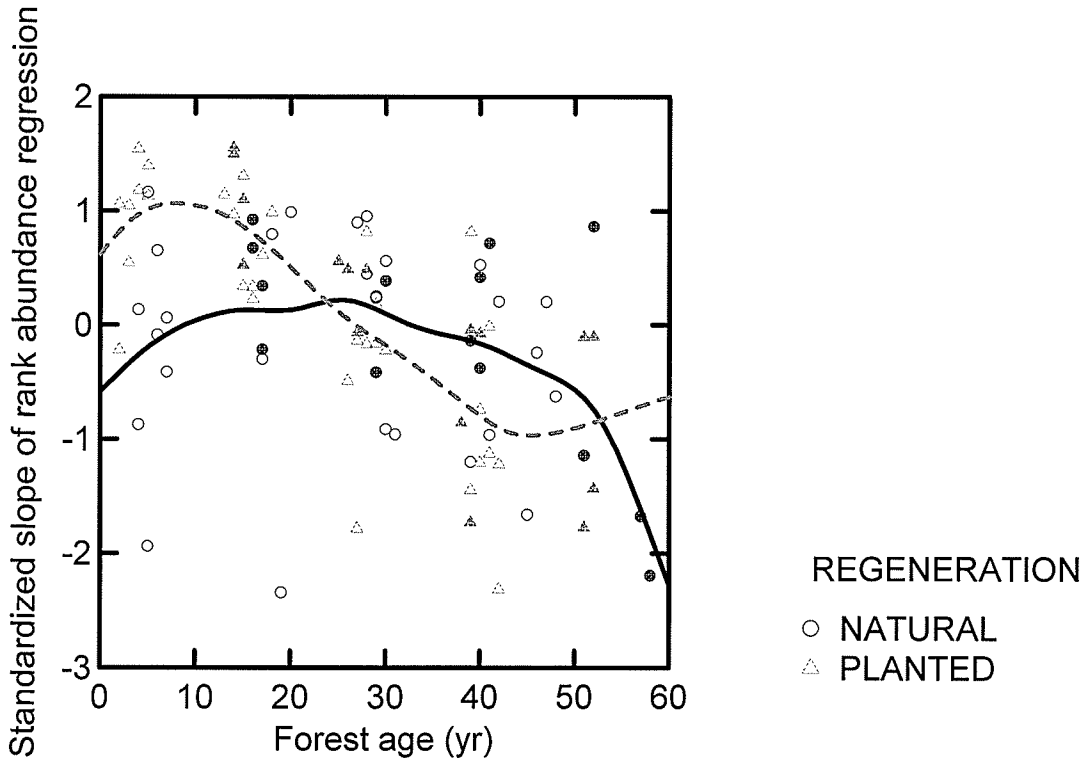


Figure 3.3.41 Standardized beta diversity (Jaccard's index) of the carabid beetle assemblages of 1991 – 1994 (open symbols) and 2003 – 2004 (filled symbols) plotted against age at the time of sampling; patterns related to forest age and regeneration type.

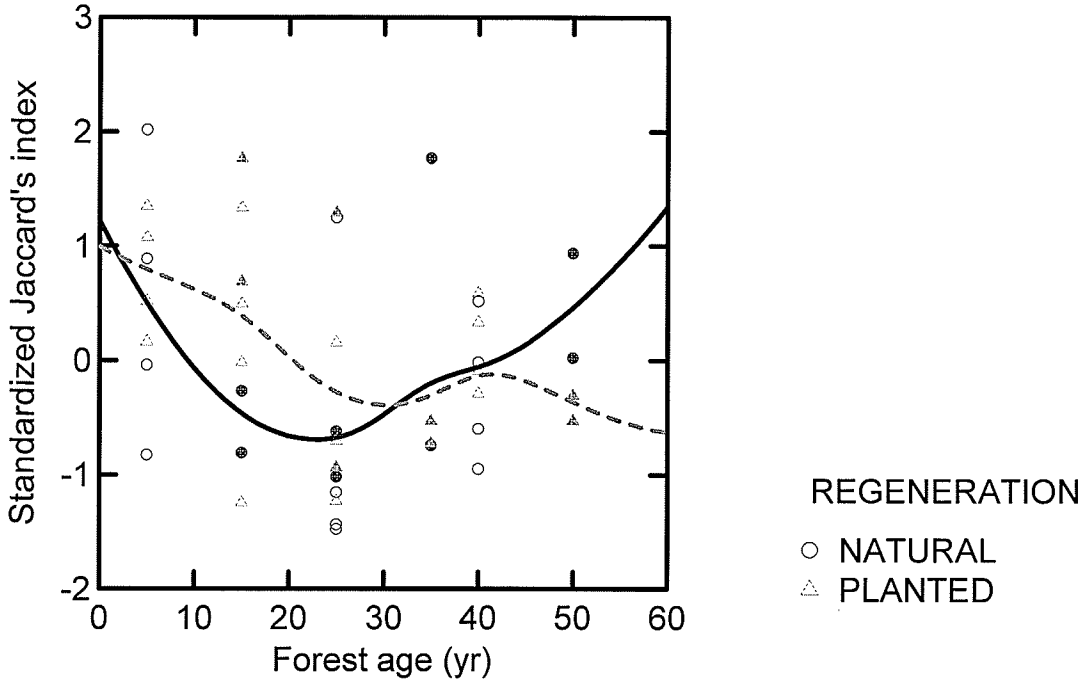


Figure 3.3.42 Standardized beta diversity (Kendall's τ) of the carabid beetle assemblages of 1991 – 1994 (open symbols) and 2003 – 2004 (filled symbols) plotted against age at the time of sampling; patterns related to forest age and regeneration type.

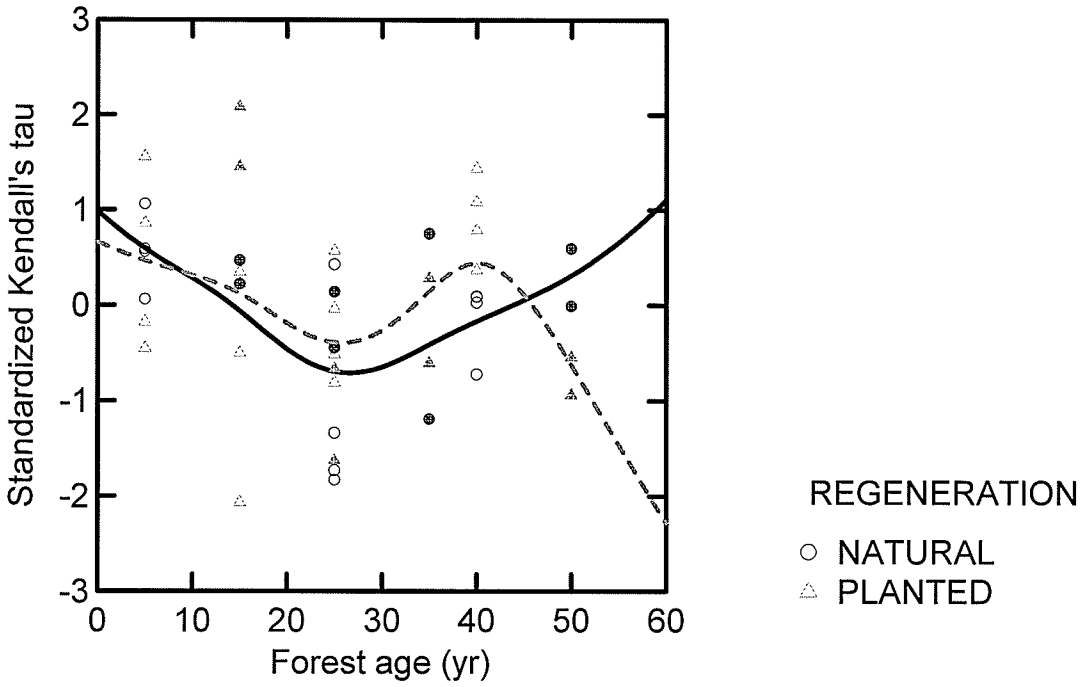


Figure 3.3.43 1991 and 2003 sites in 1991 species space; successional trajectories of sites

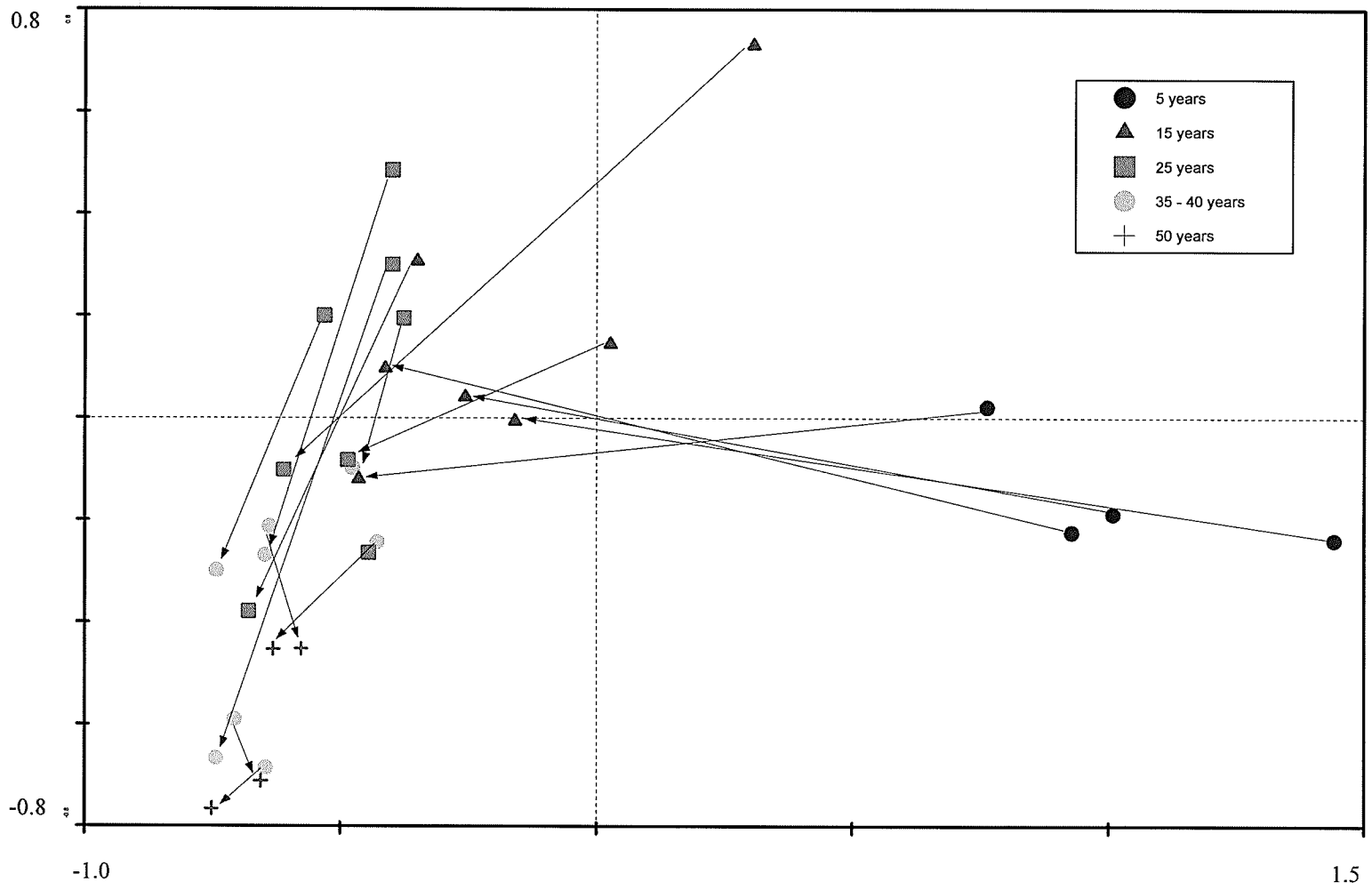


Figure 3.3.44 1992 and 2004 sites in 1992 species space; successional trajectories of sites

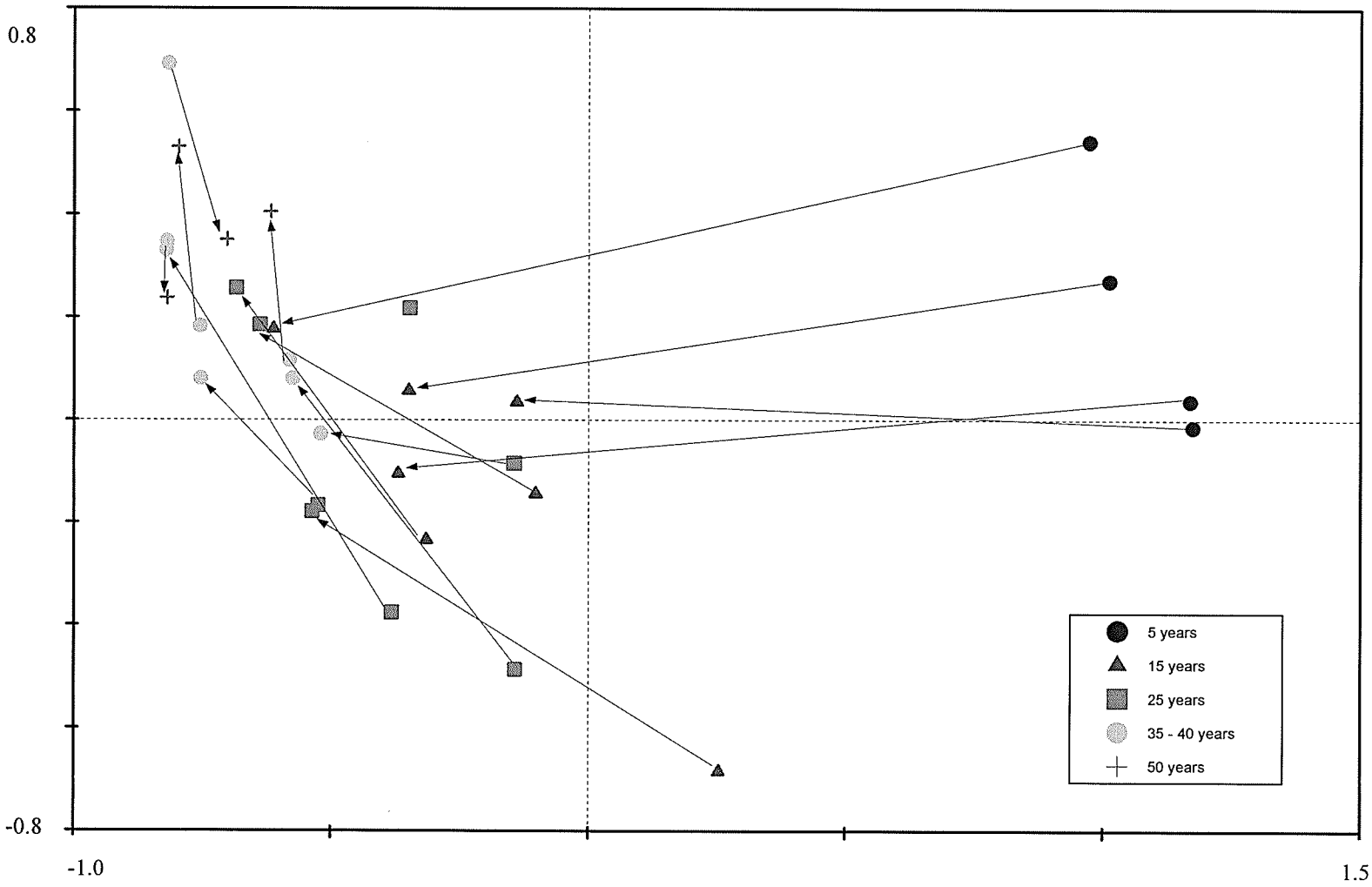


Figure 3.3.45 1991 and 2003 sites in 1991 species space: 15- and 25-year-old sites

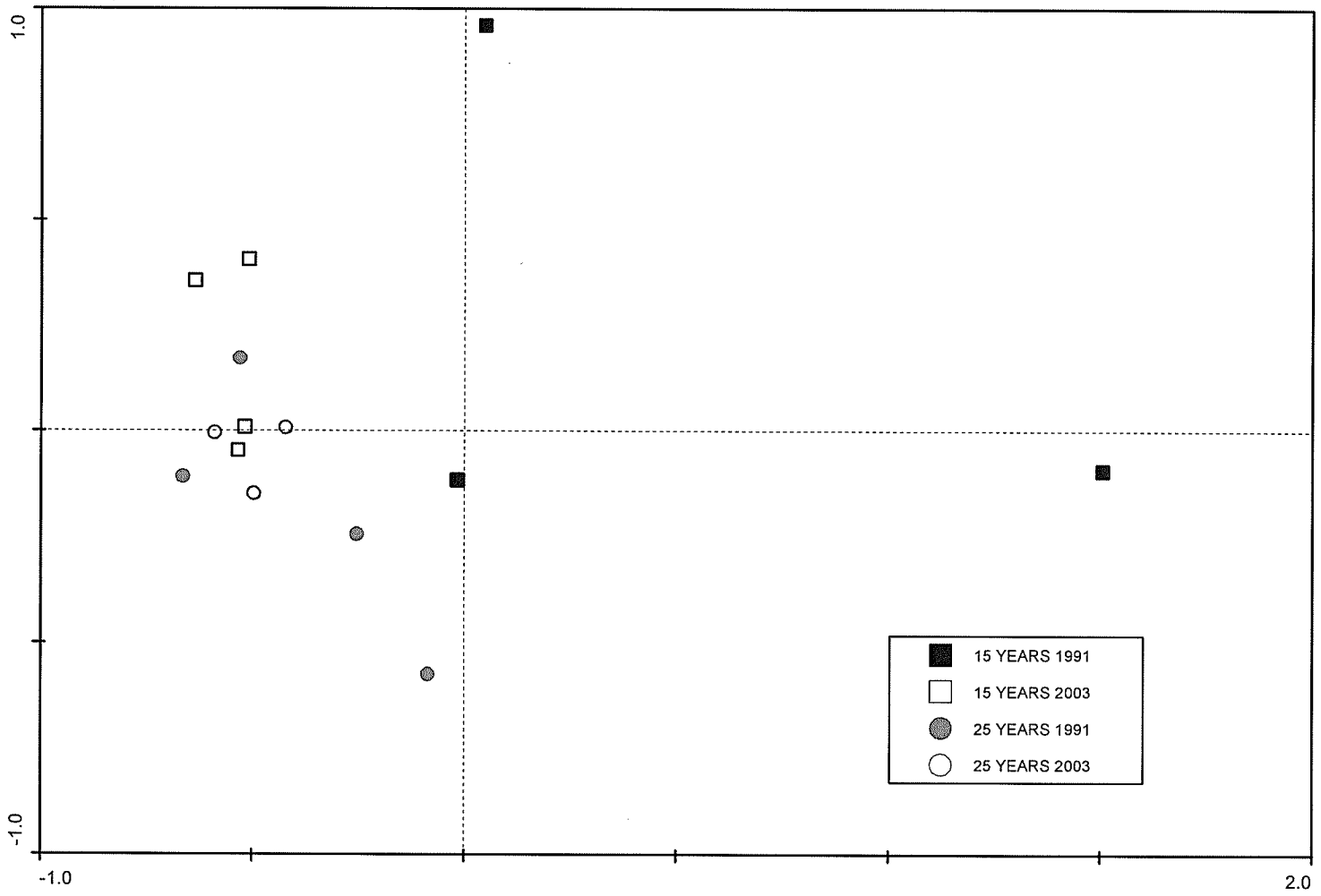
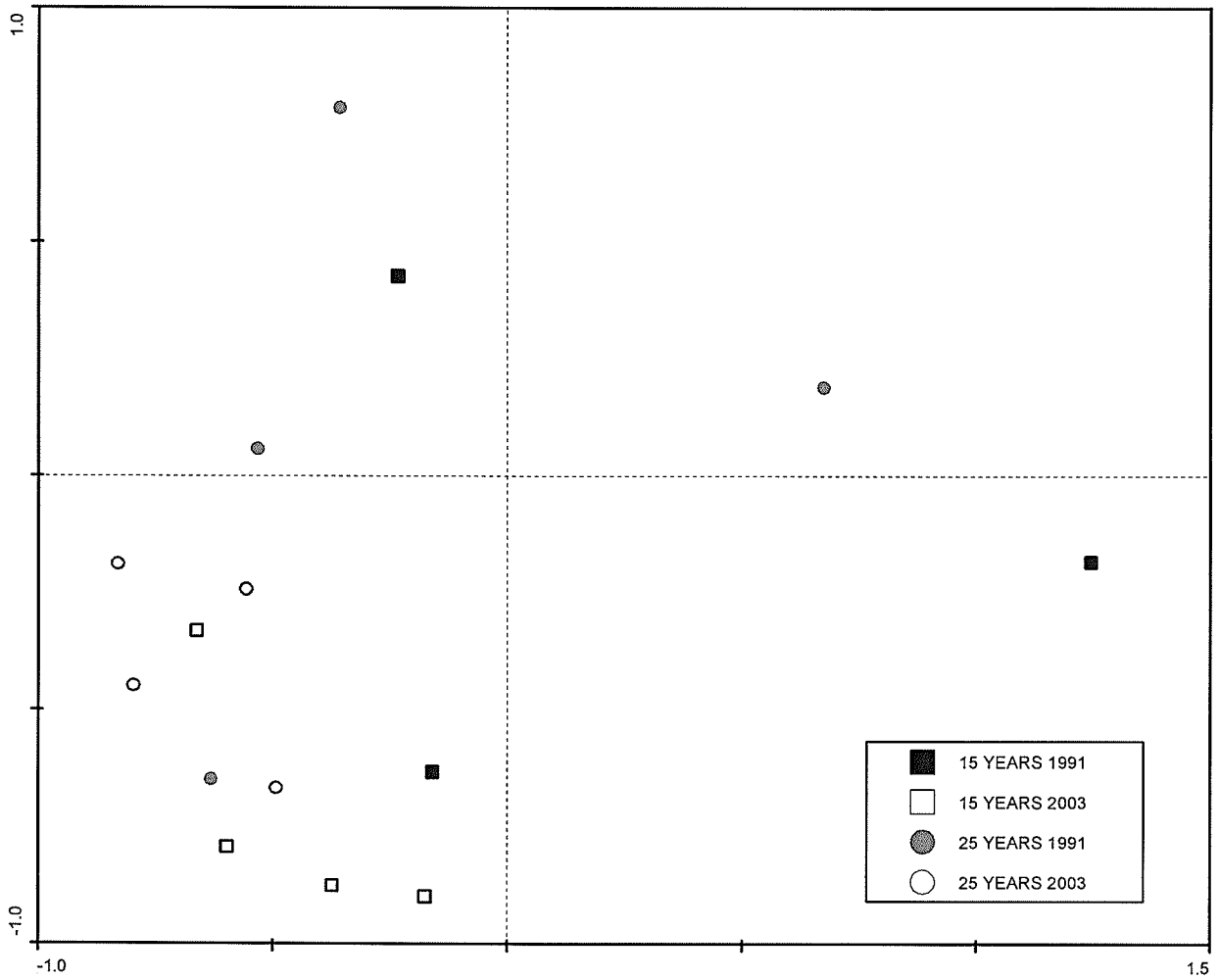


Figure 3.3.46 1992 and 2004 sites in 1992 species space: 15- and 25-year-old sites



4. General discussion

Many of the requirements of appropriate compositional indicators are quite general and are met by many groups. Certain key characteristics are required for a biological group to be a suitable indicator of boreal forest health. It must be sensitive to specific ecosystem characteristics and reflect important components of the boreal forest (Holloway and Stork 1991). It needs to be an ecologically significant group in the boreal forest. The potential indicator group must demonstrate a consistent response to environmental perturbations (Holloway and Stork 1991). Ideally it should also be capable of conveying information about other local taxa.

In this study, the ground level understory plant community, especially that of the early part of the season, responded to forest ecosystem changes associated with forest age and management. The community of ground vegetation clearly responded to environmental factors such as light attenuation and tree height, parameters associated with forest succession. Communities in young sites were distinct from those of older sites, further, the most mature forests tended to have distinct vegetation. This community also responded to differences occurring as a result of forest management and some of these effects were evident in older forests as well as younger forests. However, the response of ground vegetation to forest management shows different responses in different studies. Species richness or diversity is higher after natural disturbance than harvest in some studies, while the reverse is true in others (e.g. Abrams and Dickmann 1982; Johnston and Elliott 1996; Reich et al. 2001). Local factors such as pre fire conditions, fire season, seed supply, fire intensity, nutrient availability, microclimate and competition can all influence the subsequent plant community of the site (Ahlgren 1960).

However, so can regional conditions such as surface geology, precipitation and air temperature (Ahlgren 1960; Chipman and Johnson 2002). Rather than being contradictory findings, these results may be indicative of the strong influence of regional or site conditions on the plant community.

Based on their biology, butterflies are expected to respond to elements of stand structure and to floral diversity or quality, specific ecosystem characteristics that are important in the evaluation of forest management. However, because of the limitations of the butterfly data in this study, the results could not substantiate any response of the butterfly assemblage to these forest ecosystem characteristics. Elliott (1997) found that in jack pine stands in Manitoba, some butterfly species were found in association with their host plants while others were not. While Elliot (1997) suggests some correlation of particular butterfly species with their host plant, there is not much evidence to show that butterfly species diversity relates to plant species diversity on a stand level (Kremen 1992). Butterflies, however, have been found to correlate with aspects of stand structure in the boreal forest; Elliott (1997) noted light intensity to be the only significant factor associated with the butterfly species present.

Another limitation of the use of butterfly diversity indices in forest health evaluation is the lack of reliable response to perturbation manifested by this group. Although there were no significant findings in either year, trends in the data differed between 2003 and 2004. The lack of consistent response may be an artefact of low sample sizes; however, Elliott (1997) also found that diversity responses were inconsistent between study years.

The selection of butterflies as forest health indicators in boreal regions is not well-substantiated and there is a lack of documented studies using this test group in this area. With the exception of Elliott's (1997) work, the bulk of the research using butterflies has been in tropical or more temperate regions where butterflies may be a more significant component of the ecosystem.

The response of carabid beetles to specific structural elements of the forest is better-established than that of butterflies. In forest environments, sensitivity of carabid diversity indices and assemblage composition to certain ecosystem characteristics, such as canopy closure, tree density and understory cover, is well documented (Niemelä et al. 1993; Jukes et al. 2001; Koivula and Niemelä 2002; Koivula 2002), and these findings are corroborated by this study. The biological response of carabids to smaller scale structural aspects, such as understory or ground cover characteristics was also established in this study and this is supported by the findings of other authors (Koivula et al. 1999; Pearce et al. 2003).

Dispersal of many carabids is limited as many are brachypterous species (Thiele 1977). The limited mobility of carabids in comparison to groups such as Lepidoptera suggests their use in studies at a small, stand scale. As they may live out their whole life cycle within a few hectares, they are presumably more affected by changes in their habitat than are other groups.

Carabid diversity and assemblage composition changes associated with forest succession are highly consistent from study to study, including this one (e.g. Niemelä et al. 1994; Lafrenière 1994; Koivula et al. 2002). Monitoring forest management effects, however, requires a distinctly different degree of environmental sensitivity. While

changes in carabid assemblages were noted with environmental alteration due to forest management, no differences in diversity indices were found over the two years. There is a body of studies using this group to evaluate effects of other forest management effects in the boreal region; similar trends were found in these studies, carabid beetle assemblages differed between treatments, but diversity indices often did not (e.g. Beaudry et al. 1997; Koivula et al. 1999; Duchesne et al. 1999; Koivula 2002).

There is little evidence that any of the indicator groups selected reflected any other taxonomic or functional group. Although sites that were especially unique floristically also had unique carabid beetle assemblage, this alone is not enough to suggest that one group could serve as a proxy for another. Few diversity studies have evaluated how well the responses to environmental change of an indicator group represent those of other taxa; those that have done this evaluation have often found little similarity in response between groups (Muona and Rutanen 1994; Spence et al. 1997; Niemelä and Baur 1998; Jonsson and Jonsell 1999; Raino and Niemelä 2003). The lack of corresponding responses between taxa constitutes a serious problem in using quantitative diversity measures to infer the health of local biota beyond the context of the study group. Conclusions drawn from measures of certain taxa can only be relevant for that particular group in the region under study. Further research comparing the response of different taxa to the same perturbation is warranted.

The amount of coarse woody debris was a structural characteristic that clearly differed between planted and naturally regenerated sites. Of the biological indicators selected for study, none was selected to reflect this component. Since the quantity and quality of coarse woody debris may profoundly influence saproxylic flora and fauna and

subsequently affect the ecosystem services these biota provide, it would be warranted to select indicator species that are sensitive to this ecosystem component in future studies.

Diversity measures used to assess the influence of forest management on biological groups must be interpreted with caution. In this study and in most of the other forest health studies reviewed, there were definite, and sometimes profound, qualitative differences between treatment types, yet diversity values rarely reflected these differences. Clearly, diversity indices can generalize data to an extent that valuable information is often lost. Elliott's (1997) study provides an excellent illustration of this phenomenon. No difference in butterfly species diversity was noted between the two regeneration types, however in the younger forest stages there were considerable qualitative differences – natural stands supported assemblages made up primarily of food plant specialists while their planted counterparts were comprised of feeding generalists. Ordination analysis is more sensitive to assemblage differences and generally shows the influence of management interventions. Therefore, diversity indicators should be used in conjunction with a more qualitative evaluation of the indicator assemblage such as ordination analysis to provide a clearer picture of the effects of forest management.

Diversity indicators appear to be of more utility in describing community processes associated with forest succession in different regeneration types. Consistent, predictable changes in carabid beetle assemblages in natural and planted jack pine forests were described by diversity indicators. This was especially striking with the use of the log series alpha index. Alpha diversity tended to peak earlier in planted than naturally regenerating forests; this pattern was found in both the initial and the current study and well as in two studies combined. Diversity peaks in naturally regenerating forests did not

follow as clear a trend between studies, however the overall pattern of diversity change with succession was consistent.

Both diversity measures and ordination analysis are effective in modelling community changes associated with forest succession. This was apparent in both the understory plant assemblages and the carabid beetle assemblages. The use of the two strategies together provides the best description of the nature of the changes in these taxonomic groups.

The use of chronosequence study designs to evaluate the influences of forest succession on the carabid beetle assemblage was validated by this study. Activity and diversity measures based on the original chronosequence study predicted the community changes over the intervening 10 years. Ordination analyses also showed similar results. Carabid assemblages in forests of a particular age were similar regardless of the year they were sampled.

CONCLUSIONS

- The ground level vascular plant community responded to ecosystem alterations occurring as a result of forest succession and forest management.
- The use of butterflies as indicators in this study was hampered by small sample sizes; the use of this group would be enhanced by changes in sampling regime.

- The carabid community also responded to these differences, however, assemblage composition was more sensitive to these differences than diversity measures.
- The original chronosequence study design predicted the current study results, validating the use of chronosequence studies when examining carabid assemblages in forests.

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Appendix 1 Summary of environment measures by site

	Mean per site															
	B46A	B52B	B64A	B63B	B74A	B76B	B87A	B87B	PL52A	PL52B	PL65A	PL64B	PL78A	PL76B	PL89A	PL89B
Canopy closure and light																
Canopy closure (%)	81	69	70	74	71	67	53	29	78	81	83	53	70	73	41	15
Coefficient of varation	0.60	0.32	0.17	0.31	0.18	0.40	0.29	0.49	0.49	0.32	0.40	0.18	0.35	0.20	0.33	0.17
Light attenuation to 20cm (LUX)	-3589	-1343	-1791	-2255	-2269	-2597	-2078	-594	-2622	-2372	-3206	-2164	-2027	-2706	-1033	-940
Light attenuation to 2m (LUX)	-3383	-1626	-1258	-2280	-1685	-2493	-2160	-306	-2597	-2299	-2594	-1299	-1454	-2448	-478	-338
Light attentuation 2m to 20cm (LUX)	-207	282	-533	25	-584	-104	82	-288	-25	-73	-611	-865	-573	-258	-555	-602
Overstory																
Trees per ha (number)	5425	1425	2200	1413	5300	1266	9850	7663	1300	1525	2138	9075	1413	1288	1363	2313
Avg tree diameter (cm)	6.0	7.0	3.4	12.2	6.3	4.3	3.7	2.2	5.1	12.6	11.9	3.0	11.2	11.5	5.9	4.2
Avg jack pine diameter (cm)	16.2	12.4	9.5	12.2	6.3	9.4	3.2	2.7	16.9	12.6	11.9	13.7	11.2	11.5	5.9	4.2
Avg tree height (m)	18.1	14.0	12.8	13.3	9.8	8.8	5.5	4.0	17.1	14.9	11.5	10.1	9.2	8.8	4.5	4.1
Ground cover (% cover)																
Coarse woody debris	10	1	2	0	2	3	13	13	3	0	4	1	4	1	4	9
Fine woody debris	15	9	7	7	10	6	11	16	7	15	8	10	5	6	3	12
Coniferous litter	46	27	32	41	36	32	31	13	38	59	46	21	42	31	7	13
Deciduous litter	25	5	0	3	0	1	9	4	4	0	1	35	2	18	0	2
Grass litter	4	10	18	13	7	27	26	21	11	8	8	24	21	25	35	34
Bare ground	0	0	0	0	0	0	1	11	0	0	0	0	1	0	2	4
Rock	0	0	0	0	0	0	0	0	0	5	0	0	0	0	0	0
Moss	26	59	39	24	39	21	7	13	52	27	51	7	26	13	21	18
Lichen	0	3	24	1	15	4	6	3	0	12	0	0	29	0	15	5
Shrub	55	12	19	22	8	20	15	4	27	12	35	61	12	38	6	21
Herb	85	100	108	77	74	87	86	61	58	63	77	67	83	72	74	70

	B46A	B52B	B64A	B63B	B74A	B76B	B87A	B87B	PL52A	PL52B	PL65A	PL64B	PL78A	PL76B	PL89A	PL89B
Coarse woody debris (number pieces)																
Decay class 1	0	1	1	3	1	0	0	0	4	2	1	0	0	0	0	0
Decay class 2	2	19	1	3	1	1	0	0	2	2	1	0	1	1	0	0
Decay class 3	12	5	3	0	0	2	1	6	0	1	1	1	0	1	0	2
Decay class 4	26	1	6	0	1	1	71	56	5	0	0	0	1	2	7	26
Decay class 5	11	4	0	0	3	6	42	38	4	0	0	0	2	4	7	16
Total pieces	51	30	11	6	6	10	114	100	15	5	3	1	4	8	14	44
Snags																
Stems per ha (number)	688	225	975	550	1675	78	175	175	413	400	63	150	0	0	38	100
Avg. stem diamter (cm)	4.2	6.6	4.3	4.9	2.5	1.5	2.0	1.5	7.1	4.3	4.0	2.0	0.0	0.0	2.7	1.7

Appendix 2 Summary of tree stems per ha per site

Species	B46A	B52B	B64A	B63B	B74A	B76B	B87A	B87B	PL52A	PL52B	PL65A	PL64B	PL78A	PL76B	PL89A	PL89B
Alnus spp.	438	0	0	0	0	0	0	0	13	0	0	25	0	0	0	0
Amelanchier alnifolia (Nutt.) Nutt.	138	25	113	0	0	141	0	0	0	0	0	838	0	0	0	0
Betula papyrifera Marshall	13	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Corylus cornuta Marshall	2900	0	0	0	0	0	0	0	0	0	0	5975	0	0	0	0
Pinus banksiana Lamb.	1300	1400	2000	1413	5300	1094	9313	7425	1238	1525	2138	700	1413	1288	1363	2313
Pinus resinosa Aiton	0	0	0	0	0	31	0	0	0	0	0	0	0	0	0	0
Populus balsamifera L.	25	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Populus tremuloides Michx.	100	0	50	0	0	0	363	150	0	0	0	425	0	0	0	0
Prunus pensylvanica L. f.	125	0	38	0	0	0	0	0	25	0	0	25	0	0	0	0
Prunus virginiana L.	0	0	0	0	0	0	0	88	0	0	0	663	0	0	0	0
Quercus macrocarpa Michx	0	0	0	0	0	0	0	0	0	0	0	425	0	0	0	0
Salix spp.	388	0	0	0	0	0	0	0	25	0	0	0	0	0	0	0

Appendix 3 Spring vegetation sampled per site

	Mean % cover																Total cover
	B46A	B52B	B64A	B63B	B74A	B76B	B87A	B87B	PL52A	PL52B	PL65A	PL64B	PL78A	PL76B	PL89A	PL89B	
Tree seedlings																	
Picea spp.	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.10	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.10
Pinus banksiana Lamb.	0.00	0.00	0.15	0.50	0.10	0.00	0.35	0.70	0.00	0.37	0.10	0.00	0.45	0.00	0.00	0.15	2.87
Shrub species < 30 cm																	
Amelanchier alnifolia (Nutt.) Nutt.	0.74	0.00	0.00	0.00	0.00	0.00	0.00	0.10	0.00	0.00	0.00	0.00	0.00	0.10	0.00	0.00	0.94
Arctostaphylos uva-ursi (L.) Spreng.	0.00	13.25	13.75	18.55	19.65	15.45	0.50	15.60	3.75	10.53	1.65	0.50	10.75	3.85	18.00	10.80	156.58
Corylus cornuta Marshall	0.26	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.26
Hudsonia tomentosa Nutt.	0.00	0.00	0.00	0.00	0.00	0.00	1.00	4.50	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	5.50
Prunus pumila L.	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.20	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.20
Prunus spp.	0.11	0.00	0.00	0.45	0.00	0.10	0.05	0.10	0.10	0.26	0.00	0.00	0.10	0.00	1.05	0.00	2.32
Prunus virginiana L.	0.00	0.00	0.00	0.45	0.00	0.10	0.15	0.10	0.00	0.00	0.00	0.00	0.25	0.00	1.05	0.00	2.10
Rosa acicularis Lindl.	1.47	0.40	0.00	0.00	0.15	0.45	0.10	0.10	0.00	0.68	0.15	0.10	0.05	0.00	0.00	1.20	4.86
Rubus idaeus L.	2.84	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.10	0.35	0.10	0.00	0.00	0.00	3.39
Salix spp.	0.00	0.00	0.00	0.00	0.00	0.00	0.15	0.00	0.00	0.00	0.00	0.15	0.00	0.00	0.00	0.00	0.30
Symphoricarpos albus (L.) S.F. Blake	0.00	0.80	0.25	0.75	0.25	2.80	0.00	0.00	0.25	0.00	2.85	7.25	0.00	4.70	0.00	0.50	20.40
Symphoricarpos occidentalis Hook.	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.15	0.00	0.15
Vaccinium angustifolium Aiton	4.74	9.45	13.35	6.90	17.60	32.85	3.25	8.30	5.03	11.89	5.25	1.50	19.00	4.85	7.75	9.83	161.53
Herbaceous vegetation																	
Liliaceae																	
Maianthemum canadense Desf.	9.37	11.25	9.20	1.60	3.70	3.00	1.80	0.25	3.10	6.95	9.60	0.00	0.20	4.90	0.20	0.50	65.62
Smilacina stellata (L.) Desf.	0.00	0.25	0.35	0.00	0.60	0.00	0.00	0.20	0.00	0.21	0.00	0.00	0.00	0.00	2.70	2.10	6.41
Orhidaceae																	
Cypripedium pavriflorus Salisbury	0.00	0.00	0.10	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.10
Goodyera repens (L.) R. Br.	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.16	0.00	0.00	0.00	0.00	0.00	0.00	0.16

	Mean % cover																Total cover
	B46A	B52B	B64A	B63B	B74A	B76B	B87A	B87B	PL52A	PL52B	PL65A	PL64B	PL78A	PL76B	PL89A	PL89B	
Ranunculaceae																	
Anemone patens L.	0.00	1.00	0.70	1.15	0.75	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.75	0.20	4.55
Anemone quinquefolia L.	13.47	7.25	7.35	7.10	5.85	12.65	1.25	0.00	18.85	0.11	9.65	2.15	1.60	10.60	0.00	0.40	98.28
Anemone spp.	0.00	0.00	0.00	0.20	0.00	0.00	0.50	0.00	0.00	0.05	0.00	0.00	0.00	0.00	0.15	0.00	0.90
Thalictrum venulosum Trel.	0.00	0.55	0.50	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.35	0.00	1.35	0.00	0.00	2.75
Rosaceae																	
Fragaria virginiana Mill.	3.58	3.10	1.75	1.00	1.40	2.65	2.45	0.00	1.83	1.05	1.25	3.45	0.65	5.80	0.00	0.65	30.61
Potentilla tridentata Soland. in Ait.	0.00	0.00	0.00	0.70	0.00	0.00	0.00	0.25	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.95
Rubus pubescens Raf.	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Fabaceae																	
Fabaceae spp.	0.00	0.00	0.00	0.00	0.00	0.10	0.05	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.15
Lathyrus ochroleucus Hook.	0.68	0.15	0.65	1.25	0.20	1.75	2.35	0.30	0.68	0.00	1.70	1.20	0.00	0.60	0.00	0.00	11.51
Vicia americana Muhl. ex Willd	0.21	0.05	0.00	0.15	0.00	0.50	0.00	0.00	0.10	0.00	0.55	0.00	0.00	0.00	0.00	0.00	1.56
Violaceae																	
Viola adunca Sm.	0.00	0.15	0.10	1.35	0.30	0.40	0.65	0.00	0.15	0.32	0.00	0.00	0.00	0.00	1.25	1.05	5.72
Viola spp.	0.00	0.10	0.10	0.20	0.15	0.25	0.30	0.00	0.00	0.11	0.05	0.25	0.00	0.25	0.20	0.00	1.96
Onagraceae																	
Epilobium angustifolium L.	1.47	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.15	0.00	0.00	0.00	0.00	0.00	1.62
Lamiaceae																	
Monarda fistulosa L.	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.10	0.00	0.00	0.00	0.00	0.10
Pyrolaceae																	
Chimaphila umbellata (L.) W.P.C. Barton	0.00	1.55	0.00	0.00	0.15	0.00	0.15	0.00	0.00	0.00	0.00	0.00	0.10	0.00	0.00	0.00	1.95
Pyrola asarifolia Michx.	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.75	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.75
Pyrola secunda L.	0.79	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.20	0.00	0.00	0.00	0.99
Pyrola virens Schweigg.	2.11	13.90	10.45	0.15	0.00	0.00	2.50	3.70	17.90	8.16	0.25	0.00	0.00	0.00	0.00	1.15	60.26

	Mean % cover																Total cover
	B46A	B52B	B64A	B63B	B74A	B76B	B87A	B87B	PL52A	PL52B	PL65A	PL64B	PL78A	PL76B	PL89A	PL89B	
Apiaceae																	
Zizia aptera (A. Gray) Fernald	0.00	0.00	0.10	0.15	0.70	0.15	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	1.10
Asteraceae																	
? Solidago hispida Muhl. ex Willd.	0.00	0.00	0.00	0.00	0.00	0.00	0.75	2.65	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	3.40
? Solidago nemoralis Aiton	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.10	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.10
Antennaria neglecta Greene	0.00	1.00	0.00	8.05	4.70	0.50	8.55	1.75	0.00	9.34	4.55	0.85	0.00	0.00	0.00	0.00	39.29
Artemisia frigida Willd.	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.13	0.00	0.13
Artemisia spp.	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.40	0.00	0.00	0.00	0.00	0.40
Aster ciliolatus Lindl.	0.00	0.00	0.00	0.00	0.00	0.00	0.43	0.00	0.00	0.16	0.00	0.00	0.00	0.00	0.00	0.00	0.58
Asteraceae spp.	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.20	0.00	0.00	0.00	0.00	0.00	0.00	0.10	0.40	0.70
Solidago ?nemoralis Lindl.	0.00	0.00	0.50	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.50
Petasites palmatus (Ait.)	0.16	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.16
Taraxacum officinale Weber ex F.H. Wigg.	0.26	0.00	0.00	0.00	0.10	0.00	0.00	0.00	0.00	0.00	0.35	0.00	0.00	0.00	0.10	0.00	0.81
Poaceae																	
Oryzopsis asperifolia Michx.	3.16	2.45	7.85	0.00	0.00	3.90	0.00	0.00	10.25	0.00	4.90	3.65	2.40	2.75	0.00	0.00	41.31
Oryzopsis pungens (Torr.) Hitchc.	0.00	0.40	0.20	0.25	1.30	0.00	0.00	0.00	0.00	0.61	0.00	0.00	1.50	0.25	0.10	0.00	4.61
Unidentifiable grass - clumped	3.95	0.00	0.50	0.25	0.25	7.60	3.20	2.00	1.50	0.00	0.35	5.15	0.25	1.00	8.88	6.05	40.92
Unidentifiable grass - not clumped	1.37	1.20	0.40	5.00	0.45	1.10	5.30	3.45	1.50	0.68	3.83	6.70	1.35	3.50	1.40	1.65	38.88
Cyperaceae																	
Carex sp.	0.00	0.00	0.15	0.10	0.10	0.10	0.15	0.00	0.00	0.05	0.00	0.15	0.00	0.05	0.00	0.00	0.85
Other angiosperm families																	
Cornus canadensis L.	3.84	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	3.84
Galium boreale L.	1.05	0.35	1.05	2.00	0.65	1.85	0.20	0.00	0.35	0.00	2.40	1.10	1.40	2.55	0.83	0.00	15.78
Galium triflorum Michx.	0.11	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.11
Heuchera richardsonii R. Br.	0.26	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.10	0.00	0.00	0.00	0.00	0.00	0.36
Linnaea borealis L.	0.53	0.00	0.00	0.00	0.00	0.00	1.00	0.00	0.00	0.00	2.80	0.00	0.00	0.00	0.00	0.00	4.33
Lithospermum canescens (Michx.) Lehm.	0.00	0.45	0.40	0.00	0.10	0.10	0.10	0.00	0.00	0.00	0.60	0.00	0.00	0.10	0.65	0.10	2.60

	Mean % cover																Total cover
	B46A	B52B	B64A	B63B	B74A	B76B	B87A	B87B	PL52A	PL52B	PL65A	PL64B	PL78A	PL76B	PL89A	PL89B	
Trientalis borealis Raf.	0.26	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.26
Unidentifiable herbs	0.11	0.00	0.10	0.00	1.10	0.20	0.65	0.20	1.20	0.63	1.20	2.20	1.25	2.65	0.00	0.15	11.64
Polypodiaceae																	
Pteridium aquilinum (L.) Kuhn	0.84	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.84
Equisetaceae																	
Equisetum hyemale L.	0.05	0.50	0.40	0.00	0.00	0.00	0.20	0.00	0.00	0.05	0.00	0.00	4.15	0.00	0.00	0.00	5.36
Equisetum scirpoides Michx	1.32	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	1.32
Total cover	59.11	69.55	70.40	58.25	60.30	88.55	38.08	44.85	67.28	52.37	54.38	37.55	45.75	49.85	45.43	36.88	878.55

Appendix 4 Summer vegetation species sampled per site

	Mean % cover																
	B46A	B52B	B64A	B63B	B74A	B76B	B87A	B87B	PL52A	PL52B	PL65A	PL64B	PL78A	PL76B	PL89A	PL89B	Total cover
Tree seedlings																	
Abies balsamea (L.) Mill.	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.13	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.13
Pinus banksiana Lamb.	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.13	0.00	0.18	0.00	0.00	0.10	0.00	0.10	0.10	0.60
Populus tremuloides Michx.	0.00	0.00	0.00	0.00	0.00	0.00	0.20	0.00	0.00	0.00	0.00	0.00	0.00	0.25	0.00	0.85	1.30
Shrub species < 30cm																	
Amelanchier alnifolia (Nutt.) Nutt.	0.00	0.00	0.00	0.23	0.00	0.30	1.00	0.00	0.13	0.00	0.38	0.00	0.38	0.25	0.10	0.20	2.95
Apocynum androsaemifolium L.	0.25	0.00	1.00	0.20	0.00	0.78	0.00	0.00	0.00	0.00	0.00	0.00	0.80	1.68	1.40	0.73	6.83
Arctostaphylos uva-ursi (L.) Spreng.	0.00	6.83	11.65	18.58	14.88	11.78	1.85	11.95	0.90	8.55	0.20	3.58	10.00	2.25	21.55	11.05	135.58
Ceanothus herbaceous Raf	0.00	0.00	1.48	0.18	0.00	0.00	0.00	0.00	0.00	0.00	1.35	0.85	0.00	0.00	0.00	0.00	3.85
Corylus cornuta Marshall	0.25	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.35	0.00	0.00	0.00	0.00	0.60
Diervilla lonicera Mill.	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.50	0.00	0.00	0.00	0.50
Hudsonia tomentosa Nutt.	0.00	0.00	0.25	0.00	0.00	0.00	0.00	5.13	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	5.38
Rosa acicularis Lindl.	1.88	0.58	0.60	0.38	0.10	0.23	1.70	1.33	0.35	0.13	0.70	0.60	0.55	0.15	0.95	1.08	11.28
Rubus idaeus L.	1.50	0.00	0.00	0.00	0.00	0.00	0.50	0.00	0.00	0.50	0.75	0.00	0.43	0.00	0.00	0.00	3.68
Salix spp.	0.00	0.00	0.10	1.28	2.15	1.25	0.25	2.88	0.00	0.38	0.25	0.50	0.00	0.90	3.30	4.55	17.78
Spiraea alba Du Roi	1.25	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.30	0.00	1.55
Symphoricarpos albus (L.) S.F. Blake	0.60	2.85	0.00	1.33	0.40	2.33	0.00	0.00	0.00	0.00	0.85	6.60	0.00	5.78	0.70	0.00	21.43
Vaccinium angustifolium Aiton	1.75	9.80	9.28	4.30	10.13	27.35	4.10	7.80	0.05	12.55	13.50	1.95	18.75	1.75	8.50	15.18	146.73
Unidentifiable shrub	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	1.00	0.00	0.00	0.00	0.00	0.00	1.00
Herbaceous vegetation																	
Liliaceae																	
Maianthemum canadense Desf.	9.23	26.65	21.70	7.90	7.05	7.23	3.25	0.58	13.63	14.35	15.88	0.10	2.80	3.08	0.00	0.50	133.90
Smilacina stellata (L.) Desf.	0.00	0.60	1.58	0.00	0.00	0.00	0.00	0.05	0.00	1.45	0.00	0.00	0.00	0.00	0.30	0.10	4.08
Orchidaceae																	
Orchid 1	0.00	0.00	0.00	0.00	0.08	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.08

	Mean % cover																Total cover
	B46A	B52B	B64A	B63B	B74A	B76B	B87A	B87B	PL52A	PL52B	PL65A	PL64B	PL78A	PL76B	PL89A	PL89B	
Saxifragaceae																	
Mitella nuda L.	0.00	0.00	0.10	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.10
Ranunculaceae																	
? Anemone spp.	0.00	0.00	0.20	0.00	0.00	0.00	0.10	0.00	0.10	0.00	0.00	0.00	0.00	0.00	0.13	0.00	0.53
Anemone canadensis L.	0.00	0.00	0.00	0.50	0.00	0.00	0.00	0.00	0.00	1.00	0.00	0.00	0.00	0.00	1.25	0.00	2.75
Anemone patens L.	0.00	1.68	0.88	1.90	3.58	0.28	0.75	0.00	0.00	0.00	0.00	0.00	0.00	0.10	1.73	0.83	11.70
Anemone quinquefolia L.	1.78	2.50	2.78	0.43	0.80	0.58	0.35	0.00	3.48	0.00	1.83	0.20	0.25	0.00	0.00	0.00	14.95
Thalictrum venulosum Trel.	0.65	0.88	0.00	0.00	0.25	0.00	0.00	0.00	2.25	0.00	0.75	1.73	0.00	1.75	0.00	0.00	8.25
Rosaceae																	
Fragaria virginiana Mill.	1.83	3.30	4.38	1.38	2.23	2.48	7.63	0.00	1.08	0.50	2.53	3.65	0.00	4.73	0.00	1.35	37.03
Potentilla tridentata Soland. in Ait.	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.25	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.25
Rubus pubescens Raf.	5.65	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	5.65
Fabaceae																	
Amorpha canescens Pursh	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	1.25	0.00	16.85	0.00	0.00	18.10
Lathyrus spp.	0.73	1.80	7.13	3.03	0.25	0.68	8.78	1.00	3.53	0.00	3.35	1.68	0.00	2.13	0.00	0.00	34.05
Violaceae																	
Viola spp.	0.00	0.68	0.40	0.73	1.35	0.40	0.20	0.00	0.18	0.30	0.23	0.00	0.00	0.20	0.38	0.78	5.80
Onagraceae																	
Epilobium angustifolium L.	6.50	0.00	0.00	0.00	0.00	0.13	0.00	0.00	0.28	0.13	0.45	0.00	0.00	0.00	0.00	0.25	7.73
Scrophulariaceae																	
Melampyrum lineare	0.00	3.03	0.10	2.33	5.15	0.38	1.60	0.23	4.70	3.35	0.18	0.00	9.43	0.10	0.20	0.30	31.05
Lamiaceae																	
Monarda fistulosa L.	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.60	0.00	0.50	0.00	0.00	1.10

	Mean % cover																Total cover
	B46A	B52B	B64A	B63B	B74A	B76B	B87A	B87B	PL52A	PL52B	PL65A	PL64B	PL78A	PL76B	PL89A	PL89B	
Pyrolaceae																	
Chimaphila umbellata (L.) W.P.C. Barton	0.00	1.75	0.00	0.00	0.00	0.00	0.00	0.00	0.00	1.00	0.00	0.00	0.00	0.00	0.00	0.00	2.75
Pyrola spp.	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.50	0.00	0.00	0.00	0.50
Pyrola virens Schweigg.	0.75	12.03	8.73	0.00	0.00	0.00	2.13	5.20	5.98	1.00	0.00	0.00	0.00	0.00	0.00	1.68	37.48
Apiaceae																	
Sanicula marilandica L.	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	1.25	0.00	0.00	0.00	1.25
Asteraceae																	
? *Aster* spp.	0.00	0.00	0.00	0.00	0.00	0.00	3.20	0.00	0.00	0.00	0.00	0.00	0.00	0.13	0.00	0.70	4.03
? *Solidago* spp.	0.00	0.00	2.18	1.53	0.00	1.20	0.00	3.20	0.00	0.83	0.80	0.10	1.60	0.10	0.00	0.35	11.88
Antennaria neglecta Greene	0.00	1.88	0.75	4.75	4.30	0.00	5.88	0.75	0.00	2.60	5.25	0.75	0.00	3.10	0.00	0.00	30.00
Artemisia ludoviciana Nutt.	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.25	0.00	0.00	0.00	0.10	0.35
Aster ciliolatus Lindl.	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.05	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.05
Aster spp.	0.00	1.95	0.00	0.00	4.25	0.00	0.00	0.00	0.00	0.00	0.00	0.35	0.00	0.48	0.13	0.00	7.15
Crepis tectorum L.	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.05	0.00	0.05
Solidago nemoralis Aiton	0.00	0.00	0.00	0.00	0.00	0.13	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.13
Solidago spp.	0.00	0.18	0.00	0.23	0.13	0.63	0.00	0.00	0.00	0.00	0.00	0.00	0.23	0.10	0.10	1.05	2.63
Taraxacum officinale Weber ex F.H. Wigg.	0.00	0.00	0.25	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.25
Trientalis borealis Raf.	1.68	0.00	0.00	0.00	0.58	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	1.15	3.40
Poaceae																	
Andropogon gerardii Vitman	0.00	0.00	0.00	0.00	0.98	0.00	25.75	19.28	0.00	0.00	0.00	0.00	0.00	0.00	17.10	20.73	83.83
Danthonia spp.	0.00	0.00	0.00	0.00	0.00	0.25	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.25
Elymus innovatus Beal	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.10	0.00	0.10
Schizachne spp.	0.00	5.60	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	5.60
Unidentifiable grass (may incl. young Andropogon)	9.10	10.35	23.25	22.13	9.33	25.35	8.10	0.93	16.18	13.03	16.75	28.45	29.75	22.55	10.15	5.40	250.78

	Mean % cover																Total cover
	B46A	B52B	B64A	B63B	B74A	B76B	B87A	B87B	PL52A	PL52B	PL65A	PL64B	PL78A	PL76B	PL89A	PL89B	
Other angiosperm families																	
? Gentianella spp.	0.00	0.00	0.00	0.00	0.00	0.10	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.10
Aralia nudicaulis L.	9.50	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	9.50
Asclepias spp.	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.25	0.00	0.00	0.25
Campanula rotundifolia L.	0.00	0.00	0.00	0.15	0.15	0.10	0.00	0.00	0.00	0.13	0.05	0.00	0.00	0.00	0.35	0.00	0.93
Cornus canadensis L.	14.75	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	14.75
Galium boreale L.	1.35	2.08	4.63	2.90	1.58	1.48	0.00	0.00	1.90	0.00	2.18	3.15	1.45	1.65	3.65	0.00	27.98
Galium trifidum L.	0.00	0.00	0.10	0.00	0.00	0.00	0.00	0.00	0.05	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.15
Galium triflorum Michx.	0.65	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.05	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.70
Houstonia longifolia Gaertn.	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.30	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.30
Linnaea borealis L.	3.75	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	4.13	0.00	0.00	0.00	0.00	0.00	7.88
Lithospermum canescens (Michx.) Lehm.	0.00	2.73	3.80	0.10	3.85	1.40	1.25	0.00	1.30	0.25	1.95	1.63	0.00	0.40	1.13	0.90	20.68
Petasites palmatus (Ait.)	0.63	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.63
Physalis virginiana Mill.	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.75	0.75
Rhus radicans L.	0.00	0.00	0.75	0.63	0.00	0.00	0.00	0.00	0.00	0.00	0.00	8.33	0.00	0.25	0.00	0.00	9.95
Unidentifiable herbs	0.00	0.00	0.00	0.20	0.38	0.20	0.35	0.00	1.78	0.00	1.25	0.10	0.10	0.85	0.00	0.00	5.20
Polypodiaceae																	
Pteridium aquilinum (L.) Kuhn	7.75	0.00	0.00	0.00	0.00	0.00	7.15	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	14.90
Equisetaceae																	
Equisetum hymenale L.	0.00	0.53	0.00	0.05	0.00	0.05	0.00	0.00	0.05	0.00	0.00	0.00	3.70	0.00	0.00	0.00	4.38
Equisetum scripoides Michx	1.13	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	1.13
Total cover	84.85	100.20	108.00	77.28	73.88	87.00	86.05	60.95	58.08	62.18	76.50	66.73	82.55	72.28	73.63	70.63	1240.75

Appendix 5 Shrub species sampled per site

	Mean % cover																
	B46A	B52B	B64A	B63B	B74A	B76B	B87A	B87B	PL52A	PL52B	PL65A	PL64B	PL78A	PL76B	PL89A	PL89B	Total cover
? *Symphoricarpos albus (L.) S.F. Blake*	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.25	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.25
Alnus crispa (Aiton) Pursh	3.50	0.00	0.00	0.00	0.00	0.00	0.00	0.00	1.25	0.00	0.00	0.00	0.00	0.00	0.00	0.00	4.75
Amelanchier alnifolia (Nutt.) Nutt.	6.80	1.00	3.10	15.65	1.35	5.30	4.25	0.10	4.60	1.70	11.35	17.25	3.65	13.75	2.40	0.00	92.25
Apocynum androsaemifolium L.	0.00	0.00	0.00	0.00	0.00	0.00	0.15	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.10	0.00	0.25
Ceanothus herbaceous Raf	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.60	0.00	0.00	0.00	0.00	0.00	0.60
Cornus stolonifera Michx.	2.45	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	2.45
Corylus cornuta Marshall	11.25	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	16.60	0.00	0.00	0.00	0.00	27.85
Juniperus communis L.	0.00	0.00	0.00	1.00	0.00	4.00	0.00	0.00	0.00	0.00	0.00	0.00	4.00	0.00	0.00	0.00	9.00
Lonicera dioica L.	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.15	0.00	0.00	0.00	0.15
Pinus banksiana Lamb.	0.00	0.25	0.35	1.00	0.00	0.00	0.35	1.00	0.00	3.00	0.00	0.00	1.15	0.00	0.00	0.25	7.35
Populus tremuloides Michx.	0.20	0.00	0.50	0.00	0.00	0.00	0.00	0.00	1.75	0.00	0.00	0.10	0.00	0.00	0.00	0.00	2.55
Prunus pensylvanica L. f.	0.40	2.35	0.15	1.15	0.15	0.00	1.90	0.00	2.00	0.35	1.25	2.50	0.00	0.00	2.75	1.40	16.35
Prunus pumila L.	0.00	0.00	0.00	0.10	0.10	0.35	0.10	0.15	0.00	0.00	0.00	0.00	0.00	0.25	0.35	2.35	3.75
Prunus virginiana L.	2.35	3.10	14.05	9.45	3.50	3.95	0.25	0.00	5.20	5.70	2.90	11.50	0.40	21.25	2.25	1.65	87.50
Quercus macrocarpa Michx.	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.50	0.00	0.00	0.00	0.00	0.50
Rosa acicularis Lindl.	9.40	4.30	0.75	2.50	0.25	3.80	1.70	0.40	5.45	2.80	3.70	5.60	0.00	2.25	0.15	1.60	44.65
Rubus idaeus L.	5.25	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.85	0.00	0.00	0.00	0.00	0.10	6.20
Salix 1	0.00	0.00	0.00	0.00	0.00	0.00	0.00	2.65	0.00	0.25	0.00	0.00	0.00	0.00	0.00	0.00	2.90
Salix bebbiana or *discolor*	2.05	0.00	0.00	0.00	0.00	0.00	1.00	0.00	0.65	0.00	0.50	0.25	0.00	0.00	0.00	0.00	4.45
Salix spp.	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.75	0.00	0.00	0.00	0.00	0.00	0.75
Spiraea alba Du Roi	0.00	0.00	0.00	0.00	0.10	0.00	0.00	0.15	0.00	0.25	0.00	0.00	0.40	0.00	0.40	7.10	8.40
Symphoricarpos albus (L.) S.F. Blake	2.10	6.70	0.65	1.25	3.20	6.40	0.00	0.00	4.15	0.00	1.45	26.25	0.15	7.35	1.25	0.50	61.40
Vaccinium angustifolium Aiton	3.80	4.50	1.00	1.25	1.15	4.20	0.25	0.00	3.25	2.30	2.65	0.75	1.05	3.75	0.15	1.60	31.65
Unidentifiable shrubs	0.00	0.85	3.15	1.50	0.00	1.75	0.75	0.00	7.10	0.25	5.95	0.00	0.00	16.25	0.00	0.00	37.55
Total cover	49.55	23.05	23.70	34.85	9.80	29.75	10.70	4.45	35.65	16.60	31.95	81.30	10.95	64.85	9.80	16.55	453.50

Appendix 6 Moss species sampled per site

	Mean % cover																
	B46A	B52B	B64A	B63B	B74A	B76B	B87A	B87B	PL52A	PL52B	PL65A	PL64B	PL78A	PL76B	PL89A	PL89B	Total cover
Ceratodon purpureus (Hedw.) Brid.	0.10	0.00	0.00	0.00	0.25	0.00	2.83	9.90	0.00	0.25	0.00	0.00	0.00	0.00	0.78	5.43	19.53
Dicranum fuscescens Turn	0.00	0.15	0.00	0.00	0.00	0.00	0.00	0.00	0.25	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.40
Dicranum polysetum Sw.	0.60	6.90	1.55	1.33	6.00	7.48	0.00	0.00	1.58	3.15	1.00	0.13	8.93	0.40	0.00	0.33	39.35
Dicranum scoparium Hedw.	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	1.23	0.00	0.00	0.00	0.00	0.00	0.00	0.00	1.23
Ditrichum flexicaule (Schwaegr.) Hampe	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.25	0.00	0.00	0.00	0.25
Eurhynchium pulchellum (Hedw.) Jenn.	4.35	0.00	0.00	0.25	0.00	0.00	0.00	0.00	0.38	0.13	0.00	0.00	0.00	1.75	0.00	0.00	6.85
Hylocomium splendens (Hedw.) B.S.G.	0.00	0.75	0.00	2.25	0.00	0.00	0.00	0.00	11.80	0.25	0.00	0.00	0.00	0.00	0.00	0.00	15.05
Hypnum revolutum (Mitt.) Lindb.	0.00	0.00	0.00	0.00	0.00	0.00	0.15	2.43	0.08	0.00	0.00	0.00	0.05	0.00	2.78	3.60	9.08
Hypmum spp.	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.50	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.50
Pleurozium schreberi (Brid.) Mitt.	18.05	40.65	30.80	19.85	30.50	11.30	1.13	0.00	34.10	26.78	48.00	6.70	12.28	6.00	0.00	0.98	287.10
Polytrichum spp.	0.00	0.00	2.05	0.00	0.05	0.00	2.90	0.30	0.00	0.00	0.00	0.00	0.20	0.00	5.30	2.95	13.75
Ptilium crista-castrensis (Hedw.) De Not.	0.25	0.50	0.00	0.00	0.00	0.00	0.00	0.00	0.58	0.00	2.25	0.13	0.00	0.00	0.00	0.00	3.70
Tortella fragilis (Drumm.) Limpr.	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	2.40	0.00	2.40
Tortula ruralis (Hedw.) Gaertn., Meyer, & Scherb. (Pottiaceae)	0.00	0.00	0.25	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.75	0.00	1.00
Tortula spp.	0.00	0.00	0.00	0.75	0.15	0.00	0.00	0.00	0.00	0.10	0.00	0.00	1.30	0.00	7.05	0.00	9.35
Unidentifiable moss	0.25	0.25	0.00	0.00	0.00	0.00	0.00	0.00	0.25	0.00	0.00	0.00	0.00	0.15	0.00	4.35	5.25
Total cover	23.60	49.20	34.65	24.43	36.95	18.78	7.00	13.13	50.23	30.65	51.25	6.95	23.00	8.30	19.05	17.63	414.78

Appendix 7 Butterflies sampled by site in 2003 and 2004

		Total per species per site																
	Year	B46A	B52B	B64A	B63B	B74A	B76B	B87A	B87B	PL52A	PL52B	PL65A	PL64B	PL78A	PL76B	PL89A	PL89B	Total
Amblyscirtes vialis (W. H. Edwards)	2003	0	0	0	0	1	0	0	0	1	0	0	0	1	0	0	0	3
	2004	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Boloria bellona (Fabricius)	2003	0	0	0	4	0	0	0	0	0	0	0	0	0	0	0	0	4
	2004	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Callophrys henrici (Grote & Robinson)	2003	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	1
	2004	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Callophrys niphon (Hübner)	2003	0	0	0	4	0	3	1	0	2	2	0	1	1	2	1	1	18
	2004	0	1	1	1	0	0	0	0	0	2	0	1	1	0	1	0	8
Callophrys polios (Cook & Watson)	2003	0	2	1	1	0	0	0	2	0	1	0	0	2	0	0	0	9
	2004	0	1	0	0	0	0	0	0	0	2	0	0	1	0	0	1	5
Celastrina ladon (Cramer)	2003	3	2	9	0	3	0	0	1	0	4	2	4	1	2	0	0	31
	2004	2	2	5	2	1	0	1	0	1	5	0	2	5	0	1	0	27
Cercyonis pegala (Fabricius)	2003	0	0	1	0	0	0	1	3	1	0	0	0	0	0	3	2	11
	2004	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	1	3
Colias interior Scudder	2003	0	3	0	2	1	3	0	1	3	1	0	0	19	0	2	3	38
	2004	0	0	1	0	3	4	2	1	0	1	0	0	11	0	5	5	33
Colias philodice Godart	2003	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	1	2
	2004	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Danaus plexipppus	2003	0	2	0	1	0	0	0	0	0	1	0	1	0	1	0	0	6
	2004	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Enodia anthedon (A. H. Clark)	2003	0	6	5	6	0	6	0	0	7	0	3	1	1	8	1	0	44
	2004	0	5	1	1	0	4	0	0	1	1	7	2	0	5	0	0	27
Erynnis icelus (Scudder & Burgess)	2003	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	1
	2004	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	1
Erynnis juvenalis (Fabricius)	2003	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	1
	2004	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	1
Erynnis lucilius (Scudder & Burgess)	2003	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	2004	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	1

		Total per species per site																
	Year	B46A	B52B	B64A	B63B	B74A	B76B	B87A	B87B	PL52A	PL52B	PL65A	PL64B	PL78A	PL76B	PL89A	PL89B	Total
Euchloe ausonides (Lucas)	2003	0	0	0	0	0	0	0	1	0	0	0	0	0	0	1	0	2
	2004	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1
Everes amyntula (Boisduval)	2003	0	0	0	1	0	1	3	0	0	0	0	0	1	0	0	0	6
	2004	0	0	0	0	0	0	2	0	0	0	0	0	0	0	0	0	2
Glaucopsyche lygdamus (Doubleday)	2003	4	2	2	6	3	8	5	4	6	1	1	9	2	3	0	1	57
	2004	1	3	3	0	0	3	2	0	2	0	0	6	0	0	2	0	22
Limenitis arthemis (Drury)	2003	0	2	2	0	0	4	0	0	1	0	1	0	0	2	0	1	13
	2004	0	0	0	0	0	0	0	0	0	0	0	0	0	2	0	0	2
Megisto cymela (Cramer)	2003	0	0	0	0	0	0	0	0	0	1	0	1	1	3	0	0	6
	2004	1	0	1	0	0	0	2	0	1	0	0	4	0	3	0	0	12
Oeneis macounii (W. H. Edwards)	2003	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	2004	0	0	1	6	1	0	0	0	0	1	0	0	4	1	0	2	16
Papilio glaucus (Linnaeus)	2003	0	0	0	2	0	0	0	0	0	0	0	0	1	0	0	0	3
	2004	0	0	0	1	0	0	0	0	1	0	0	0	0	0	0	0	2
Phyciodes batesii (Reakit)	2003	0	1	1	0	0	1	0	0	1	0	0	2	0	2	2	1	11
	2004	0	0	0	0	0	0	1	0	0	0	0	0	0	3	1	0	5
Phyciodes cocyta (Cramer)	2003	0	0	0	2	0	1	2	1	0	0	1	0	0	3	0	0	10
	2004	0	0	0	1	0	1	0	0	0	1	0	0	0	0	2	1	6
Phyciodes tharos (Drury)	2003	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	1
	2004	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Pieris oleracea Harris	2003	0	2	0	0	0	0	0	0	0	0	0	1	0	0	0	0	3
	2004	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	2
Pieris rapae (Linnaeus)	2003	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1
	2004	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Poanes hobomok (Harris)	2003	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	2004	0	0	0	0	0	0	0	0	0	0	0	2	0	0	0	0	2
Polites peckius (W. Kirby)	2003	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
	2004	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0

		Total per species per site																
	Year	B46A	B52B	B64A	B63B	B74A	B76B	B87A	B87B	PL52A	PL52B	PL65A	PL64B	PL78A	PL76B	PL89A	PL89B	Total
Satyrium liparops (Leconte)	2003	0	0	0	0	0	0	0	0	0	0	0	1	1	1	0	0	3
	2004	0	0	0	0	0	1	0	0	0	0	0	0	0	2	0	0	3
Satyrium titus (Fabricius)	2003	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	1
	2004	0	0	0	0	0	0	0	2	0	0	0	0	0	0	0	0	2
Speyeria aphrodite (Fabricius)	2003	0	0	3	0	1	0	0	0	0	0	0	0	0	0	0	0	4
	2004	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Speyeria atlantis (W. H. Edwards)	2003	0	0	0	1	0	0	1	0	1	0	0	1	1	0	0	1	6
	2004	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	1
Speyeria cybele (Fabricius)	2003	0	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	3
	2004	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Speyeria electa (W. H. Edwards)	2003	0	0	0	1	0	0	0	0	0	0	0	0	0	0	1	0	2
	2004	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Thorybes pylades (Scudder)	2003	1	2	0	1	0	0	0	0	1	0	1	0	0	0	0	0	6
	2004	0	0	0	0	0	1	1	0	1	0	1	0	0	1	0	0	5
Total	2003	9	25	26	33	9	27	13	16	24	11	9	23	33	28	11	11	308
	2004	4	12	13	12	5	14	13	3	7	14	9	18	23	17	15	10	189
Number of species	2003	4	11	10	14	5	8	6	10	10	7	6	11	13	11	7	8	32
	2004	3	5	7	6	3	6	9	2	6	8	3	7	6	7	8	5	24

Appendix 8 Carabid beetles caught per site in 2003 and 2004

		Total per species per site																
	Year	B46A	B52B	B64A	B63B	B74A	B76B	B87A	B87B	PL52A	PL52B	PL65A	PL64B	PL78A	PL76B	PL89A	PL89B	Total
Agonum cupreum Dejean	2003	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1
	2004	0	1	0	0	0	2	0	0	1	0	1	0	1	0	0	0	6
Agonum gratiosum (Mannerheim)	2003	0	1	0	0	0	0	0	0	0	0	0	0	1	1	0	0	3
	2004	0	1	0	0	0	1	0	0	0	0	0	0	2	1	0	0	5
Agonum placidum (Say)	2003	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	1
	2004	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	1	2
Agonum retractum LeConte	2003	114	0	1	0	1	0	0	0	6	0	21	178	3	16	0	0	340
	2004	43	1	1	1	0	0	3	0	1	1	5	21	4	0	0	0	81
Agonum thoreyi Dejean	2003	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	2004	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	1
Agonum trigeminum Lindroth	2003	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	2004	0	1	0	0	0	3	0	0	0	0	0	1	0	0	0	0	5
Amara cupreolata Putzeys	2003	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	2004	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	1
Amara farcta LeConte	2003	0	0	0	0	0	0	0	0	0	0	0	0	3	0	0	0	3
	2004	0	1	0	0	1	0	0	0	0	0	0	0	1	0	1	0	4
Amara impuncticollis (Say)	2003	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1
	2004	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Amara laevipennis Kirby	2003	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	2004	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1
Amara latior (Kirby)	2003	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	2004	0	0	0	0	0	1	0	0	0	0	0	0	0	0	5	0	6
Amara obesa (Say)	2003	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1
	2004	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	1	2
Amara schwarzi Hayward	2003	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	1	3
	2004	0	1	0	0	1	2	0	0	0	0	0	0	0	0	0	1	5
Amara sinuosa (Casey)	2003	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1
	2004	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0

		Total per species per site																
	Year	B46A	B52B	B64A	B63B	B74A	B76B	B87A	B87B	PL52A	PL52B	PL65A	PL64B	PL78A	PL76B	PL89A	PL89B	Total
Anisodactylus harrisii LeConte	2003	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	2004	0	0	0	0	0	1	0	1	0	0	0	0	0	0	0	0	2
Anisodactylus merula (Germar)	2003	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	2004	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	1
Anisodactylus sanctaecrucis (Fabricius)	2003	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	1
	2004	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	1
Badister obtusus LeConte	2003	0	0	0	0	0	1	0	0	0	0	1	1	0	2	0	0	5
	2004	2	0	0	3	0	1	0	0	0	0	1	0	0	0	1	0	8
Bembidion mimus Hayward	2003	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	2004	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1
Bembidion new species	2003	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	2004	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	1
Bembidion quadrimaculatum Say	2003	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	2004	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
Bembidion versicolor (LeConte)	2003	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	2004	0	0	0	0	0	0	0	0	0	0	0	0	0	2	0	0	2
Blethisa multipunctata aurata Fischer von Waldheim	2003	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	2004	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	1
Bradycellus lugubris (LeConte)	2003	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	2004	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	1
Calathus ingratus Dejean	2003	14	1	26	0	24	2	1	0	30	13	8	4	0	0	1	1	125
	2004	9	2	2	0	3	0	1	0	9	9	3	1	0	0	2	0	41
Calosoma calidum (Fabricius)	2003	0	0	0	0	0	3	1	1	0	0	0	0	2	0	0	0	7
	2004	1	0	0	0	1	1	1	0	0	0	0	0	0	0	0	0	4
Calosoma frigidum Kirby	2003	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	1
	2004	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	1
Carabus serratus Say	2003	0	0	3	1	2	2	1	0	0	0	0	0	0	0	1	3	13
	2004	0	1	3	0	0	1	1	0	0	3	3	0	0	2	3	3	20
Carabus taedatus agassii LeConte	2003	1	0	10	1	2	2	4	2	0	4	1	15	6	8	2	8	66
	2004	0	0	4	1	1	4	6	6	0	3	0	28	2	7	8	9	79

	Year	Total per species per site																
		B46A	B52B	B64A	B63B	B74A	B76B	B87A	B87B	PL52A	PL52B	PL65A	PL64B	PL78A	PL76B	PL89A	PL89B	Total
Chlaenius niger Randall	2003	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	2004	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	1
Chlaenius pensylvanicus pensylvanicus Say	2003	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	1
	2004	0	1	0	0	0	0	0	0	0	0	0	0	0	1	0	0	2
Chlaenius platyderus Chaudoir	2003	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	2004	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	1
Chlaenius sericeus sericeus (Forster)	2003	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	2004	0	0	0	0	0	0	0	1	0	0	0	0	0	0	1	0	2
Cymindis borealis LeConte	2003	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1
	2004	0	0	0	0	0	0	0	0	0	0	0	0	0	0	8	1	9
Cymindis cribicollis Dejean	2003	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	1
	2004	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Cymindis neglectus Haldeman	2003	0	0	0	0	0	0	0	0	0	0	0	1	0	0	3	1	5
	2004	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	1
Dicaelus sculptilis upiodes Ball	2003	0	10	5	5	9	7	3	0	0	13	8	0	0	6	0	3	69
	2004	0	9	12	8	8	10	15	1	1	32	29	1	1	3	2	12	144
Dromius piceus Dejean	2003	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	2004	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	1
Harpalus fulvilabris Mannerheim	2003	1	10	9	2	9	3	3	0	7	2	13	7	1	4	1	0	72
	2004	0	11	5	1	7	2	3	1	2	3	9	7	1	4	0	4	60
Harpalus herbivagus Say	2003	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	2004	0	0	0	0	1	0	0	0	0	1	0	0	0	0	0	0	2
Harpalus laticeps LeConte	2003	0	0	0	0	0	1	0	0	0	1	0	0	0	0	0	0	2
	2004	0	1	0	0	0	4	2	0	0	0	0	1	0	0	2	0	10
Harpalus lewisii LeConte	2003	0	0	0	0	0	1	1	3	0	0	0	0	0	0	7	2	14
	2004	0	1	0	0	0	2	0	5	0	0	0	0	0	0	4	1	13
Harpalus nigritarsus C.R. Sahlberg	2003	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	2004	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1
Harpalus opacipennis (Haldeman)	2003	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	2004	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1

	Year	Total per species per site																
		B46A	B52B	B64A	B63B	B74A	B76B	B87A	B87B	PL52A	PL52B	PL65A	PL64B	PL78A	PL76B	PL89A	PL89B	Total
Harpalus pensylvanicus (DeGreer)	2003	0	0	0	0	0	0	1	0	0	0	0	0	0	0	1	0	2
	2004	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Harpalus plenalis Casey	2003	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	2004	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	1
Harpalus solitaris Dejean	2003	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	2004	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1
Harpalus somnulentus Dejean	2003	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	2004	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1
Notiophilus semistriatus Say	2003	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	1	3
	2004	0	0	0	0	0	0	1	0	0	0	0	0	0	0	2	0	3
Pasimachus elongatus LeConte	2003	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	1
	2004	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Platynus decentis (Say)	2003	2	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	3
	2004	9	0	0	0	0	0	0	0	0	0	0	2	0	1	0	0	12
Poecilus lucublandus lucublandus (Say)	2003	0	0	0	0	0	0	0	0	0	0	0	2	3	0	0	0	5
	2004	0	1	0	0	2	1	0	0	1	2	0	1	3	0	1	1	13
Pterostichus adstrictus Eschscholtz	2003	1	0	1	0	1	0	0	0	1	0	2	1	0	0	0	0	7
	2004	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
Pterostichus commutabilis (Motschulsky)	2003	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	2004	0	0	0	0	1	0	0	0	0	2	0	0	0	0	2	0	5
Pterostichus femoralis (Kirby)	2003	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	1
	2004	0	2	2	0	1	0	2	0	0	0	0	0	2	0	0	0	9
Pterostichus melanarius (Illiger)	2003	3	0	1	0	0	0	0	0	0	1	0	1	1	0	1	0	8
	2004	0	1	0	0	0	1	1	0	1	1	0	0	0	1	0	1	7
Pterostichus mutus (Say)	2003	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	1
	2004	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	1
Pterostichus novus Straneo	2003	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	2004	0	0	0	0	0	2	0	0	0	0	0	0	0	0	0	0	2
Pterostichus pensylvanicus LeConte	2003	97	23	46	1	27	29	16	1	35	38	51	12	21	8	1	1	407
	2004	286	85	130	7	109	48	47	11	133	136	115	29	101	18	2	0	1257

	Year	Total per species per site																
		B46A	B52B	B64A	B63B	B74A	B76B	B87A	B87B	PL52A	PL52B	PL65A	PL64B	PL78A	PL76B	PL89A	PL89B	Total
Scaphinotus bilobus (Say)	2003	9	0	0	0	0	0	0	0	2	3	0	0	0	0	0	0	14
	2004	3	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	3
Scaphinotus elevatus coloradensis Van Dyke	2003	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	2004	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	1
Sphaeroderus stenostomus lecontei Dejean	2003	1	5	3	3	0	0	0	0	2	4	3	2	0	0	0	0	23
	2004	17	7	9	7	4	9	2	0	12	13	5	6	4	2	0	1	98
Syntomus americanus (Dejean)	2003	0	1	1	2	0	11	1	0	0	1	0	4	7	7	9	1	45
	2004	0	9	3	5	3	13	8	0	0	1	0	2	10	18	13	2	87
Synuchus impunctatus (Say)	2003	116	23	22	19	12	43	22	3	47	43	83	43	35	31	2	15	559
	2004	116	200	44	16	95	154	149	105	50	90	171	73	78	14	210	182	1747
Total	2003	359	74	128	35	88	107	56	10	130	124	192	272	85	83	32	41	1816
	2004	487	338	216	53	239	267	243	134	211	298	342	174	211	74	271	222	3780
Number of species	2003	11	8	12	9	10	14	13	5	8	12	11	14	13	9	14	15	38
	2004	10	21	12	13	16	25	16	11	10	15	10	14	15	13	21	15	59