EFFECTS OF FOREST MANAGEMENT ON CLICK BEETLE (COLEOPTERA: ELATERIDAE) ASSEMBLAGES IN THE ACADIAN FOREST OF MAINE

By

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By Shelly L. Thomas

Thesis Advisor: Robert G. Wagner

An Abstract of the Thesis Presented
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Click beetle (Coleoptera: Elateridae) assemblages were examined in three experiments in the Acadian forest of Maine. First, I used flight intercept traps to compare Elaterid assemblages in stands that developed after clearcut, shelterwood, and selection harvests. Click beetle richness was highest in stands managed under a selection system and lowest in stands regenerated using the clearcut method. The abundance of click beetle species was lower in stands managed by clearcutting than in stands managed using the shelterwood and selection methods. Hardwood basal area was the best environmental predictor for both species richness and species abundance.

Second, I examined whether Elaterid assemblages in soil were associated with hardwood (Maple, Birch, Aspen, Blueberry, and Oak) and softwood (Spruce-Fir-Pine, Pine, Hemlock, and Fern-Hemlock) cover types. Elaterid diversity was generally higher in hardwood than softwood stands. Species richness was lowest in the Spruce-Fir-Pine and highest in the Oak cover type. Species abundance was lowest in the Spruce-Fir-Pine and Pine and highest in the Oak, Maple, and Hemlock cover types. Assemblages in

hardwood stands were less similar to those in coniferous stands than they were to each other, with assemblages in oak stands being least similar to those in coniferous or other hardwood stands. Four species of click beetle were more abundant in softwood stands, and seven species were associated with increases in specific softwood tree and shrub species. Nine species of click beetle were more abundant in hardwood stands, and fifteen species were associated with increases in specific hardwood tree and shrub species, including six species associated with oak stands.

Third, I examined how the species richness, abundance, diversity, and assemblage similarity of click beetles inhabiting coarse woody material (CWM) were affected by gap harvesting and characteristics of the CWM (diameter, degree of decay, and wood type) in Maine’s Acadian forest. Species assemblages varied between harvest treatments, canopy conditions, CWM wood type (hardwood vs. softwood), and especially between CWM decay classes and among diameter classes. Size of harvest gap did not influence the species abundance of click beetles across the small range of gap sizes studied (0.01 to 0.21 ha), and there were few differences between the two harvest treatments. Four of the most common species had higher abundances in closed canopy than harvest gaps. Click beetle species richness and species abundance were higher in CWM that had larger diameters and were more decayed. Click beetle diversity was higher in softwood than hardwood CWM.

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PROLOGUE

I arrived in Maine with the goal of studying the effects of forest management on a family of beetles. My overall research interests were motivated by questions about how to use our natural resources (especially forest ecosystems) while still protecting and caring for all the creatures that depend on these resources. My interests have paralleled directions that conservation biology has taken over the last few decades, first in the conservation of biodiversity in forests reserves and then in managed forests (Hunter 1999, Lindenmayer and Franklin 2002).

To meet this goal, we need to know which species exist in our forests and their habitat preferences. This basic information is still largely unknown for the majority of invertebrate species in North American temperate forests (Danks and Foottit 1989, Carlton and Robison 1998). Insects are an important group to investigate because they are highly diverse, far outnumbering other higher taxa (MEA 2005), and perform many important functions in forest ecosystems (Crowson 1981, Wilson 1992). Because forest management affects insect populations (Niemelä 1997, Grove 2002a), they can serve as important indicators of ecological sustainability (Kremen *et al*. 1993, Taylor and Doran 2001). Coleoptera (beetles) is the largest order of insects and includes approximately 40% of all arthropods (Grove and Stork 2000), and Elateridae (click beetles) is the ninth most biodiverse family of Coleoptera, with approximately 10,000 described and many undescribed species (Johnson, 2002).

I find click beetles to be entertaining and quite lovely, so I was surprised to discover that relatively little was known about most species of this family. Click beetles are a delight to observe, both in the field and in the lab. Beyond their ability to snap suddenly and propel themselves into the air, they may scamper rapidly or fly in dizzying vertical circles at the first opportunity; other times they may tuck only their head in moss, apparently to hide, leaving the rest of their body visible. These small creatures have fascinating, minute details in their sclerites (the hardened parts of the exoskeleton), antennae, and tarsal claws. The species have an amazing diversity of colors, shapes, divots, and tufts of "hair" that are only visible under magnification; this is a constant reminder of the infinite amount of diversity and activity occurring right under our noses of which we have almost no knowledge or concept. Other scientists can have those ever so commonly studied mammals, birds, and amphibians; I was blessed to have this opportunity to study these little-known beetles!

Although some species of Elateridae are considered pests in agricultural systems, this family does not cause serious damage to forest trees (Craighead 1950, Anderson 1960, and Williams 1985). The larvae live in soil or plant materials in various stages of decomposition, including duff and deadwood- both upright snags and material on the forest floor (Owen 1986, Kaila *et al*. 1997, Jacobs 2004). In soil they are omnivorous, preying on insects or eating decaying plant materials; some species are herbivorous on highly metabolic tissues, such as meristematic regions, sprouting seeds, or high sugar content tubers (Johnson 2002 and personal communication). In wood they are often predators of small invertebrates or saprophagous on decaying plant materials or other saprophagous organisms like slime molds (Morris 1951, Wolters 1989, Johnson 2002). Although many studies found that the larval stage can last up to six years (e.g. Miles 1942, Strey 1972), Johnson (personal communication) insisted that this extended life span was due to faulty rearing conditions and that larvae take 1-3 years to develop, depending on food availability and quality. Elaterid adults are common in temperate forests, usually active in the afternoon and evening during the summer months. Many species feed on plant parts (on floral parts, nectar, pollen, and decaying or overripe fruit, or at glandular trichomes, extra-floral nectaries, and phloem weeps) or fungal fruiting bodies, and some are predators on the soft bodies and honey-dew exudates of the insects in suborder Sternorrhyncha (ex. psyllids, aphids, scale insects, and white flies) or caterpillars and larvae of other insects (Balduf 1935, Morris 1951, Johnson 2002).

Click beetles are notable predators of forest insect pests (Morris 1951, Yano *et al.* 1984), prey for birds and other biota (Barron and Walley 1983, Holmes and Robinson 1981, Heinrich and Bell 1995), and mediators of nutrient cycling (Wolters 1989). Some species are considered threatened or endangered (Anon. 1999, Alexander 2003, Zach 2003). Elaterids are valuable for forest biodiversity studies because the family is numerically abundant and species rich, they can be collected using comparably simple trapping methods, and the species have diverse food and habitat preferences. However, the deficiency of detailed information regarding most species in this family is an impediment to their conservation.

The knowledge of European species is much greater than for North American species. Are there click beetles here that are dependent very specific habitats like large, hollow trees as in Nilsson and Baranowski (1997)? Are there species that are ought to be listed as endangered, like in Alexander (2003) and Zach (2003)? Are there larval predators that clue in on the sex pheremones of its prey (Svensson *et al.* 2004)? Even just the basics are still unknown. What species exist in the Acadian forest? Which ones are common or uncommon? Do they have habitat preferences? How do our traditional forest harvesting methods affect click beetle populations? Can we use forest resources (harvest trees) in such a way that we still provide the habitat these species need? To address these information gaps, three experiments were designed to examine click beetle assemblages and habitat preferences for the species living in Maine's Acadian forests, a transitional ecotone between the eastern temperate and boreal forests.

In the first experiment, the effect of harvest systems (clearcut, shelterwood, and selection) and stand characteristics (vegetation composition and structural diversity, hardwood. softwood, and snag basal area, and coarse woody material volume) on click beetle abundance and assemblage composition was investigated. Changes in the richness and abundance of click beetles at various heights in the forest canopy were investigated using flight-intercept traps. Because flight-intercept traps only capture flying adults that have already emerged, it was not possible to identify where click beetles spend the majority of their years as larvae. Adult beetles may disperse some distance from their emergence points, but click beetle dispersal distances have not been widely studied (but see Kishita *et al*. 2003 and Yamamura *et al*. 2003).

Based on findings and limitations from this first experiment, two additional studies were designed to determine whether click beetle assemblages were related to the composition of forest vegetation and the characteristics of deadwood within the stand. To investigate these site-specific relationships, emergence traps were used in the subsequent studies.

In the second study, the relation between click beetle assemblages emerging from soil on sites dominated by common plant species in the Acadian forest (blueberry, aspen, maple, birch, oak, spruce, fir, pine, fern, and/or hemlock) was examined. Of particular interest was assessing whether dominant plant species affected the abundance and composition of click beetle assemblages and whether specific species of click beetle had any specific habitat preferences.

The third study focused on whether harvest gaps that were designed after patterns of natural disturbance in the Acadian forest provided adequate habitat for click beetles, thus providing for Elaterid diversity and abundance in managed forests. A unique aspect of this study was examining whether the abundance and composition of click beetles living in coarse woody material (CWM) were affected by gap harvesting and CWM characteristics, including decay class, diameter, and wood type (softwood or hardwood).

I believe that results from the three studies described in the following dissertation have significantly advanced our understanding about Elateridae occupying the Acadian forest, as well as how management practices in this forest can potentially influence assemblages and individual species of click beetles.

Chapter 1

EFFECT OF SILVICULTURAL METHODS AND ASSOCIATED STAND CHANGES ON CLICK BEETLE (COLEOPTERA: ELATERIDAE) ASSEMBLAGES IN THE MAINE REGION OF THE ACADIAN FOREST

1.1. Abstract

Click beetle (Coleoptera: Elateridae) communities were sampled using flight intercept traps at 1, 3, 5, 7, 9, and 11 m above the ground in a long-term experiment comparing clearcut, shelterwood, and selection silvicultural methods in the Acadian forest of central Maine, USA. We used forest stand characteristics (vegetation composition and structural diversity, hardwood and softwood basal area, and amount of deadwood) to predict click beetle assemblages. Click beetle richness was highest in stands managed under a selection system and lowest in stands regenerated using the clearcut method. The abundance of click beetle species was lower in stands managed by clearcutting than in stands managed using the shelterwood and selection methods. Silvicular method was the best predictor of click beetle richness, however, hardwood basal area was the best environmental predictor. Hardwood basal area was a better predictor of click beetle species abundance than silvicultural method. Species richness decreased with increasing height above the ground and was best predicted using relative canopy height rather than absolute canopy height. Species abundance increased with trap height in selection stands and decreased with trap height in clearcut and shelterwood stands, but relative canopy height was a better predictor than trap height, suggesting click beetle species respond to the forest canopy rather than absolute height above the ground.

Click beetle species composition varied with the forest stand characteristics, indicating that differences in habitat characteristics created by different silvicultural methods determined long-term differences in click beetle assemblages.

1.2. Introduction

The conservation of biodiversity has become a concern in management of natural resources (Hunter 1999, Lindenmayer and Franklin 2002). Balancing this goal with meeting human demands for wood requires that forest management be based on sound ecological principles (Seymour and Hunter 1999, Lindenmayer and Franklin 2002). Much of the Acadian forest, a transition ecoregion between the boreal spruce-fir forest to the north and the deciduous eastern temperate forest to the south (Bailey 1995, Lorimer and White 2003), is managed using traditional silvicultural methods and harvesting techniques (Maine Forest Service 2005**.** Therefore, it is important to understand how traditional silvicultural methods (such as clearcut, shelterwood, and selection harvesting) influence biodiversity by creating forest stands of different compositional and structural characteristics.

At least two thirds of the world's terrestrial species inhabit forests (Salim and Ullsten 1999), and these taxa are affected by changes in stand characteristics such as vegetation composition, vertical structure, and the amount of deadwood. The composition of forest vegetation can affect invertebrate assemblages through insect-plant associations within a stand (Saetre *et al.* 1999, Paquin and Coderre 1997, and Ohsawa 2004). Tree species composition is closely related to vertical structure (Palik and Engstrom 1999), and structural diversity is associated with the abundance, diversity or richness of other species (Wilson 1974, Schowalter 1995, DeGraaf *et al*. 1998, and Walla *et al*. 2004). Finally, the importance of deadwood, both dead-standing trees (snags) and coarse woody material (CWM), has been recognized as vital for conserving biodiversity in forests (Speight 1989, Elton 1966, Harmon *et al*. 1986, Lohr *et al*. 2002) because it supports a wide variety of animals, fungi, and plants (Speight 1989, Lindenmayer and Franklin 2002, Machmer 2002).

The method of forest harvesting and other silvicultural interventions can have a strong influence on the long-term structure and composition of forest stands. Regeneration methods such as clearcutting remove the entire stand in one operation to produce future even-aged stands of desired composition (Smith *et al*. 1997). Shelterwood cutting removes the entire stand in a succession of harvests to provide seed and shaded micro-environments suitable for regenerating an even-aged stand when the overstory is removed. Selection harvesting removes single trees or small groups of trees on a regular cutting cycle to produce a continuous flow of regeneration, recruit trees into larger diameter classes, and maintain an uneven-aged stand. All three harvest methods are used to regenerate hardwood, mixedwood, or softwood stands in northern temperate forests. Depending on how each of the methods is implemented across a forest landscape, various patterns of stand composition and structure can be established. Unless it is designed into the silvicultural system, all harvest systems can deplete snags and CWM through removal of large living trees (potential CWM), stand preparation, and slash disposal (Fridman and Walheim 2000). Different harvest methods can modify the distribution of size and decay class of snags and CWM through the addition of small diameter slash and through the mechanical crushing of larger pieces in late-stage decay (Freedman *et al*. 1996, Fraver *et al*. 2002).

Harvesting affects the flora and fauna of a forest ecosystem, including insects, the most plentiful and richest group of higher organisms (MEA 2005). Although many important natural processes within forest ecosystems are facilitated by insects (Crowson 1981, Wilson 1992), most species are poorly understood (Danks and Foottit 1989). Beetles (Coleoptera) are the largest order of insects and include approximately 40% of all arthropods (Grove and Stork 2000). Elateridae (click beetles), including approximately 10,000 described and many undescribed species, is the ninth most biodiverse family of Coleoptera (Johnson 2002).

Click beetles are well known as pests in agricultural systems, but many species live in forest soil and deadwood without causing serious damage to living trees. Moreover, click beetles have been shown to be beneficial as prey for birds and other forest biota (Barron and Walley 1983, Holmes and Robinson 1988, Heinrich and Bell 1995), as predators of forest pests (Morris 1951, Yano *et al*. 1984), and as mediators of nutrient cycling (Wolters 1989). Some species of click beetles have been determined to be threatened or endangered (Anon. 1999, Alexander 2003, Zach 2003), but the paucity of information regarding most species in this family (especially outside Europe) is an impediment to their conservation. Elaterids are useful for studying the effects of forest management on biodiversity because the many species have diverse habitat and food preferences. In addition, the family is numerically abundant, species rich, and can be sampled using relatively simple trapping methods.

In this study, we hypothesized that 1) long-term differences in the forest stand development created by various silvicultural methods (such as clearcut, shelterwood, and selection harvesting) in the Acadian forest would create varied click beetle assemblages at different heights in the forest canopy and among silvicultural methods, and 2) stand characteristics (vegetation structure, composition, deadwood, and relative canopy height) would better predict click beetle assemblages than using silvicultural methods alone.

1.3. Methods

1.3.1. Study Site

This study took place in the Penobscot Experimental Forest (PEF) in east-central Maine (44°50’ N, 68°35’ W, Figure 1.1). Dominant tree species in the forest included softwoods such as red (*Picea rubens* Sarg.), white (*P. glauca* (Moench) Voss) and black spruce (*P. mariana* (Mill.) B.S.P.), balsam fir (*Abies balsamea* (L.) Mill.), eastern white pine (*Pinus strobus* L.), eastern hemlock (*Tsuga canadensis* (L.) Carr.), and northern white cedar (*Thuja occidentalis* L.), and hardwoods such as red maple (*Acer rubrum* L.), paper (*Betula papyrifera* Marsh.) and gray birch (*B. populifolia* Marsh.), and quaking (*Populus tremuloides* Michx.) and bigtooth aspen (*P. grandidentata* Michx.). The PEF has a complicated history of insect outbreaks and repeated partial cuttings that resulted in multi-cohort stand structures of many species (R. Seymour, unpublished data). Soils range from glacial till ridges with well-drained or sandy loams to flat areas between ridges with poorly to very poorly drained loams and silt loams (Brissette 1996).

Table 1.1. Silvicultural system, size, and dates of harvest of the stands studied in the Penobscot Experimental Forest. Stand titles: c = clearcut, s = selection, w = shelterwood.

Stand	Management System	Acres	Dates of Harvest
c8	Commercial Clearcut	43.2	53, 83
c22	Commercial Clearcut	33.8	57, 88
s12	10-year Selection	31.1	54, 65, 75, 84, 94
s20	10-year Selection	21.2	57, 67, 76, 86, 98
s25	Crop Tree Selection	44.8	57, 77, 86, 95
s26	10-year Selection	31	57, 64, 68, 73, 83, 93
s52	15-year Selection	17.9	93
w2	Irregular Shelterwood	47.9	51, 66, 84
w7A	2-stage Shelterwood	29.4	69, 79
w7B	2-stage Shelterwood	26	69, 79
w21	2-stage Shelterwood	27.3	57, 67
w23	3-stage Shelterwood	24.3	55, 66, 72; (PCT half stand) 81
w29	3-stage Shelterwood	16.8	57, 68, 74; (PCT half stand) 83

Thirteen stands were selected in long-term research plots established by the USDA Forest Service on the PEF (Sendak *et al*. 2003). All the stands were approximately 10 ha in size and were created over a 50-year period following the application of various silvicultural methods. Although there was some variability in harvest dates and procedures used to apply the silvicultural methods among stands, we divided the stands into those managed using clearcut, shelterwood, and selection methods (Table 1.1). In the two stands where commercial clearcuts were applied, most or all merchantable trees were removed with no plan for regeneration. The culls and unmerchantable trees were left scattered or in patches.

The six stands that were shelterwood harvested in 2- or 3-stages produced a single-age class of red spruce, balsam fir, and white pine. The shelterwood harvests removed much of the overstory in one or two stages; a residual overstory was retained as seed and shade trees to promote regeneration of softwood trees. Final overstory removal occurred six to ten years later. Some shelterwood harvests included precommercial thinning (PCT) of the regeneration to 2 x 3m spacing. In the irregular shelterwood cut, half the stand was whole-tree harvested by hand-felling and cable skidding with advanced regeneration protected (Kenefic, personal communication). The second half included whole-tree harvesting and chipping on non-merchantable parts of the harvested trees that destroyed advanced regeneration, but scarified the soil and resulted in pine-dominated regeneration.

The five stands that have been continuously managed using three methods of selection harvesting created uneven-aged stands. Single tree and group selection harvesting used 10- or 15-year cutting cycles and produced stands dominated by red spruce, eastern hemlock, and balsam fir in mixture with other softwood and hardwood species. In the crop tree selection treatment, trees were released and additional trees recruited by diameter limit cutting at 15-year intervals.

1.3.2. Measurements

1.3.2.1. Beetle Sampling

We sampled insects in the thirteen stands using non-baited flight intercept traps designed to form a four-panel intercepting surface. Each trap was constructed with two panes of clear plastic (approximately 60 cm tall x 44 cm wide) that were intersected in the middle and perpendicular to one another. A funnel and collecting jar were attached at the top and bottom of the intersecting panes. A 15 mm^2 section of Vapona (2,2-Dichlorovinyl dimethyl phosphate) was placed in each jar as a killing agent. Six traps were suspended from nylon cord at heights of 1, 3, 5, 7, 9, and 11 m above the ground on 16.8 m high towers made of metal pipe. Two towers were installed (no less than 10 m apart) near the center of each stand (26 towers total; see Su and Woods 2001 for a more detailed description). We also used three pitfall traps and one malaise trap at each tower, but very few click beetles were trapped by these methods; no analyses were performed on these samples.

We extracted samples from the traps at approximately one-week intervals from June 24 to August 21, 1997 and at two-week intervals from May 19 to August 18, 1998. Because of uneven sampling effort due to weather-damaged traps, capture from each trap was standardized to capture per trap week, and then summed between towers in each stand. Insects were sorted to order and stored in 70% ethanol. Elaterid specimens were identified to species, stored in alcohol or pinned, and incorporated into the University of Maine Insect Collection. A reference collection for verification of species identification was sent to E.C. Becker and Serge LaPlante in Ottawa, Ontario, Canada. All further identifications were made by S. L. Thomas following the nomenclature of Dietrich (1945) and Downie and Arnett (1996).

1.3.2.2. Vegetation Sampling

We measured overstory trees, understory vegetation, and deadwood in 1997 using four 2 x 200 m belt transects (1,600 m^2 total area) in each stand. Hardwood and softwood basal area, vegetation species and structural diversity indices, and snag basal area and CWM class volume indices (Table 1.2) were calculated to characterize the structure and composition of the forest stands. To test the degree of colinearity among these variables, Pearson's correlations with Bonferonni probabilities were calculated for all pairs of variables. No significant correlation was found ($p > 0.05$).

To quantify overstory trees greater than 2 cm DBH and 5 m height, we recorded the species and measured DBH, lower canopy height, and upper canopy height. Mean canopy length for the stand was calculated by summing the crown lengths at 3 m height intervals for all trees by species . The basal area of hardwoods and softwoods were calculated for each stand, and the density (numbers of stems per m^2) was also calculated for each understory species.

The Shannon diversity index (Hill 1973) was used to quantify plant species diversity and stand structural diversity. Shannon's index was calculated as: $H' = -\Sigma p_i \ln(p_i)$, where p_i is a measure of relative abundance (proportion of S made up of the ith species or canopy lengths), and i ranges from 1 to S. For plant species diversity, S =

number species occurring in a stand and p_i = proportion of S made up of the *i*th species. For stand structural diversity (overstory only), S = total canopy length across all species at each height interval in each stand, and p_i = proportion of S made up of the *i*th three meter height interval. Relative canopy height was determined by dividing each trap height by the mean height of the tallest 10% of trees in each stand.

To quantify deadwood, we measured the DBH and height of each snag located in the transect. The length and the diameter of each piece of CWM > 4 cm diameter was measured where they crossed the central transect. The decay condition of each snag and piece of CWM was categorized into four decomposition classes following Fraver *et al.* (2002). We calculated the basal area for each snag decay class. The total volume of CWM pieces greater than 7 cm in diameter was calculated using the formula of Van Wagner (1968): CWM Volume = $(\text{sum of diameters} \times \pi)^2/8L$, where L is the length of transect. However, we tallied all logs rather than disregarding those described in Van Wagner, so our measure was a volume index rather than an absolute volume. Click beetles tend not to be found in fresh deadwood, so we analyzed only decay classes 2, 3, and 4. The snag basal area was relatively low in each stand, so we summed classes 2-4.

1.3.3. Analytical Approach

We examined relationships between click beetle species abundance and the stand variables (vegetation diversity, stand structural diversity, hardwood and softwood basal area, and snag basal area and CWM volume index by decay class) by ordinating stands in species-space with non-metric multidimensional scaling (NMS; Kruskal 1964) using PC-ORD (McCune and Mefford 1999). NMS is an iterative ordination method based on ranked distances between sample units. This method searches for low stress, measured by the relationship between the ranked distances in the original multidimensional space and the reduced dimensions produced by the ordination. NMS is an effective ordination method for community data; it is robust to a large proportion of zero values and does not assume normality (Clarke 1993, McCune and Grace 2002). In an initial NMS analysis, we examined the relative positions of species and found little difference between years. As a result, we pooled click beetle samples from both years for all click beetle species. Random starting configurations and the quantitative version of the Sorensen distance measure were used; the run with the lowest stress (14.6) was selected for the final analysis. We assessed the dimensionality of six axes and selected two axes; both axes had significant Monte Carlo test results ($p < 0.05$), and described 30.0% and 47.3% of the variation in the click beetle assemblages. Subsequently, Pearson and Kendall Correlations were compared between the ordination axes with the beetle species and the stand variables, and joint-plotted these variables. A high correlation between any stand variable and an NMS axis indicated a persuasive association between that variable with the beetle species associated with the axis.

We assessed the relation between click beetle richness (total number of species) and species abundance (abundance of each species per trap week) with stand variables using linear models for each stand (stand scale) and for trap-height within each stands (trap-height scale). At the stand scale, we derived elaterid richness from the summed elaterid species abundances within each stand; we used year, harvest treatment, and stand within harvest treatment as predictor variables. To determine which stand variables best predicted the patterns, we substituted stand variables (vegetation species and stand structural diversity, hardwood and softwood basal area, and snag basal area and CWM volume) for harvest treatment and stands. At the trap-height scale, we based click beetle richness and species abundances on data from each trap height within each stand; we used year, harvest treatment, stand within harvest treatment, and trap heights as predictor variables. To determine which trap-height variables best predicted the patterns, we subsequently a exchanged height-related variable (relative canopy height) for trap heights, harvest treatment, and stands. PROC GLM (SAS Institute 2000) was used for the click beetle species richness models. Because the data were over-dispersed, PROC GENMOD (SAS Institute 2000) with a negative binomial error distribution was used for species abundance models of the sixteen most abundant click beetle species. We generated models based on the main effects and their interactions, selecting a biologically meaningful optimal model with the second order Akaike Information Criterion (Akaike 1974). Therefore, four models each of species richness and species abundance were used- a harvest treatment model and environmental variable model for both the stand scale and trap-height scale.

We examined the relation between the click beetle assemblages with the following stand variables: vegetation diversity, stand structural diversity, hardwood and softwood basal area, and snag basal area and CWM volume index by decay class. The stands produced a range of results for each stand variable, so we arranged stands into two groups (low and high) by sorting the stands and searching for the largest difference between successive values. These groups were used to compare click beetle assemblage measurements for each year individually and both years combined; the text description refers to the total between years. We used a *t*-tests to determine differences in click beetle richness and total abundance between stands.

Click beetle assemblage was measured using species richness, total abundance, assemblage similarity, and diversity, as each addressed different aspects of beetle assemblage. We used a cluster analysis of the Jaccard percent similarity measure, calculated using internet-based software provided by Brzustowski (2002). Higher percent similarity referred to greater overlap in species composition between the two assemblages. Rarefaction takes into account both richness and abundance, so it can be used as a measure of species diversity; herein we use “diversity” to refer to rarefaction-estimated species richness. PAST (Hammer *et al*. 2001) was used to calculate the expected number of species derived from random subsamples of the total abundance, and compared species diversity between subsamples of similar sizes (Sanders 1968, Hurlbert 1971). We considered diversity between two groups of stands to be different when 95% confidence intervals did not overlap.

1.4. Results

1.4.1. Beetle Taxa

We collected 2,823 click beetles of 60 different species, including two species (*Isorhiphis obliqua* Say and *Fornax canadensis* Brown) from Eunemidae, the false click beetles (Tables A.1 and A.2). *Ctenicera triundulata* Randall, *Agriotes stabilis* LeC., *Ampedus mixtus* Herbst, and *Sericus brunneus* L. were the most common species, representing 52%, 9%, 5%, and 4% of the total abundance, respectively. Twelve species were singletons, and 23 species were represented by only two to nine individuals. Click beetle

Table 1.2. Environmental variables for each stand. Stand codes; c = clearcut, s= selection cut, and w = shelterwood. Diversity is Shannon diversity; CWM volume index refers to the Van Wagner formula.

Stand	Average (Tallest 10%) Canopy Height (m)	Vegetation Species Diversity	Vegetation Structural Diversity	Hardwood Basal Area (m^2 / ha)	Softwood Basal Area (m^2 / ha)	Snag Classes 2-4 Basal Area (m^2 / ha)	CWM Class 2 Volume Index	CWM Class 3 Volume Index	CWM Class 4 Volume Index
c22	13.1	3.29	1.29	3	4	0	20.07	2.52	4.41
c8	9.0	2.81	1.09	3	5	1	2.05	14.74	2.66
s12	16.2	2.63	1.43	3	8	0	1.98	4.57	4.09
s20	17.1	3.06	1.68	2	23	2	10.59	4.67	7.21
s25	16.0	3.18	1.48	8	10	2	7.67	6.22	7.59
s26	20.3	2.88	1.86	6	18	3	1.91	5.78	9.36
s52	20.4	2.69	1.95	16	9	2	2.57	3.71	6.19
w2	9.8	3.40	1.13	3	9	0	3.24	10.62	6.09
w21	10.9	2.56	1.18	6	24	6	3.48	10.69	6.41
w23	10.4	2.31	1.20	2	22	0	0.00	1.70	10.94
w29	8.9	2.96	1.09	1	9	0	1.48	3.65	3.08
w7a	9.1	2.82	1.10	2	8	1	0.14	2.24	5.19
w7b	7.9	3.07	0.92	2	5	0	0.41	6.76	11.36

species abundance per trap week was 37% higher in 1997 than in 1998 ($p = 0.013$, Table 1.3, Table A.4).

1.4.2. Effect of Silvicultural Methods

At the stand scale, stands managed using the selection method contained 4.3 more species of click beetles than in stands initiated by clearcutting ($p = 0.016$, Tables 1.3a and A.3a, Figure A.1a). Model comparisons using AIC$_c$ indicated that the best model predicting click beetle species richness at the stand scale included silvicultural method rather than any environmental variables (Table A.5a). At the trap-height scale, species richness decreased with increasing trap height ($p < 0.001$, Tables 1.3c and A.3c and Figure A.2a). However, model comparisons using AIC$_c$ indicated that the best model predicting click beetle species richness at the trap-height scale included relative canopy height instead of silvicultural method and height (Table A.5b).

At the stand scale, click beetle species abundance per trap week was 194% and 264% higher in the shelterwood and selection stands, respectively, than in the clearcut stands ($p < 0.001$, Tables 1.4a and A.4a). However, model comparison with AIC_c indicated that the best model predicting the abundance of click beetle species at the stand scale included hardwood basal area (Table A.5c). NMS ordination separated stands according to harvest treatment (Figure 1.2a), suggesting a correlation between the harvest treatments and click beetle assemblages. At the trap-height scale, species abundance in selection stands increased with trap height, while abundance in clearcut and shelterwood stands decreased with increased trap height ($p < 0.001$, Tables 1.4c, A.4c, Figure A.2c). Model comparisons using AIC_c indicated that the best model for click beetle species abundance at the trap-height scale included relative canopy height (Table A.5d).

1.4.3. Effect of Vegetation

1.4.3.1. Relative Canopy Height

Model comparisons using AIC_c indicated that the strongest model predicting click beetle species richness and species abundance at the trap-height scale contained relative canopy height rather than silvicultural method and height (Table A.5b and d). Both species richness ($p < 0.001$, Tables 1.3d, A.3d, Figure A.2b) and species abundance ($p < 0.001$, Tables 1.4d, A.4d, Figure A.2d) decreased with increasing relative canopy height.

1.4.3.2. Stand Structural and Vegetation Species Diversity

Click beetle species richness, total abundance, and diversity per trap week were 18% ($p = 0.10$), 19% ($p = 0.10$), and 19% ($p = 0.05$) higher in stands of high stand structural diversity than in stands of low stand structural diversity, respectively (Table 1.5). Assemblage similarity, a measure of the overlap of species between groups of stands, was 65%, indicating that 35% of the species were found only in stands of high

Table 1.3. Results for the Site and Height general linear models of click beetle species richness.

Source	DF	F Value	Pr > F
a) Site Model- Harvest Treatment			
Year	1	2.84	0.118
Treatment	2	6.05	0.015
Site within Treatment	10	3.79	0.016
b) Site Model- Environmental Variable			
Year	1	1.50	0.234
Hardwood Basal Area	1	9.60	0.005
c) Height Model- Harvest Treatment			
Year	1	3.66	0.058
Treatment	2	22.09	<.001
Site within Treatment	10	2.16	0.024
Trap Height	1	93.93	<.001
d) Height Model- Environmental Variable			
Year	1	2.56	0.112
Relative Canopy Height	1	57.4	<.001

Table 1.4. Results for the Site and Height general linear models of click beetle species abundance.

Source	DF	Chi-Square	Pr > ChiSq
a) Site Model- Harvest Treatment			
Year	1	6.13	0.013
Beetle Species	15	318.4	<.001
Treatment	2	26.51	<.001
Site within Treatment	10	15.31	0.121
b) Site Model- Environmental Variable			
Year	1	5.5	0.019
Beetle Species	15	154.73	<.001
Hardwood Basal Area	1	1.04	0.308
Hardwood Basal Area* Beetle Species	15	28.11	0.021
c) Height Model- Harvest Treatment			
Year	1	9.57	0.002
Species	15	558.88	<.001
Treatment	2	15.74	<.001
Site within Treatment	10	17.52	0.064
Trap Height	1	16.87	<.001
Trap Height*Treatment	2	38.45	<.001
d) Height Model- Environmental Variable			
Year	1	9.77	0.002
Beetle Species	15	568.6	<.001
Relative Canopy Height	1	13.39	<.001

Table 1.5. Summary of richness (number of species) per stand, total abundance (number of individuals per trap week) per stand, and rarefaction-estimated species diversity of click beetles for 1997-1998.

Source	Species Richness	Total Abundance	Diversity[a]
Hardwood Basal Area			
Low (0-3.4; n = 9)	21.0	17.1	26.5+/-1.8 (70)
High (5.7-15.8; n = 4)	27.8[b]	22.5[b]	36.0+/-0.0 (70)[b]
Softwood Basal Area			
Low (0-9.6; n = 9)	23.3	18.7	24.9+/-2.1 (50)
High (17.6-23.6; n = 4)	22.5	19.1	25.3+/-1.3 (50)
Vegetation Species Diversity			
Low (0-3.0; n = 8)	24.0	19.7	27.7+/-2.1 (60)
High (3.1-3.4; n = 5)	21.6	17.3	25.9+/-0.9 (60)
Vegetation Structural Diversity			
Low (0-1.2; n = 7)	21.3	17.3	30.0+/-0.0 (100)
High (1.3-2.0; n = 6)	25.2[c]	20.6[c]	35.7+/-0.5 (100)[b]
Snag Classes 2-4 Basal Area			
Low (0-0.2; n = 9)	20.4	16.5	26.8+/-2.1 (60)
High (0.4-2.0; n = 4)	26.2[b]	21.5[b]	30.4+/-0.6 (60)
CWM Class 2 Volume Index			
Low (0-123.9; n = 9)	22.4	18.8	34.0+/-0.0 (78)
High (147.7-292.5; n = 4)	23.8	18.8	31.1+/-1.8 (78)
CWM Class 3 Volume Index			
Low (0-123.9; n = 9)	23.1	19.1[c]	32.8+/-1.3 (92)
High (147.7-292.5; n = 4)	23.0	18.5	34.0+/-0.0 (92)
CWM Class 4 Volume Index			
Low (0-123.9; n = 9)	23.5	18.6	30.0+/-2.1 (70)
High (147.7-292.5; n = 4)	22.4	19.1	30.5+/-0.6 (70)

[a] Rarefaction-estimated number of species +/- SD (number of individuals in subsample). [b,c] Significantly higher ([b] $p < 0.05$, [c] $p < 0.10$).

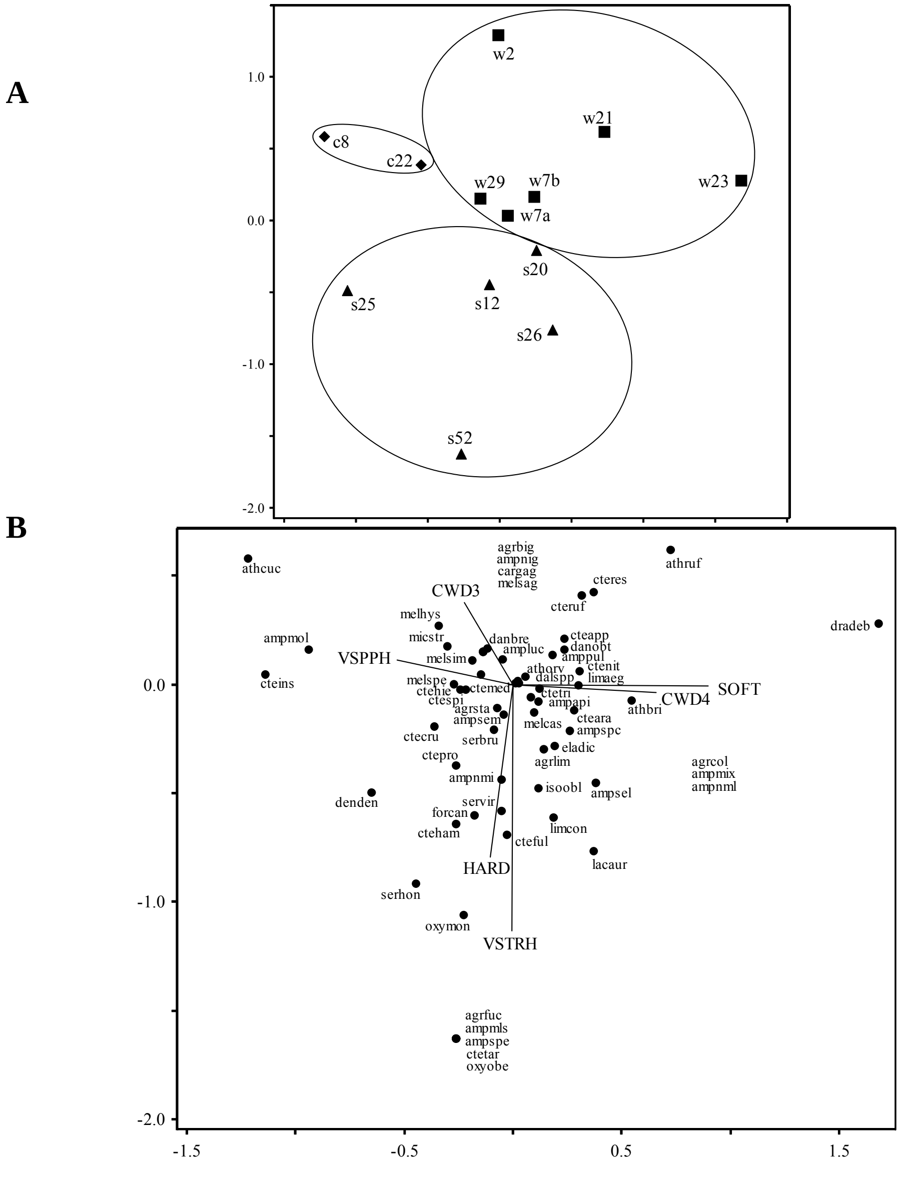
Table 1.6. Pearson and Kendall correlations of click beetle species and environmental variables with site locations along two NMS ordination axes. The horizontal and vertical axes explain 30.0% and 47.3% of the variation in the click beetle community structure, respectively. Note: Only the environmental variables with significant correlations with one or both ordination axes are shown. *, ($p < 0.1$); **, ($p < 0.05$); ***, ($p < 0.001$).

Source	Abbre-viation	Horizontal Axis		Vertical Axis	
		r	*tau*	r	*tau*
Click Beetle Species					
Agriotella bigeminata	agrbig	-0.06	-0.13	0.06	0.00
Agriotes collaris	agrcol	0.02	0.12	0.02	0.00
Agriotes fucosus	agrfuc	-0.11	-0.2	-0.67***	-0.39**
Agriotes limosus	agrlim	0.13	0.24	-0.27	-0.34**
Agriotes stabilis	agrsta	-0.42	-0.26	-0.57**	-0.39**
Ampedus apicatus	ampapi	0.20	0.07	-0.14	0.07
Ampedus luctuosus	ampluc	-0.11	0.24	0.28	0.11
Ampedus mixtus	ampmix	0.23	0.08	0.09	-0.21
Ampedus melsheimeri	ampmls	-0.11	-0.2	-0.67***	-0.39**
Ampedus molestus	ampmol	-0.72***	-0.62***	0.13	0.12
Ampedus nigricollis	ampnig	-0.06	-0.13	0.06	0.00
Ampedus near melantoides	ampnmi	-0.04	-0.12	-0.34	-0.21
Ampedus near mixtus	ampnml	0.02	0.15	0.01	-0.03
Ampedus pullus	amppul	0.44	0.30*	0.35	0.12
Ampedus sellatus	ampsel	0.35	0.16	-0.42	-0.31
Ampedus semicinctus	ampsem	-0.15	0.14	-0.43	-0.12
Ampedus species C	ampspc	0.10	0.20	-0.09	-0.13
Ampedus species E	ampspe	-0.11	-0.2	-0.67***	-0.39**
Athous brightwelli	athbri	0.33	0.44**	-0.04	0.00
Athous cucullatus	athcuc	-0.49*	-0.39**	0.24	0.26
Athous orvus	athorv	0.02	0.07	0.02	-0.07
Athous rufifrons	athruf	0.29	0.33*	0.26	0.33*
Cardiophorus gagates	cargag	-0.06	-0.13	0.06	0.00
Ctenicera appropinquans	cteapp	0.34	0.23	0.32	0.15
Ctenicera arata	cteara	0.63**	0.51***	-0.27	-0.14
Ctenicera cruciata	ctecru	-0.69***	-0.59***	-0.36	-0.31*
Ctenicera fulvipes	cteful	-0.03	-0.05	-0.63**	-0.49***
Ctenicera hamata	cteham	-0.16	-0.02	-0.39	-0.45**
Ctenicera hieroglyphica	ctehie	-0.53**	-0.44**	-0.04	0.31*
Ctenicera insidiosa	cteins	-0.68***	-0.53***	0.03	0.00

Table 1.6 continued.

Source	Abbre-viation	Horizontal Axis		Vertical Axis	
		r	*tau*	r	*tau*
Click Beetle Species					
Ctenicera mediana	ctemed	-0.21	-0.24	0.08	-0.04
Ctenicera nitidula	ctenit	0.27	0.37**	0.06	0.02
Ctenicera propola	ctepro	-0.48*	-0.33*	-0.67***	-0.62***
Ctenicera resplendens	cteres	0.22	0.17	0.26	0.26
Ctenicera rufopleuralis	cteruf	0.39	0.24	0.52**	0.42*
Ctenicera spinosa	ctespi	-0.38	-0.10	-0.03	-0.10
Ctenicera tarsalis	ctetar	-0.11	-0.20	-0.67***	-0.39**
Ctenicera triundulata	ctetri	0.47*	0.46**	-0.35	-0.28*
Dalopius species	dalspp	0.39	0.26	-0.05	0.03
Danosoma brevicornis	danbre	-0.26	-0.08	0.37	0.14
Danosoma obtectus	danobt	0.10	0.13	0.07	0.07
Denticollis denticornis	denden	-0.61**	-0.57***	-0.47*	-0.34**
Drasterius debilis	dradeb	0.68***	0.39**	0.12	0.13
Elathous dicalceatus	eladic	0.18	0.20	-0.26	-0.37**
Fornax canadensis	forcan	-0.20	-0.15	-0.66***	-0.53***
Isoriphis obliqua	isoobl	0.12	0.10	-0.51**	-0.33*
Lacon auroratus	lacaur	0.15	0.26	-0.31	-0.33*
Limonius aeger	limaeg	0.42	0.37**	0.00	0.06
Limonius confusus	limcon	0.11	0.07	-0.37	-0.07
Melanotus castanipes	melcas	0.38	0.19	-0.51*	-0.64***
Melanotus hyslopi	melhys	-0.21	-0.29*	0.17	0.15
Melanotus sagitarius	melsag	-0.06	-0.13	0.06	0.00
Melanotus similis	melsim	-0.24	-0.26	0.15	-0.02
Melanotus species	melspe	-0.16	-0.02	0.00	0.02
Microhypnus striatulus	micstr	-0.23	-0.16	0.14	0.16
Oxygonus montanus	oxymon	-0.17	-0.14	-0.80***	-0.65***
Oxygonus obesus	oxyobe	-0.11	-0.2	-0.67***	-0.39**
Sericus brunneus	serbru	-0.19	' 0.03	-0.45*	-0.39**
Sericus honesticus	serhon	-0.34	-0.36**	-0.71***	-0.56***
Sericus viridanus	servir	-0.06	-0.05	-0.63**	-0.47**
Environmental Variables					
Vegetation Species Diversity	VSTRH	0.00	0.03	0.65***	-0.51***
Vegetation Structural Diversity	VSPPH	0.31**	-0.28*	0.07	0.10
Hardwood Basal Area	HARD	0.06	-0.13	0.45***	-0.10
Softwood Basal Area	SOFT	0.51***	0.39**	0.00	0.00
CWM Class 3	CWD2	0.13	-0.05	0.22*	0.18
CWM Class 4	CWD4	0.38**	0.46**	0.02	-0.18

Figure 1.2. NMS ordination plots based on 16 click beetle species. The horizontal and vertical axes explain 30.0% and 47.3% of the variation in the click beetle community structure, respectively. Only significant correlation vectors (*r* or *tau* of at least $p < 0.1$) are shown. Length of vectors indicates the strength of the correlation. (A) Symbols code for site type (diamond = clearcut, square = shelterwood, and triangle = selection cut. (B) Abbreviations based on Table 1.6. Species agrcol, ampmix, and ampnmi are located at the center dot, and agrbig, ampnig, cargag, and melsag are at the dot below danbre.



structural diversity or only in stands of low structural diversity. Beetle assemblage similarity was 65% between stands of low and high vegetation species diversity. Stand structural diversity was correlated with the horizontal axis of the NMS ordination and associated with the 17 beetle species correlated with that axis; vegetation diversity was correlated with the vertical axis and associated with the 25 beetle species correlated with that axis (Table 1.6, Figure 1.2b).

1.4.3.3. Basal Area of Hardwoods and Softwoods

Model comparisons using AIC_c indicated that the best model for click beetle species richness at the stand scale contained silvicultural method; however, the best model of environmental variables included basal area of hardwoods (Table A.5a). Furthermore, model comparisons using AIC_c suggested that the best model predicting click beetle species abundance at the stand scale included hardwood basal area rather than silvicultural method (Table A.5c). Click beetle richness increased with hardwood basal area ($p = 0.005$, Tables 1.3b, A.3b, Figure A.2e). The abundance of three click beetle species (*A. semicinctus*, *Ctenicera hieroglyphica* Say, and *Oxygonus montanus* Schaeffer) increased with hardwood basal area ($p = 0.021$, Table 1.4b and A.4b, Figure A.2f).

Click beetle species richness, total abundance, and diversity per trap week were 32%, 31%, and 36% higher in stands of high hardwood basal area than in stands of low hardwood basal area, respectively ($p = 0.05$, Table 1.5). Beetle assemblage similarity was 63% between stands of high and low hardwood basal area and 62% between stands of high and low softwood basal area. Hardwood basal area was correlated with the NMS vertical axis and the associated 25 click beetle species, and softwood basal area was correlated with the horizontal axis and the associated 17 click beetle species (Table 1.6, Figure 1.2b).

1.4.4. Effect of Deadwood Conditions

1.4.4.1. Snag Classes 2-4

Click beetle species richness and total abundance per trap week were 28% and 31% higher in stands of high snag basal area than in stands of low snag basal area, respectively (*p* = 0.05, Table 1.5). Click beetle assemblage similarity was 65% between stands of low and high snag basal area, indicating a difference in beetle species composition among the stands.

1.4.4.2. CWM Classes 2, 3, and 4

Click beetle total abundance per trap week was 3% higher in stands of high decay class 3 CWM volume than in stands of low decay class 3 CWM (*p* = 0.10, Table 1.5). Beetle assemblage similarity was 62%, 63%, and 67% between stands of low and high decay class 2, 3, and 4 CWM volume, respectively. The volume of decay class 3 CWM was correlated with the NMS vertical axis and the associated 25 click beetle species, and the volume of decay class 4 CWM was correlated with the horizontal axis and the associated 17 click beetle species (Table 1.6, Figure 1.2b).

1.5. Discussion

This study demonstrated that the species richness and abundance of click beetles differed among stands created by clearcut, shelterwood, and selection silvicultural methods in the Acadian forest of Maine. The primary factors affecting differences in the click beetle richness and abundance among stands that were managed using different methods appeared to be associated with differences in relative canopy height and the presence of hardwoods. Vegetation composition, stand structural diversity, and amount of deadwood were also important stand characteristics determining habitat suitability for individual species of click beetles.

1.5.1. Effect of Silvicultural Methods

Management practices have been previously shown to affect insect assemblages in forest stands (Niemelä 1997, Grove 2002a). We found that silvicultural method was a better predicted click beetle richness than any of the environmental variables. However, hardwood basal area was a better predictor of click beetle species abundance than silvicultural method. Species richness of click beetles was higher in stands developed from repeated selection harvesting than clearcut harvesting. Species abundance of click beetles was lower in stands created by clearcutting than in either shelterwood or selection harvesting. These differences among harvest treatments were supported by the NMS ordination that separated harvest treatments based on the abundance of each click beetle species.

Su and Woods (2001) also found differences among silvicultural methods for Elateridae in a study based on a similar experimental design using some of the stands sampled in this study. In several cases, more than one elaterid species were grouped into a single morphospecies, and several individual species were separated into two morphospecies. As a result, findings by Su and Woods (2001) are difficult to compare with our study, where all Elateridae specimens were identified to species. Three morphospecies (*O. montanus*, *Ctenicera fulvipes* Bland, and one morphospecies of *A. stabilis*) were associated with selection harvested stands, three morphospecies (*A. semicinctus*, *C. triundulata*, a second morphospecies of *A. stabilis*, and one of the morphospecies of *A. mixtus*) were associated with stands that developed following clearcutting, and one morphospecies (made up of at least two species, *A. mixtus* and *Ampedus pedalis* Germar) was associated with shelterwood harvested stands. However, the models that best predicted species abundance did not included an interaction term between click beetle species abundances and silvicultural method; therefore we did not test for specific species differences among silvicultural methods.

Studies of other invertebrate taxa have found varied results depending on the taxa and forest management treatments. For example, ground beetles (Coleoptera: Carabidae) are commonly studied as indicators of ecosystem perturbations. In many instances, clearcutting appears to increase carabid species richness, abundance, and/or diversity (Jennings *et. al*. 1986, Beaudry *et al*. 1997, Heliola *et al*. 2001, Koivula 2002). On the other hand, Moore *et al*. (2004) found no significant effect of selective cutting (6-8 years after treatment) or strip clear-cutting (12-13 years after treatment) on carabids in northern hardwoods stands. Other beetle taxa often have differing results. For example, even 30-80 years after a clearcut, longicorn beetle (Coleoptera: Cerambycidae and Disteniidae) richness was lower than in uncut conifer and evergreen broad-leaved forests (Maeto *et al*. 2002). Sippola *et al*. (2002) found that an old-growth pine forest had lower overall beetle richness than a one year-old selection cut and lower non-saproxylic richness than a 15 year-old selection cut. No difference in overall beetle richness was found between the old-growth sites and the clearcut, but rare saproxylic beetle species were much lower in the clearcut than in the old growth. The authors accounted for these differing results by different habitat requirements among species. For example, the higher richness or abundance in clearcut areas was often due to disturbed regions hosting open-habitat species that did not penetrate into the forest, but species that require deeper forest were reduced in disturbed habitats.

Click beetle larvae (called wireworms) are well-known as agricultural and grassland (i.e., open habitat) pests. One might therefore expect, as with many carabid species, that a forest disturbance (such as clearcuts) might result in increased richness and abundance. In our study, however, species richness and species abundance were lowest in stands created by clearcutting, and species richness was highest in stands that had been created from repeated selection harvesting. This result suggests that differing responses among species of click beetles may be attributed to forest stand characteristics and species-specific requirements, rather than from a simple dichotomy between open versus forested habitat. Furthermore, we found environmental variables to be better predictors of click beetle richness and abundance than silvicultural method. This result may reflect the fact that varying degrees of environmental variables (such as hardwood basal area, stand structure, and deadwood content) can be achieved through using different silvicultural approaches.

1.5.2. Influence of Vegetation

1.5.2.1 Canopy Height

Many studies have demonstrated a change in insect species assemblage with height in or near forests (Rodgers and Kitching 1998, Fermon *et al*. 2003, Schowalter and

Zhang 2005), likely due to dispersal barriers, habitat requirements, management practices, and differences in tree species in the overstory and understory. In our study, click beetle abundance in selection stands increased with trap height, while abundance in clearcut and shelterwood stands decreased with trap height; however, click beetle species richness and species abundance decreased with relative canopy height. This result suggested that click beetles were responding to the canopy rather than simply to height above the ground.

Su and Woods (2001) also found differences among heights for Elateridae in the study discussed above. Recognizing the limitations of the groups of morphospecies, three morphospecies (later identified by S.L. Thomas from the reference collection as *A. stabilis*, *A. semicinctus*, and several *Melanotus* species) were consistently more abundant in upper traps among silvicultural treatments (clearcut, shelterwood, and selection), and one morphospecies (*O. montanus*) was consistently more abundant in lower traps. Four morphospecies (*C. triundulata*, *Dalopius* spp. Brown, several *Melanotus* species, and one of the *A. mixtus* morphospecies- formerly *A. rubricus*) were more abundant in the lower traps than the upper traps, but this difference depended upon the type of silvicultural method. The change among silvicultural method likely corresponded to differences in canopy height resulting from the patterns of harvest, which would corroborate our finding about the importance of relative canopy height.

Boiteau *et al*. (2000), however, indicated that click beetles responded to absolute height rather than canopy height, as there was no overstory canopy in their study. They examined Carabidae and Elateridae vertical flight distribution above a 0.22 ha meadow, surrounded by a forest on one side (at approximately 130 m from the traps) and field crops on all other sides. While Carabidae and Elateridae abundance decreased with height, many species were caught in the highest traps (14.3 m), and the authors concluded that flights for these species extended above the highest traps. Eight species of Elateridae were caught in sufficient numbers to establish vertical distribution profiles; the intercept varied among the species, demonstrating that, although they all decreased in numbers with height, the vertical profile varied among species. Of the 46 species of Elateridae collected, 32 species were also found in our study.

There are various reasons why adult click beetles may be found in the canopy. Click beetle adults may be actively dispersing to find new territory; Yamamura *et al*. (2003) found a mean dispersal distance of over 140m, and Boiteau *et al*. (2000) trapped click beetles at 14.3m off the ground. They may use vertical flight for escape. Click beetle adults may also be occupying the canopy to search for food, as some species of adults feed on aphid honeydew, aphids, other herbivores, or flower nectar or pollen (Yano *et al*. 1984, Johnson 2002).

1.5.2.2. Stand Structural Diversity

In our study, click beetle richness, abundance, and diversity were higher in stands of high stand structural diversity, and there were differences in species composition among stands. Seventeen species of Elateridae were correlated with increased stand structural diversity. It may be that some species of click beetles responded to the increased habitat provided by greater amounts of vegetation structure. This suggestion may be supported by Linit *et al*. (1986) in a study of insects inhabiting 80 year-old northern red oak (*Quercus rubra*) stands that had been harvested (clearcut or thinned) and replaced with red oak seedlings. They collected adults of a click beetle (*Limonius* spp.) on red oak (*Quercus rubra*) seedlings, but did not capture any adults emerging from soil. Therefore, this species likely dispersed to these sites as adults. All of the specimens were collected in the partial cut rather than in the clearcut, suggesting that adults preferred greater vegetation structure.

Structural diversity in forest stands is often related to canopy height, with taller stands providing more diverse stand structures and foliage, and therefore more structural complexity (Brokaw and Lent 1999). Even- and uneven-aged silvicultural methods, such as shelterwood and selection systems, alter canopy structure by affecting the amount and distribution of foliage. As a result, silvicultural practices can directly and indirectly influence invertebrates through the vertical placement of food and shelter, and by affecting microclimate and prey items (Pettersson 1996, Phillips and Cobb 2005). For example, Hamer *et al*. (1997) rated forest stands according to forest structure (measured primarily as tree density, height, and diameter) and found that overall butterfly diversity was highest in the most heavily disturbed forest stand (with intermediate tree size and low tree density), but the most common species in these sites had wide-ranging geographical distributions. On the other hand, biogeographical distinctness (a measure of endemism) was higher on sites with greater forest structure, demonstrating that species with small geographical ranges required greater stand structure.

1.5.2.3. Forest Composition

The abundance of hardwood or softwood tree species also can have a large influence on the invertebrate populations occupying forest stands (Hughes *et al*. 2000, Novotny *et al.* 2006). For example, Work *et al.* (2004) found that differences in the epigaeic arthropod community among forest stands were influenced by the relative proportion of coniferous and deciduous trees in the overstory and understory. Grove (2002b) found that, although the volume of CWM was most strongly correlated with saproxylic species richness, basal area was also an appropriate surrogate measure. However, the basal area of larger-diameter trees was a better measure than total basal area.

In our study, the basal area of hardwoods was the best predictor of species abundance in all models, and it was the best predictor of species richness among the environmental variables examined. There were differences in beetle assemblages between stands of low or high vegetation species diversity, and eighteen click beetle species were correlated with vegetation species diversity. Stands of high or low hardwood and softwood basal area also varied in click beetle species composition. Click beetle species richness, total abundance, and diversity were higher in stands of high hardwood basal area, and hardwood basal area was the best predictor of both click beetle species richness and species abundance. Although click beetles are clearly found in softwood-dominated stands and to emerge from softwood logs (see Chapters 2 and 3), click beetle species richness, total abundance, and diversity were similar between stands of high and low softwood basal area. Assemblage similarity measures demonstrated differences in click beetle assemblages between stands of high and low softwood or hardwood content. Twenty-five species of Elateridae were correlated with increased hardwood basal area, and seventeen species were correlated with increased softwood basal area, further demonstrating click beetle assemblage response to hardwood or softwood content.

Click beetles generally spend 1 to 3 years as larvae in soil and/or deadwood (Johnson 2002). Adults captured by our traps may have emerged from these stands and/or dispersed to these sites as adults and were responding to above-ground conditions such as food or habitat conditions in the aboveground portions of the plants (see above). On the other hand, adults captured by our traps may have emerged from these stands and were responding to humus, leaf litter, or deadwood conditions influenced by forest composition. Saetre *et al*. (1999) studied soil fauna in spruce and mixed spruce-birch stands, finding that the abundance of many taxa, including Elateridae, was higher in the mixed stands than in the pure spruce stands. They concluded that the birch leaf litter was important in determining soil fauna composition by addition of substrate and by sustaining leaf litter moisture. However, Scheu *et al*. (2003) studied soil fauna in pure and mixed stands of beech and spruce; although most invertebrate species had higher biomass in the pure beech or mixed stands, click beetles had higher biomass in the spruce forests. Beech leaves are a more favorable food resource than spruce needles, so they speculated that these elaterid larvae are able to live on poor food substrates due to their slow growth and long larval development. Linit *et al*. (1986) collected adults of one unidentified elaterid species emerging from soil in stands of 80 year-old northern red oak (*Quercus rubra*) that had been cut and replaced with red oak seedlings. Because no specimens were collected on the seedlings themselves, it is likely this species inhabited the stand only at the larval stage, and responded to soil or humus conditions. Invertebrates living in deadwood are also affected by forest composition; Jacobs (2004) found that saproxylic beetle richness was influenced by stands dominated by deciduous or coniferous trees.

1.5.3. Deadwood Influences

Saproxylic insects depend on dying or dead wood (or taxa associated with deadwood) for at least part of their life cycle (Speight 1989). Studies of saproxylics are becoming more common as ecologists recognize their importance to the conservation of biodiversity in the management of forests. Deadwood includes snags, CWM, and live trees with hollows or dead parts (Siitonen 2001, Ranius 2002, Ranius and Jansson 2002). There are many factors affecting saproxylic insect assemblages, including deadwood characteristics such as species, stage of decay, diameter, point of origination (i.e. trunk, branch, roots), and fungi and other saproxylic species assemblages, but also including stand and landscape conditions such as amount of surrounding CWM, sun exposure, forest fragmentation, and forest successional stage and cover type (Schiegg 2000, Siitonen 2001, Jacobs 2004).

CWM is increasingly studied as crucial habitat for forest biodiversity. There are twice as many saproxylic beetles as all terrestrial vertebrates combined (Parker 1982), and saproxylics comprise a substantial percentage of forest insects (Martikainen *et al.* 2000, Siitonen 2001). Many studies have established a strong link between species richness and CWM volume (Økland *et al.* 1996, Martikainen *et al.* 2000, Grove 2002a and b). Snags, although less commonly studied, are also important habitat with different assemblage successional patterns from downed logs (Siitonen 2001). Siitonen (1994) collected saproxylic beetles in two old spruce forests. Common generalist species were abundant in both forests, but specialists on spruce (including four elaterid species) or birch snags were more abundant in the forest with more decaying wood. Jacobs (2004) studied beetle assemblages on girdled and natural snags in stands of several cover types. Beyond differences between girdled (aspens did not die as readily as spruce trees) and natural snags, he found that stand scale snag and CWM volume and cover type were important to beetle communities. Therefore, it is not surprising that click beetle assemblages in our study differed among stands with varying amounts of deadwood.

Click beetle richness and total abundance in our study also were higher in stands of high snag (decay classes 2-4) basal area, and click beetle total abundance was higher in stands with high CWM (decay class 3) volume. Click beetle assemblage similarity differed between stands of high and low classes 2-4 snag basal area and CWM classes 2, 3, and 4 volume. Twenty-five species of click beetles were correlated with CWM class 3 volume, and seventeen species were correlated with CWM class 4 volume.

The apparent effect of deadwood on the click beetle species assemblage is consistent with their natural history. Click beetles are known to inhabit both snags and CWM as larvae, and those inhabiting soil can be influenced by the proximity to CWM (Chershire 1988, Marra and Edmonds 1998). Both snags and CWM undergo a succession of insect species as the wood decays. Insects that inhabit newly dead wood often require fresh phloem or sapwood (Hammond *et al*. 2004). The species richness of predators, fungivores, and scavengers increases in response to further wood decomposition (aided by suites of fungus) and greater microhabitat diversity (Siitonen 2001). Elateridae are not common to fresh deadwood, but in our study, the later classes of decay were important forest stand characteristics that showed positive relationships with their species assemblages.

Chapter 2

RELATION BETWEEN VEGETATION COMPOSITION AND CLICK BEETLE (COLEOPTERA: ELATERIDAE) ASSEMBLAGES IN MAINE'S ACADIAN FOREST

2.1. Abstract

I examined whether populations and communities of click beetles (Coleoptera: Elateridae) were associated with habitats dominated by specific plant species in the Acadian forest of Maine. Emergence traps were used to collect adult beetles as they emerged from soil beneath hardwood (Maple, Birch, Aspen, Blueberry, and Oak) and softwood (Spruce-Fir-Pine, Pine, Hemlock, and Fern-Hemlock) cover types. Forty species of click beetle were collected, with *Ctenicera triundulata*, *Dalopius* spp., and *Agriotes stabilis* being most abundant. Click beetle assemblages, measured with richness, abundance, diversity and similarity, varied among the five hardwood and four softwood plant communities. Species richness was lowest in the Spruce-Fir-Pine and highest in the Oak cover type. Species abundance was lowest in the Spruce-Fir-Pine and Pine and highest in the Oak, Maple, and Hemlock cover types. Diversity was generally higher on hardwood cover types than softwood cover types. Assemblage similarity was generally low between hardwood and softwood cover types, indicating that species composition differed between these stands. Assemblages in non-oak hardwood cover types were more similar to each other than to the Oak cover type. Four species of click beetle were more abundant in softwood stands, and seven species were associated with increases in specific softwood tree and shrub species. Nine species of click beetle were more abundant in hardwood stands, and fifteen species were associated with increases in

specific hardwood tree and shrub species, including six species associated with oak stands.

2.2. Introduction

Conserving biodiversity has been identified as an important concern in forest management (Hunter 1999, Lindenmayer and Franklin 2002). Identifying species that are present in forests, their habitat preferences, and how management practices affect these relationships are keys to addressing this concern. This basic information is unknown for the majority of invertebrate species in North American temperate forests (Danks and Foottit 1989, Carlton and Robison 1998). Insects are an important group of organisms to understand because they are highly diverse, outnumbering all other higher taxa (MEA 2005), and perform many important functions in forest ecosystems (Crowson 1981, Wilson 1992). Furthermore, since forest management practices affect insect populations (Niemelä 1997, Grove 2002), insects may serve as important indicators of ecological sustainability (Kremen *et al.* 1993, Taylor and Doran 2001).

There are approximately 10,000 described species in the family Elateridae (click beetles), making it the ninth most species rich family of beetles (Johnson, 2002). Often considered pests in agricultural systems, this family does not cause serious damage to forest trees. Living in forest soils and deadwood as larvae, click beetles are notable predators of forest insect pests (Morris 1951, Yano *et al.* 1984), prey for birds and other biota (Barron and Walley 1983, Holmes and Robinson 1981, Heinrich and Bell 1995), and influences in nutrient cycles (Wolters 1989). Several species of click beetle are considered threatened or endangered in Europe (Anon. 1999, Alexander 2003, Zach

2003), but the dearth of detailed information about most species in this family currently limits strategic attempts at their conservation. Elaterids are ideal for forest biodiversity research because the family is numerically abundant and species rich, they can be collected using relatively simple trapping methods, and the species are characterized by diverse food and habitat preferences.

I designed a series of studies to investigate the habitat preferences of Elaterid species living in the Acadian forest in Maine. In a previous study, I determined that plant species diversity and the basal area of hardwoods and softwoods were important predictors of adult Elaterid assemblages in the Acadian forest of Maine (Chapter 1). Other studies have also demonstrated that the composition of forest vegetation can affect invertebrate assemblages through hardwood or softwood-specific insect-plant associations within a stand (Saetre *et al*. 1999, Paquin and Coderre 1997, and Ohsawa 2004).

Trees and shrubs influence the temperature and moisture of the soil (Phillips and Shure 1990 and Kapos 1989), both of can strongly impact the presence and movement of click beetle larvae in the soil (Lees 1943a&b, Zacharuk 1962, and LaFrance 1968). Leaf litter can also influence click beetle assemblages, as several species are considered to be saprophagous on dead leaves (Zacharuk 1963, Wolters 1989, and David *et al*. 1993), and carnivorous larvae will become detritivorous or saprophagous in the absence of prey (Balduf 1935). Because of this, Saetre *et al*. (1999) and Scheu *et al*. (2003) interpreted changes in click beetle assemblages across different forest stands as responses to nutrients from leaf input.

In this study, I tested whether the composition of click beetle assemblages and abundance of individual species emerging from soil were affected by the species composition of overstory and understory vegetation in the Acadian forest of central Maine. Previous studies by Paquin and Coderre (1997) and Saetre *et al*. (1999) found higher click beetle abundance in hardwood stands than softwood stands. In addition, my previous work (Chapter 1) found greater numbers of species associated with hardwood basal area than softwood basal area. Therefore, I hypothesized in this study that species richness and abundance of click beetles would be lower in stands dominated by softwood than hardwood species, and that some species (including *Agriotes stabilis LeC.*, *Ctenicera cruciata*, *Ctenicera hieroglyphica* Say, *Ctenicera propola* LeC., *Ctenicera triundulata* Randall, *Elathous dicalceatus* Say, *Fornax canadensis* Brown, *Isorhipis obliqua Say*, *Melanotus castanipes*, *Oxygonus montanus* LeC., *Sericus brunneus* LeC., and *Sericus viridanus Say*) would be associated with hardwood stands and other species (including *Ctenicera arata* LeC., *Ctenicera nitidula* LeC., and *Limonius aeger* LeC.) would be associated with softwood stands (Chapter 1).

2.3. Methods

2.3.1. Study Site

This study took place in the Penobscot Experimental Forest (44°50’ N, 68°35’ W), east-central Maine, USA (Figure B.1). The forest is part of the Acadian forest region (Bailey 1995, Lorimer and White 2003), which is considered transitional between the eastern temperate forest to the south and the boreal forest to the north. Common softwood tree species on the Penobscot Experimental Forest (PEF) include red (*Picea* *rubens* Sarg.), white (*P. glauca* (Moench) Voss) and black spruce (*P. mariana* (Mill.) B.S.P.), balsam fir (*Abies balsamea* (L.) Mill.), eastern white pine (*Pinus strobus* L.), eastern hemlock (*Tsuga canadensis* (L.) Carr.), and northern white cedar (*Thuja occidentalis* L.), and common hardwoods include red maple (*Acer rubrum* L.), white (*Betula papyrifera* Marsh.) and gray birch (*B. populifolia* Marsh.), and quaking (*Populus tremuloides* Michx.) and bigtooth aspen (*P. grandidentata* Michx.). The PEF has a complicated history of periodic partial harvests and insect outbreaks resulting in multi-cohort stand structures of many species (R. Seymour, unpublished data). Soils vary between glacial till ridges with sandy or well-drained loams to flat areas between ridges with poorly to very poorly drained loams and silt loams (Brissette 1996).

2.3.2. Cover Types

Most forest stands selected for sampling in this study were established as part of a long-term silvicultural experiment by the USDA Forest Service (Sendak *et al*. 2003). Silvicultural treatments that are part of this 60 year-long experiment produced stands of widely different composition- and structures. In addition, one red oak (*Quercus rubra* L.) stand (oak05) was located on the nearby University of Maine campus, and one eastern white pine plantation (pin07) was located on private land near Hampden, Maine.

In this study stand was defined as a relatively uniform area that was dominated by specific hardwood and softwood plant species common to the Acadian forest, including low blueberry (*Vaccinium angustifolium* Aiton), interrupted fern (*Osmunda claytoniana* L.), quaking (*Populus tremuloides* Michx.) and bigtooth aspen (*P. grandidentata* Michx.), white birch (*Betula papyrifera* Marsh.), red maple (*Acer rubrum*

Table 2.1. Tree basal area (m^2/ha) for each stand for A) 2001 and B) 2002.

Site	*Abies balsamea* Balsam Fir	*Acer rubrum* Red Maple	*Betula papyrifera* White Birch	*Picea rubra* Red Spruce	*Pinus strobus* White Pine	*Populus* species Aspen species	*Quercus rubra* Red Oak	*Thuja occidentalis* Northern White Cedear	*Tsuga canadensis* Eastern Hemlock
A) 2001									
asp22	0	0	0	0	0	31	0	0	0
bir08	0	0	13	0	0	0	0	0	0
bir22	1	0	11	0	0	0	0	0	0
blu08	0	0	0	0	0	0	0	0	0
blu22	1	0	3	0	0	1	0	0	0
hem12	2	0	0	11	2	0	0	0	15
hem20	5	5	0	3	0	0	0	1	7
inf12	1	0	0	4	0	0	0	0	8
inf20	6	2	0	2	0	0	0	3	5
map25	1	22	0	1	0	0	0	0	5
map26	0	17	1	0	0	0	0	0	5
spr21	17	5	0	5	2	0	0	0	0
spr23	5	0	0	7	21	0	0	0	0
B) 2002									
asp02	0	2	1	0	0	13	0	0	0
asp22	0	7	0	0	0	14	0	0	0
bir08	0	10	7	0	0	0	0	0	0
bir22	0	1	5	0	0	0	0	0	0
hem12	0	0	0	8	0	0	0	1	18
hem20	0	1	0	2	0	0	0	1	10
oak04	0	0	0	0	0	0	24	0	2
oak05	0	2	0	0	2	0	15	0	0
pin06	0	0	0	0	27	0	0	0	0
pin07	0	0	1	0	36	0	0	0	0
spr21	16	0	0	5	2	1	0	1	0
spr23	12	0	0	2	12	0	0	0	1

L.), northern red oak (*Quercus rubra* L.) eastern hemlock (*Tsuga canadensis* (L.) Carr.), red spruce (*Picea rubens* Sarg.), balsam fir (*Abies balsamea* (L.) Mill.), and eastern white pine (*Pinus strobus* L.). "Cover type" was defined as a stand condition dominated by a specific plant species or group of plant species and served as a treatment in the experimental design. Two stands were selected as replicates for each cover type. The one exception was the Aspen cover type in 2001, which had only one replicate. Three trap locations within each stand were selected based on the dominance and relatively uniform distribution of desired plant species. Plant species were considered dominant if at least 50% of the overstory basal area within 5 m of the center of the site or at least 50% of the understory canopy width within 2 m of the trap location was composed of that vegetation. In 2001, the cover types included Aspen (asp22), Birch (bir22, bir08), Blueberry (blu22, blu08), Maple (map25, map26), Fern-Hemlock (inf12, inf20, Hemlock (hem12, hem20), and Spruce-Fir-Pine (spr21, spr23). In 2002, the cover types included Aspen (asp02, asp22), Birch-Maple (bir08, bir22), Oak (oak04, oak05), Hemlock (hem12, hem20), Spruce-Fir-Pine (spr21, spr23), and Pine (pin06, pin07). Therefore, I used thirteen stands of seven cover types in 2001, and twelve stands of six cover types in 2002.

2.3.3. Beetle and Vegetation Sampling

Emergence traps were designed to collect adult insects as they emerged from the soil and were located at the center of each trap location. The traps, which covered 1 m^2 of soil, were constructed as dark mesh tents with clear collecting bottles, containing propylene glycol, located at the approximately 1.0 m high peak (Figure B.1). An inverted upper collecting bottle was fitted with a funnel to catch strong flying insects, and a lower collecting bottle, positioned directly below the upper bottle, was used to capture weaker flying insects that could not maneuver into the funnel. The traps were positioned over areas of soil with little or no coarse woody material (CWM) within one meter. The edges of the traps were sealed against the ground with weights to prohibit insects from entering or escaping the traps.

Insect samples were collected from the bottles biweekly from the beginning of June through the end of August of 2001 and 2002, and stored in a solution of 70% alcohol. Adult elaterid specimens were identified to species, stored in alcohol or pinned, and incorporated into the University of Maine Insect Collection. A reference collection for verification of species identification was sent to E.C. Becker and Serge LaPlante in Ottawa, Ontario, Canada. All further identifications were made by S.L. Thomas following the nomenclature of Dietrich (1945) and Downie and Arnett (1996).

Overstory and understory vegetation were sampled around each trap location during July of 2001 and 2002. For the overstory, a 10-factor prism was used to determine the basal area of each tree species. For the understory (ferns, shrubs, and small trees), canopy width at the widest point of each individual plant was measured within a 2 m distance from the trap location. I calculated the total canopy width for each understory species. Vegetation data were averaged between trap locations within each stand (Tables 2.1. and B.1).

2.3.4. Analytical Approach

I compared click beetle richness (numbers of species), abundance (numbers of individuals of each species), assemblage similarity, and diversity among cover types. Cluster analysis of Jaccard percent similarity measures using internet-based software provided by Brzustowski (2002) was used to measure assemblage similarity, the overlap of click beetle species among cover types. The rarefaction index takes into account both species richness and abundance, so it can be used as a measure of species diversity (Heck *et al*. 1975, Raup 1975); herein I use "diversity" to refer to rarefaction-estimated species richness. PAST (Hammer *et al*. 2001) was used to calculate the expected number of species derived from random subsamples of the total abundance, and compared species diversity among subsamples of similar sizes (Sanders 1968). I considered diversity between two groups significantly different when respective 95% confidence intervals did not overlap.

Two ordination analyses were used to examine the relation between click beetle species abundance and the vegetation community. I used non-metric multidimensional scaling (NMS; Kruskal 1964) to determine the strongest gradients in the click beetle assemblage structure among cover types and to associate click beetle species with particular vegetation species. Canonical correspondence analysis (CCA, Ter Braak 1986) was used to determine the amount of the variation in the click beetle assemblage that could be accounted for by vegetation variables. To exclude bias provided by including rare species (Jongman *et al*. 1995), I included only the 20 and 17 most common species for 2001 and 2002, respectively, in the analyses. A cube root transformation was used to reduce dominance of the most abundant species (McCune & Grace 2002).

For NMS, I used PC-ORD (McCune and Mefford 1999) with random starting configurations and the quantitative version of the Sorensen distance measure; the run with the lowest stress was used for the final analysis. For each year, six axes were assessed and three axes were selected. I presented results for only the two axes that had significant Monte Carlo test results ($p < 0.05$). The final stresses were was 5.96 and 6.11, and the two axes were 93.6% and 99.9% orthogonal for 2001 and 2002, respectively. I subsequently performed Pearson and Kendall correlations between the ordination axes with the beetle species and the vegetation species, and joint-plotted the vegetation species. A high correlation between a vegetation species and an NMS axis indicated a strong association between that vegetation species with the click beetle species associated with the axis. I overlaid polygons encircling the stands of major vegetation types.

For CCA, I used CANOCO version 4.5A (Ter Braak 2003) to employ an automatic CCA of click beetle species with overstory and understory vegetation. Monte Carlo analysis was performed using 1,000 permutations to test each CCA model at a significance level of alpha = 0.05. The results from the CCA showed that no multicollinearity was detected in any of the models. For each model the CCA stand ordination plots were very similar to the NMS ordination plots; therefore, I presented only the NMS site ordinations, but included the variation explained in the results (Appendix B.2).

I assessed the relationship between click beetle species richness and species abundance with the cover types using general linear models. For species richness, numbers of species were totaled within each stand; the main effect was cover type with PROC GLM (SAS Institute 2000). For species abundance, the abundances of each species were totaled within each stand; the main effects were species, cover type, and stand within cover type, and I used PROC GENMOD (SAS Institute 2000) with a negative binomial distribution because the data were over-dispersed. I used post-hoc contrasts with LSMEANS (SAS Institute 2000) to compare click beetle species richness and species abundances among cover types. In addition, I used post-hoc comparisons of relative abundances of all individual species of at least 5 specimens with 95% confidence intervals. I compared the softwood cover types to the hardwood cover types, excluding the 2001 aspen stand from the 2001 analysis to standardize numbers of stands within cover types. I also compared the three cover types within hardwoods and within softwoods, retaining all species in each analysis.

2.4. Results

2.4.1. Description of Beetle Taxa

I collected 998 click beetles of 41 different species, including one species (*Isorhipis obliqua*) from the family Eunemidae, the false click beetles (Table B.2). *Ctenicera triundulata*, *Dalopius* spp. Brown, and *Agriotes stabilis*, were the most common species, representing 36.0%, 19.2%, and 11.7%, of the total abundance, respectively. Nine species were singletons, and seventeen species were represented by only two to nine individuals.

2.4.2. Relation of Click Beetle Assemblages with Cover Types

In 2001, click beetle species richness varied among cover types (DF = 6,6, F = 6.03, p = 0.023); the Blueberry (p = 0.041), Maple (p = 0.019), Fern-Hemlock (p = 0.028), and Hemlock (p = 0.093) cover types had 110%, 650%, 120%, and 450% more species than the Spruce-Fir-Pine cover type, respectively (Figure 2.1a). In 2002, richness varied slightly among cover types (DF = 5,6, F = 3.77, $p = 0.069$); the Oak had 163% more species than the Spruce-Fir-Pine cover type ($p = 0.093$, Figure 2.1b).

In 2001, species abundance varied slightly among cover types ($p = 0.083$, Table 2.2a, Figure 2.1c). The Maple cover type had 147%, 87%, and 166% higher abundance than the Aspen ($p = 0.044$), Blueberry ($p = 0.074$), and Spruce-Fir-Pine ($p = 0.006$) cover types, respectively, and Hemlock ($p = 0.021$) and Fern-Hemlock ($p = 0.048$) had 219% and 263% greater abundance than the Spruce-Fir-Pine cover type, respectively. In 2002, species abundance varied among cover types ($p < 0.001$, Table 2.2b and Figure 2.1d). The Aspen ($p = 0.008$ and $p = 0.099$), Birch ($p < 0.001$ and $p = 0.007$), Hemlock ($p < 0.001$ and $p = 0.004$), and Oak ($p < 0.001$ and $p = 0.001$) cover types had 163% and 75%, 260% and 140%, 279% and 152%, and 357% and 205% higher abundance than the Spruce-Fir-Pine and Pine cover types, respectively. The Oak cover type had 74% higher abundance than the Aspen cover type ($p = 0.073$).

In 2001, click beetle diversity ($p = 0.05$, Table 2.3b) in the Blueberry and Aspen cover types was 35-100% and 48-67% higher than all other cover types, respectively, except Aspen was not different from Maple cover type. Diversity was 49%, 18%, and 49% higher in the Maple treatment than the coniferous Hemlock, Fern-Hemlock, and Spruce-Fir-Pine cover types, respectively. Diversity was 28% and 23% lower in Hemlock stand than in Birch or Fern-Hemlock cover types, respectively. In 2002, click beetle diversity ($p = 0.05$, Table 2.4b) was 32% and 28-58% higher in the Aspen than in Birch-Maple or the coniferous cover type (Pine, Spruce-Fir-Pine, and Hemlock), respectively. Diversity was 50% and 41-83% higher in Aspen than in Birch-Maple or the

Table 2.2. General linear model results of click beetle species abundance for A) 2001 and B) 2002. See Figure 2.1.

Source	DF	Chi-Square	Pr > ChiSq
A) 2001			
Species	30	217.37	<.0001
Compartment within Treatment	6	0.560	0.997
Treatment	6	11.17	0.083
B) 2002			
Species	32	223.75	<0.001
Compartment within Treatment	6	9.59	0.143
Treatment	5	28.47	<0.001

coniferous cover types, respectively. Diversity in Hemlock was 9% higher than in the Birch-Maple cover type.

In 2001, click beetle assemblage similarity (Table 2.3a) was low among all cover types; being most similar between Hemlock and Fern-Hemlock (58.8%), and between Birch and Maple cover types (52.4%). Similarity was lowest (20-35%) between hardwood-dominated and softwood-dominated cover types, although Birch were more similar to Hemlock and Fern-Hemlock cover types. Click beetle species assemblage similarity was slightly higher overall in 2002 (Table 2.4a). Assemblage similarity was lowest between the hardwood and softwood cover types (26.1-38.9%), although Birch-Maple was slightly more similar to Hemlock (41.7%), and Hemlock was less similar to the Spruce-Fir-Pine cover type (23.8%). Non-oak hardwoods were more similar to each other (60%) than the Oak cover type was to either the Aspen (48.0%) or Birch-Maple cover types (54.2%).

Table 2.3. Click beetle Jaccard assemblage similarity and rarefaction diversity results between vegetation treatments for 2001.

Source	Aspen	Birch	Blueberry	Maple	Hemlock	Fern-Hemlock	Spruce-Fir-Pine
A) Similarity							
Aspen	100.0	43.8	21.1	31.6	33.3	21.1	23.1
Birch	43.8	100.0	30.4	52.4	42.1	42.9	27.8
Blueberry	21.1	30.4	100.0	33.3	35.0	25.0	21.1
Maple	31.6	52.4	33.3	100.0	45.0	39.1	25.0
Hemlock	33.3	42.1	35.0	45.0	100.0	58.8	33.3
Fern-Hemlock	21.1	42.9	25.0	39.1	58.8	100.0	43.8
Spruce-Fir-Pine	23.1	27.8	21.1	25.0	33.3	43.8	100.0
B) Diversity							
Aspen	8.0+/-0.0 (15)						
Birch	5.4+/-1.3 (15)[a]	15.0+/-0.0 (94)	9.2+/-1.5 (40)[a]				9.9+/-1.5 (46)
Blueberry	8.5+/-1.3 (15)		15.0+/-0.0 (40)				
Maple	6.5+/-1.4 (15)	15.8+/-1.0 (94)	11.1+/-1.5 (40)[a]	17.0+/-0.0 (115)			11.9+/-1.5 (46)[a]
Hemlock	5.1+/-1.2 (15)[a]	10.8+/-0.9 (94)[a]	8.0+/-1.3 (40)[a]	11.4+/-0.7 (115)[a]	12.0+/-0.0 (150)	11.6+/-0.6 (127)[a]	8.5+/-1.3 (46)
Fern-Hemlock	4.9+/-1.3 (15)[a]	13.0+/-1.2 (94)	8.3+/-1.5 (40)[a]	14.3+/-0.8 (115)[a]		15.0+/-0.0 (127)	9.0+/-1.5 (46)
Spruce-Fir-Pine	4.8+/-1.0 (15)[a]		7.5+/-0.7 (40)[a]				8.0+/-0.0 (46)

Note: Rarefaction diversity is the estimated number of species +/- standard deviation for (number of individuals). Compare columns (main category with fewest number of individuals) to vegetation treatments in rows. Empty spaces indicate number of individuals in row was lower than that of the column. [a]Significantly different: respective 95% confidence intervals do not overlap.

Table 2.4. Click beetle Jaccard assemblage similarity and rarefaction diversity results between vegetation treatments for 2002.

Source	Aspen	Birch-Maple	Oak	Pine	Spruce-Fir-Pine	Hemlock
A) Similarity						
Aspen	100.0	60.0	48.0	38.9	33.3	36.0
Birch-Maple	60.0	100.0	54.2	38.9	33.3	41.7
Oak	48.0	54.2	100.0	36.4	26.1	34.5
Pine	38.9	38.9	36.4	100.0	41.7	42.1
Spruce-Fir-Pine	33.3	33.3	26.1	41.7	100.0	23.8
Hemlock	36.0	41.7	34.5	42.1	23.8	100.0
B) Diversity						
Aspen	17.0+/-0.0 (110)			15.8+/-1.0 (92)[a]	13.0+/-1.5 (60)[a]	
Birch-Maple	12.9+/-1.5 (110)[a]	17.0+/-0.0 (202)	14.7+/-1.3 (148)[a]	11.9+/-1.6 (92)	9.8+/-1.6 (60)	
Oak	19.7+/-1.3 (110)		22.0+/-0.0 (148)	18.3+/-1.5 (92)[a]	15.0+/-1.7 (60)[a]	
Pine				10.0+/-0.0 (92)	8.7+/-1.0 (60)	
Spruce-Fir-Pine					9.0+/-0.0 (60)	
Hemlock	13.3+/-1.7 (110)[a]	18.6+/-0.6 (202)[a]	15.6+/-1.5 (148)[a]	12.1+/-1.7 (92)		19.0+/-0.0 (209)

Note: Rarefaction diversity is the estimated number of species +/- standard deviation for (number of individuals). Compare columns (main category with fewest number of individuals) to vegetation treatments in rows. Empty spaces indicate number of individuals in row was lower than that of the column. [a]Significantly different: respective 95% confidence intervals do not overlap.

Figure 2.1. General linear model results for by treatment for click beetle (A&B) species richness and (C&D) species abundance (performed on log data) for (A&C) 2001 and (B&D) 2002 with standard error bars. See Table 2.5.

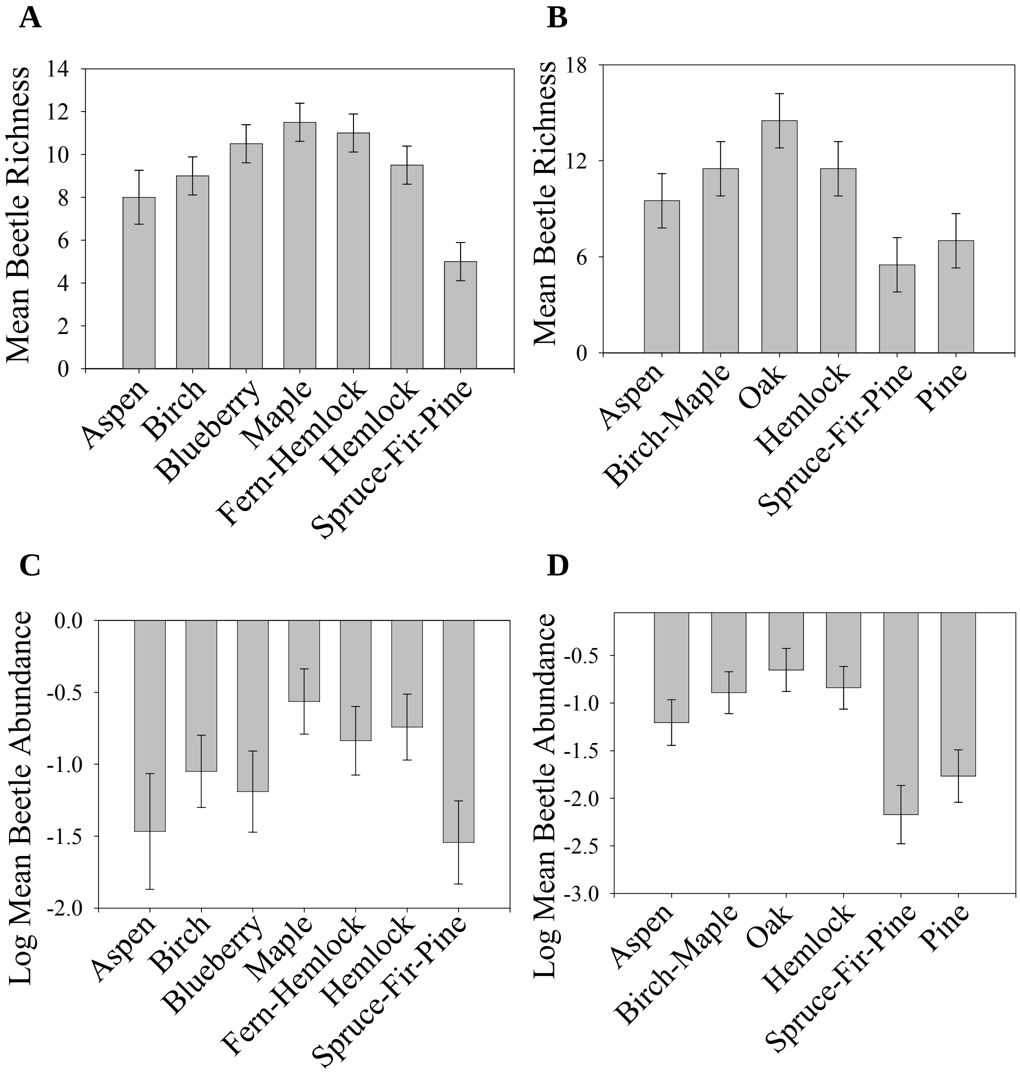


Figure 2.2. Relative abundance of the most common click beetle species in Hardwood and Softwood treatments (three stands in each) in A) 2001 and B) 2002. Asterisk denotes treatment with significantly higher relative abundance within a species.

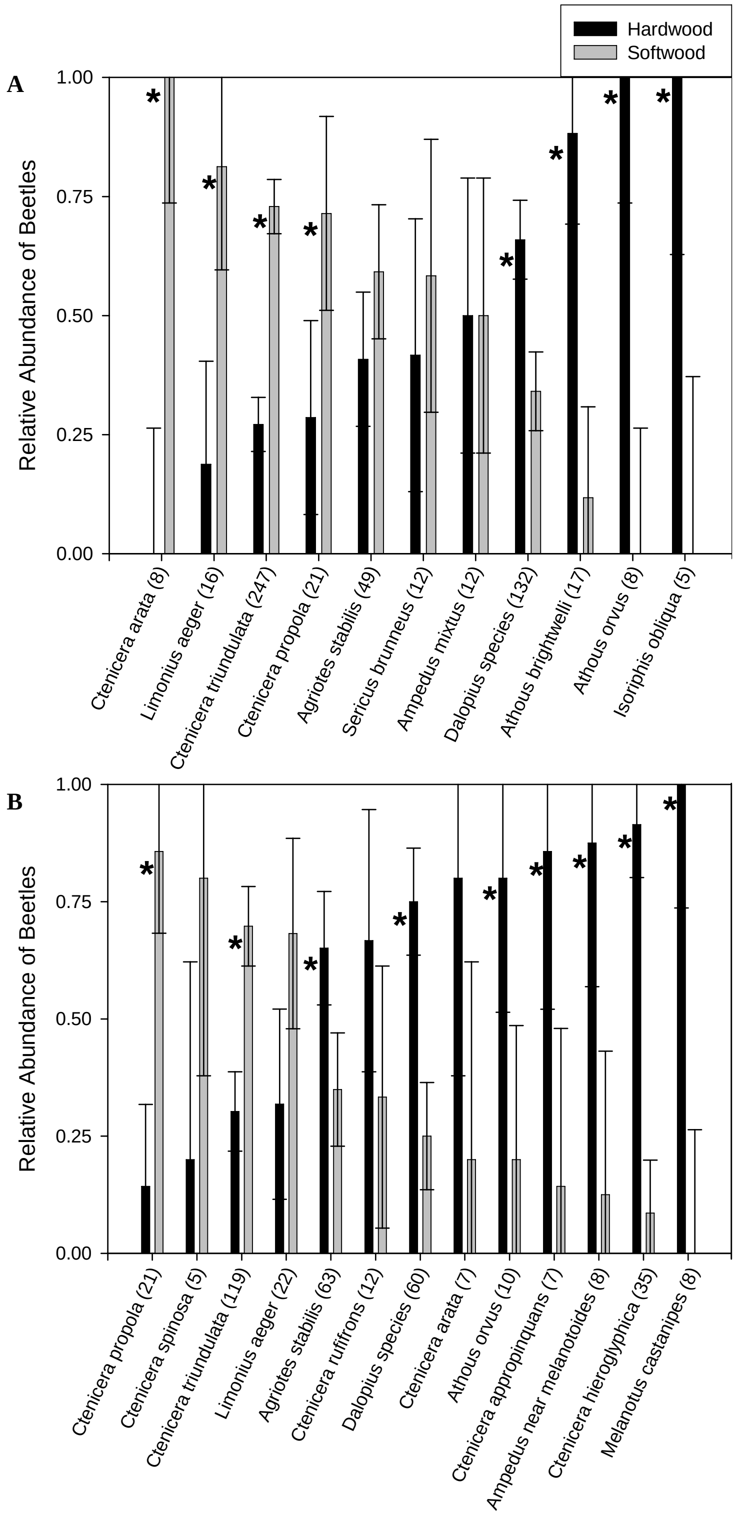


Figure 2.3. Relative abundance of beetle species in (A & B) 2001 and (C & D) 2002 in (A & C) Hardwood treatments and (B & D) Softwood treatments with confidence interval bars. Letters refer to differences among treatments within a species; only species with significant responses are included.

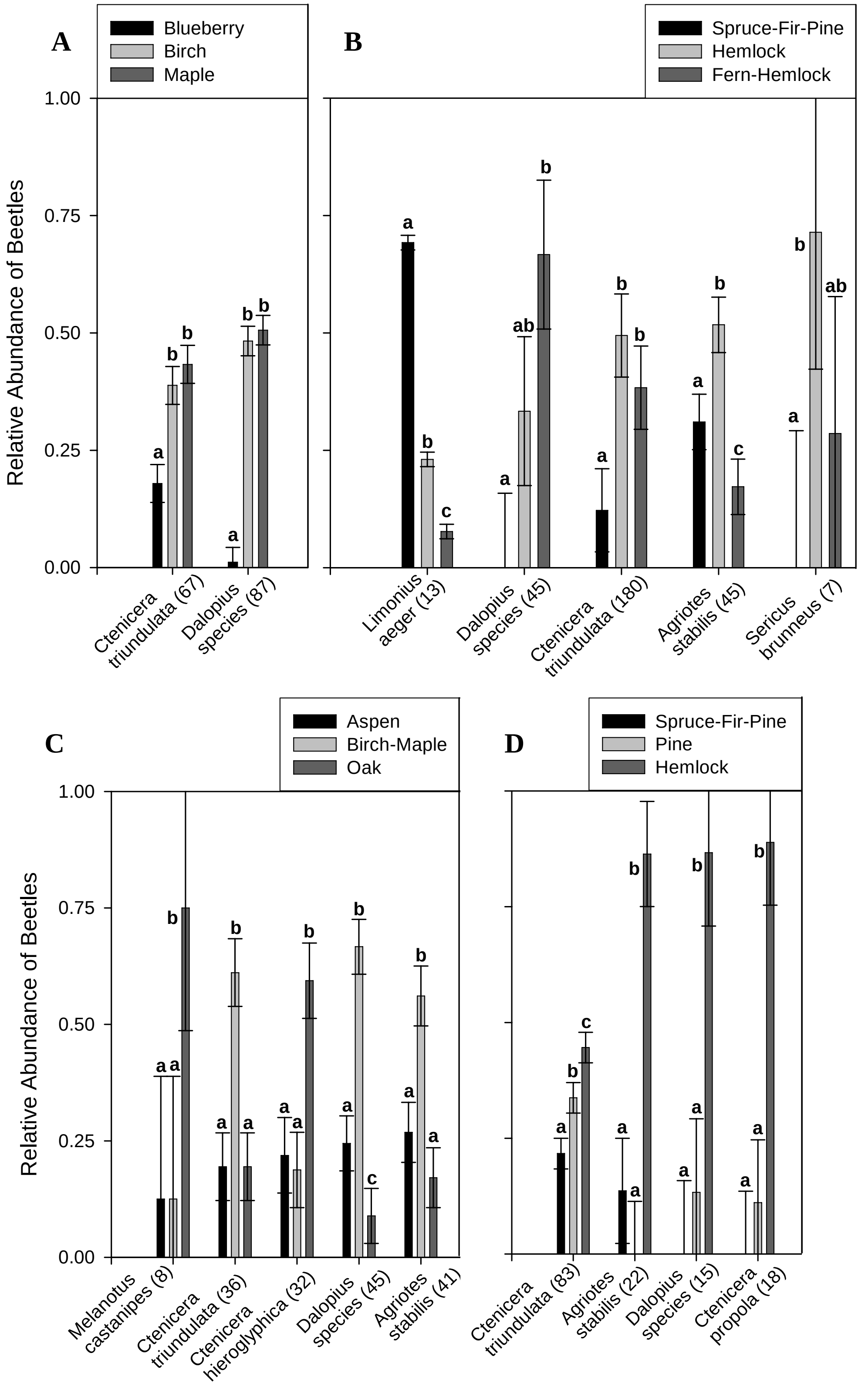


Figure 2.4. The NMS ordination plots based on 17 click beetle species from 2001 (A&C) and 20 click beetle species from 2002 (B&D). The 2001 vertical and horizontal axes explain 19.5% and 63.9% of the variation in the click beetle assemblage structure, respectively. The 2002 vertical and horizontal axes explain 29.5% and 41.7% of the variation in the click beetle assemblage structure, respectively. Note the different scales. Only significant correlation vectors (*r* or *tau* at least p < 0.1) are shown. Length of vectors indicates the strength of the correlation. (A&B) Symbols code for site type (square = hardwoods, diamond = softwoods). (C&D) Beetle and plant species abbreviations based on Table 2.6.

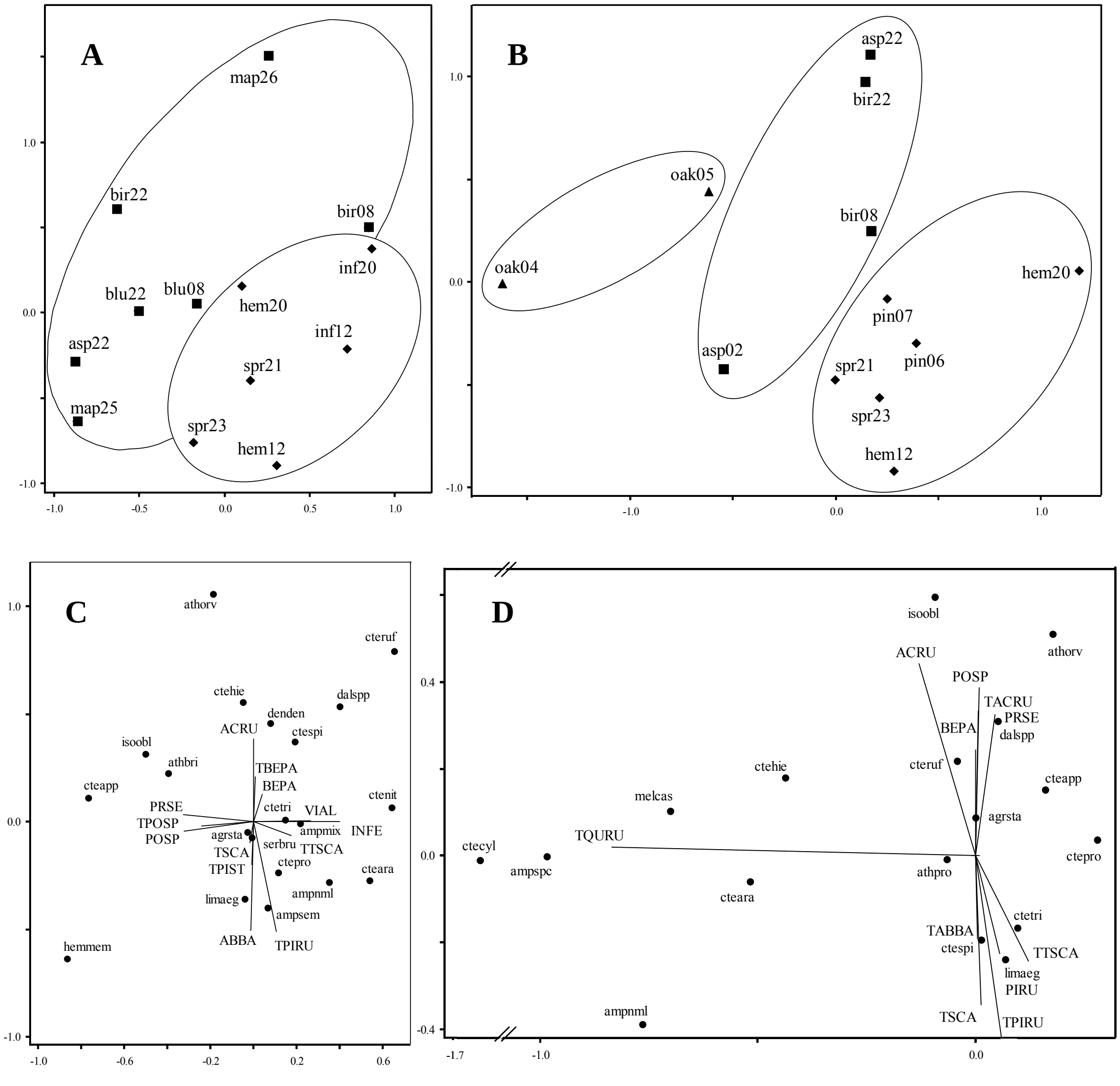


Table 2.5. Pearson and Kendall correlations of 2001 click beetle species abundance, tree species basal area, and shrub species canopy width with site locations along two NMS ordination axes. Only significant plant species are shown. The vertical and horizontal axes explain 19.5% and 63.9% of the variation in the click beetle community structure, respectively. See Figure 2.4.

Source	Abbreviation	Horizontal Axis		Vertical Axis	
		r	*tau*	r	*tau*
Click Beetle species					
Agriotes stabilis	agrsta	-0.22	-0.10	-0.33	-0.21
Ampedus mixtus	ampmix	0.46*	0.35**	-0.02	-0.08
Amedus near melanotoides	ampnml	0.33	0.24	-0.24	-0.16
Ampedus semicinctus	ampsem	0.07	0.08	-0.42	-0.34**
Athous brightwelli	athbri	-0.72***	-0.49**	0.38	0.28
Athous orvus	athorv	-0.14	-0.10	0.72***	0.53***
Ctenicera appropinquans	cteapp	-0.56**	-0.50	0.07	0.12
Ctenicera arata	cteara	0.59**	0.53***	-0.28	-0.24
Ctenicera hieroglyphica	ctehie	-0.05	-0.04	0.49*	0.33*
Ctenicera nitidula	ctenit	0.74***	0.60***	0.07	0.11
Ctenicera propola	ctepro	0.20	0.12	-0.38	-0.29*
Ctenicera rufopleuralis	cteruf	0.62**	0.54***	0.69***	0.54***
Ctenicera spinosa	ctespi	0.22	0.23	0.40	0.23
Ctenicera triundulata	ctetri	0.80***	0.62***	0.05	-0.05
Dalopius species	dalspp	0.66***	0.47**	0.81***	0.73***
Denticollis denticornis	denden	0.07	0.08	0.40	0.25
Hemicrepidius memnonius	hemmem	-0.43	-0.33*	-0.29	-0.26
Isoriphis obliqua	isoobl	-0.57**	-0.43**	0.33	0.18
Limonius aeger	limaeg	-0.07	-0.12	-0.57**	-0.42**
Sericus brunneus	serbru	-0.01	0.05	-0.10	-0.02
Tree species					
White Birch	TBEPA	0.18	0.00	0.48	0.49***
Red Spruce	TPIRU	0.35	0.21	-0.48	-0.59***
White Pine	TPIST	-0.04	0.02	-0.48	-0.53***
Aspen species	TPOSP	-0.45*	-0.45**	-0.13	-0.12
Eastern Hemlock	TTSCA	0.30	0.34**	-0.31	-0.12
Shrub species					
Balsam Fir	ABBA	-0.10	-0.19	-0.64**	-0.61**
Red Maple	ACRU	-0.03	-0.06	0.55**	0.06
White Birch	BEPA	0.18	-0.22	0.32	0.35**
Interrupted Fern	INFE	0.57**	0.45**	0.02	0.07
Aspen species	POSP	-0.51*	-0.49***	0.19	-0.26
Black Cherry	PRSE	-0.51*	-0.35**	0.16	0.14
Eastern Hemlock	TSCA	-0.12	-0.13	-0.28	-0.32*
Hobblebush	VIAL	0.46*	0.26	0.05	-0.02

Note: Significance: *, ($p < 0.1$); **, ($p < 0.05$); ***, ($p < 0.001$).

Table 2.6. Pearson and Kendall correlations of 2002 click beetle species abundance, tree species basal area, and shrub species canopy width with site locations along two NMS ordination axes. Only dominant and/or significant plant species are shown. The vertical and horizontal axes explain 29.5% and 41.7% of the variation in the click beetle community structure, respectively. See Figure 2.4.

Source	Abbre-viation	Horizontal Axis		Vertical Axis	
		r	*tau*	r	*tau*
Click Beetle species					
Agriotes stabilis	agrsta	0.00	-0.02	0.27	0.27
Ampedus near melanotoides	ampnml	-0.66	-0.32*	-0.37	-0.27
Ampedus species C	ampspc	-0.86***	-0.66***	0.00	0.07
Athous orvus	athorv	0.27	-0.09	0.85***	0.77***
Athous protervus	athpro	-0.06	-0.17	-0.01	-0.12
Ctenicera appropinquans	cteapp	0.17	-0.02	0.18	0.18
Ctenicera arata	cteara	-0.56	-0.31*	-0.07	0.02
Ctenicera cylindriformis	ctecyl	-0.75	-0.41**	-0.01	0.04
Ctenicera hieroglyphica	ctehie	-0.79	-0.64***	0.36	0.27
Ctenicera propola	ctepro	0.44	0.47**	0.06	0.11
Ctenicera rufopleuralis	cteruf	-0.11	-0.11	0.62**	0.53***
Ctenicera spinosa	ctespi	0.01	0.10	-0.23	-0.15
Ctenicera triundulata	ctetri	0.36	0.55***	-0.70***	-0.34*
Dalopius species	dalspp	0.11	-0.02	0.75***	0.63***
Isoriphis obliqua	isoobl	-0.08	-0.21	0.59**	0.55***
Limonius aeger	limaeg	0.17	0.29*	-0.66**	-0.23
Melanotus castanipes	melcas	-0.74***	-0.59***	0.12	0.22
Tree species					
Balsam Fir	TABBA	0.06	-0.08	-0.39	-0.40*
Red Maple	TACRU	0.07	-0.14	0.52**	0.56***
Red Spruce	TPIRU	0.24	0.28*	-0.64**	-0.56***
Red Oak	TQURU	-0.82***	-0.56***	0.12	0.19
Eastern Hemlock	TTSCA	0.31	0.31*	-0.44	-0.36
Shrub species					
Red Maple	ACRU	-0.32	-0.31*	0.59**	0.35*
Paper Birch	BEPA	0.03	-0.09	0.44	0.42**
Red Spruce	PIRU	0.21	0.28	-0.43	-0.40**
Aspen species	POSP	0.08	0.09	0.56**	0.05
Black Cherry	PRSE	0.19	0.09	0.51*	0.36
Eastern Hemlock	TSCA	0.10	0.24	-0.52*	-0.28

Note: Significance: *, (p <0.1); **, (p<0.05); ***, (p<0.001).

2.4.3. Relation of Click Beetle Species with Cover Types and Plant Species

In the 2001 individual species contrasts ($p < 0.05$), *Athous brightwelli*, *Athous orvus* Becker, *Dalopius* spp., and *I. obliqua*, were more abundant in the hardwood cover types, while *Ctenicera arata*, *Ctenicera propola*, *C. triundulata*, and *Limonius aeger* were more abundant in the softwood cover types (Figure 2.2a). Of the specimens captured in the hardwood cover types (Figure 2.3a), *C. triundulata* and *Dalopius* spp., were less abundant in the Blueberry than in either the Birch or the Maple. Of the specimens collected in softwood cover types (Figure 2.3b), *L. aeger* was the only species most abundant in the Spruce-Fir-Pine; it was intermediate in the Hemlock and least abundant in the Fern-Hemlock. *Dalopius* spp. was most abundant in Fern-Hemlock and least abundant in Spruce-Fir-Pine. *Sericus brunneus* was also least abundant in Spruce-Fir-Pine, but it was most abundant in Hemlock. *C. triundulata* was least abundant in the Spruce-Fir-Pine, while *A. brightwelli* was least abundant in Hemlock. *A. stabilis* was most abundant in Hemlock, less abundant in Fern-Hemlock, and least abundant in Spruce-Fir-Pine. In the 2002 individual species contrasts ($p < 0.05$), *A. stabilis*, *Ampedus near melanotoides*, *A. orvus*, *Ctenicera appropinquans* Randall, *Ctenicera hieroglyphica*, *Dalopius* spp., and *Melanotus castanipes* LeC. were more abundant in hardwood cover types, while *C. propola* and *C. triundulata* were more abundant in softwood cover types (Figure 2.2b). Of the specimens captured in the hardwood cover types (Figure 2.3c), *C. hieroglyphica* and *M. castanipes* were most abundant in Oak. *A. stabilis* and *C. triundulata* were most abundant in Birch-Maple. *Dalopius* spp. was least abundant in Oak, more abundant in Aspen, and most abundant in Birch-Maple. Of the click beetles collected in softwood cover types (Figure 2.3d), *A. stabilis*, *C. propola*, and *Dalopius* spp. were most abundant in Hemlock. *C. triundulata*, was least abundant in Spruce-Fir-Pine, more abundant in Pine, and most abundant in Hemlock.

The first four axes of the models of the CCA ordinations demonstrated that the understory and overstory vegetation explained 66.4% and 70.6% of the variation in the click beetle assemblage structure for 2001 and 2002, respectively (Appendix B.2). The NMS ordinations separated stands according to hardwood and softwood dominance in 2001 (Figure 2.4a), and according to dominance by oak, non-oak hardwoods, and softwoods in 2002 (Figure 2.4b), suggesting a relationship between the click beetle assemblages and cover types. The 2001 NMS ordination explained 83.4% of the variation in the click beetle assemblage structure, and correlations described the association between click beetle species with the vegetation species (Table 2.5 and Figure 2.4c). Four click beetle species (*A. orvus*, *C. hieroglyphica*, *Ctenicera rufopleuralis*, and *Dalopius* spp.) were associated with white birch and understory red maple. Four click beetle species (*A. brightwelli*, *C. appropinquans*, *Hemicrepidius memnonius* Herbst, and *I. obliqua*) were associated with aspen and understory black cherry. Three click beetle species (*Ampedus semicinctus* Randall, *C. propola*, and *L. aeger*) were associated with understory fir and hemlock and overstory pine and spruce. Six click beetle species (*Ampedus mixtus* Herbst, *C. arata*, *Ctenicera nitidula*, *C. rufopleuralis*, *C. triundulata*, and *Dalopius* spp.) were associated with overstory hemlock and understory hobblebush and interrupted fern. The 2002 NMS ordination accounted for 71.2% of the variation in the click beetle assemblage structure (Table 2.6 and Figure 2.4d). Click beetle assemblages associated with the Oak cover type were more different from the other cover types than those species associated with softwoods were from the other hardwood species. This relationship was indicated by the horizontal axis, which accounted for 41.7% of the variation in the click beetle assemblages, separating the beetle species associated with oak stands from those of other stands. The vertical axis, which accounted for only for 29.5% of the variation, separated click beetle assemblages associated with softwoods from those associated with hardwoods. Four click beetle species (*A. orvus*, *C. rufopleuralis*, *Dalopius* spp., and *I. obliqua*) were associated with maple and understory birch, aspen, and black cherry. Seven click beetle species (*A. near melanotoides*, *Ampedus* species C, *C. arata*, *Ctenicera cylindriformis* Herbst, *C. hieroglyphica*, *C. propola*, and *M. castanipes*) were associated with overstory oak and understory maple. Two click beetle species (*C. triundulata* and *L. aeger*) were associated with spruce, hemlock, and overstory fir.

2.5. Discussion

2.5.1. Click Beetle Assemblages and Plant Cover Types

My hypotheses for click beetle species richness and species abundance were partially supported. Species richness was lowest in Spruce-Fir-Pine and highest in Oak. Species abundance was lowest in Spruce-Fir-Pine and Pine and highest in Oak and Maple. However, both species richness and species abundance were higher than expected in Hemlock. Diversity was also generally higher in hardwood cover types than softwood cover types. Similarity was generally low between hardwood and softwood cover types. This indicated that in addition to species richness, abundance, and diversity being lower in coniferous cover types (excluding hemlock), assemblages between these cover types are different (Appendix B.3). The difference in species abundance, diversity, and assemblage similarity between Oak and other non-oak hardwood cover types was also noteworthy.

Many invertebrate communities living in forest soils are affected by the composition of forest vegetation, and several studies have found differences in Elaterid assemblages between hardwood- or softwood-dominated stands. Paquin and Coderre (1997) conducted a survey in Canada of soil macroarthropod communities in three forest types and ages-- deciduous (47 years), mixed (147 years), and coniferous (241 years). The average abundance in the click beetle family was highest in the mixed forest and lowest in the coniferous forest. Saetre *et al*. (1999) also found that the abundance of many soil fauna taxa, including Elateridae, was higher in mixed spruce-birch stands than in pure spruce stands in Sweden. They suggested that the birch leaf litter added substrate and sustained moisture and therefore greatly influenced the soil fauna composition. In contrast, Scheu *et al*. (2003) found that Elaterid biomass was greater in 30 year-old pure spruce forests than in either pure beech or mixed stands; however, this result did not hold over time, as the Elaterid biomass in the 120 year-old stands were not different between the three cover types. The authors postulated that predators were of little importance for Elaterids. Instead, the structuring factors seemed to be associated with the relatively early growing stages of the stands. As spruce needles are less favorable than beech leaves, they suggested the elaterid larvae may be able to survive on poorer food substrates because of their long larval development and slow growth. This contrasting result may be due to species-specific preferences. Since these three studies presented only family-level information, it was not possible to determine vegetation preferences of particular click beetles species. Ohsawa (2004) did identify click beetles to species and found species-specific preferences for click beetles in Japan, identifying two species of click beetles that preferred larch plantations, three species that were specific to stands dominated by oaks but mixed with other broadleaved trees (secondary forest), and one species that was specific to stands dominated by oak but mixed with coniferous species (primary forest). Although the numbers of species among the three forest types were similar, overall click beetle composition varied significantly.

2.5.2. Softwood Associates

Five species (*A. near melanotoides*, *C. arata*, *C. propola*, *C. triundulata*, and *L. aeger*) were more abundant in the softwood cover types. In the softwood cover types, all species except two (*L. aeger* and *A. stabilis*) had the lowest abundances in Spruce-Fir-Pine and Pine. *L. aeger*, on the other hand, had the highest abundance in the Spruce-Fir-Pine. *C. triundulata* is the only species that showed a difference in abundance between Pine and Spruce-Fir-Pine, with higher abundance in Pine. All species except *L. aeger* (*A. stabilis*, *A. brightwelli* Kirby, *C. propola*, *C. triundulata*, *Dalopius* spp., and *S. brunneus*) had the highest abundances in Hemlock or Fern-Hemlock.

In 2001, three species (*A. semicinctus*, *C. propola*, and *L. aeger*) were correlated with an increase in understory balsam fir and overstory white pine, red spruce, and eastern hemlock. Six species (*A. mixtus*, *C. arata*, *C. nitidula*, *C. rufopleuralis*, *C. triundulata*, and *Dalopius* spp.) were correlated with an increase in the overstory eastern hemlock and red spruce and the understory interrupted fern and hobblebush, both located in hemlock-dominated cover types. In 2002, likely due to a different array of vegetation conditions sampled, *C. triundulata* and *L. aeger* were correlated with an increase in understory and overstory red spruce and hemlock, and *C. propola* was correlated with an increase in overstory red spruce. My results indicated that Spruce-Fir-Pine and Pine were the least favored habitats within the softwood cover types for most click beetle species (except *L. aeger*).

Most studies of click beetle species in coniferous forest types compared forest to non-forest conditions rather than among coniferous types. For example, Strong *et al*. (2002) compared click beetle assemblages in spruce-fir forest and edge to ski trails in Vermont. Although low in numbers, five species (including *L. aeger*) were associated with spruce-fir forest or edge or forest. Levesque and Levesque (1993) studied Elaterid assemblages in Canada in non-forest habitats and a forest type dominated by white pine. Of the 25 species captured in the stands dominated by white pine, 15 were also caught in my study. Four of these species (*C. propola*, *C. triundulata*, *L. aeger*, and *S. brunneus*) seemed to show preferences for specific softwood cover types in my study. However, three of these species (*C. appropinquans*, *C. cylindriformis*, *Dalopius* spp., and *M. castanipes*) had higher abundances in hardwood than softwood cover types. Brooks (1960) described the regional habitats of Elaterids in southern Canada, separating the coniferous forest formations from the grassland formations. Fifteen species (including *A. mixtus*, *C. nitidula*, *C. rufopleuralis*, *Ctenicera spinosa* LeC., and *S. brunneus*) found in my study are listed by Brooks (1960) as associated with the coniferous forest formations of the Montane, Submontane, and Boreal Forest regions. Of these, my study found three (*C. arata*, *C. propola*, and *C. triundulata*) were associated with softwoods, two (*Agriotes limosus* LeC. and *Athous rufifrons* Randall) were species with few specimens but found only in softwoods, one (*C. appropinquans*) was associated with hardwoods, and four

(*Ampedus pullus* Germar, *Ctenicera mediana* Germar, *Denticollis denticornis* Kirby, and *Lacon brevicornis* [now named *Danosoma brevicornis* LeC.]) were species with few specimens but found only in hardwoods. Six species (*Agriotes fucosus* LeC., *A. stabilis, Ctenicera cruciata L., C. hieroglyphica, L. aeger,* and *M. castanipes*) found in forest stands in my study are listed by Brooks as associated with the grassland formations of the True Prairie and Eastern Parkland regions.

In a previous study (Chapter 1), three species of click beetles (*C. arata*, *C. nitidula*, and *L. aeger*) were correlated with an increase in softwood basal area ($p < 0.05$, at least 1 specimen per trap week summed between years). All three species were associated with softwood vegetation species in this study, supporting my hypothesis of click beetle species associated with softwood species.

2.5.3. Hardwood Associates

Ten species (*A. stabilis*, *A. near melanotoides*, *Ampedus* species C, *A. brightwelli*, *A. orvus*, *C. appropinquans*, *C. hieroglyphica*, *Dalopius* spp., *I. obliqua*, and *M. castanipes*) were more abundant in hardwood cover types. Blueberry was the least favored by all species of click beetle identified in this study. *C. hieroglyphica* and *M. castanipes* were most abundant in Oak. *Dalopius* spp. was least abundant in Oak, more abundant in Aspen, and most abundant in Birch-Maple. *A. stabilis* and *C. triundulata* were most abundant in Birch-Maple.

In 2001, four species (*A. orvus*, *C. hieroglyphica*, *C. rufopleuralis*, and *Dalopius* spp.) were correlated with an increase in hardwood species, such as understory red maple and understory and overstory white birch. Three click beetle species (*A. brightwelli*, *C.*

appropinquans, and *I. obliqua*) were correlated with an increase in understory black cherry, and understory and overstory aspen. In 2002, although there was not a completely distinct click beetle assemblage in Oak, other hardwood, or coniferous cover types, assemblages in Oak were less similar to cover types with birch, maple, or aspen than these assemblages were to each other. Assemblages in all hardwood cover types were less similar to coniferous cover types than they were to each other, with Oak the least similar to coniferous cover types. This difference was evident from the assemblage similarity measures, which included only the presence or absence of a species.

There was further evidence from the NMS ordination, which included species abundance, that differences between click beetle assemblages associated with Oak (versus all other cover types) was greater than the difference between assemblages associated with softwoods versus other hardwood cover types. Six click beetle species (*A. near melanotoides*, *Ampedus* species C, *C. arata*, *C. cylindriformis*, *C. hieroglyphica*, and *M. castanipes*) were associated with an increase in overstory red oaks and weakly associated with understory red maple and overstory aspen. Four click beetle species (*A. orvus*, *C. rufopleuralis*, *Dalopius* spp., and *I. obliqua*) were correlated with an increase in understory aspen, black cherry, and white birch and understory and overstory red maple. Therefore, in 2001, *C. hieroglyphica* was correlated with hardwood species in general and *C. arata* was associated with softwood species, but each was associated with red oak when this treatment was added in 2002.

Elaterid assemblages vary in stands composed of different hardwood species. Axelsson *et al*. (1984) studied soil fauna in deciduous woodlands in Sweden and found that Elateridae had the highest biomass within Coleoptera at both sites. While the oak/birch/hazel site included several species the authors considered rhizophagous (e.g. *Agriotes* species), the beech/ woodrush site was dominated by an omnivorous species. Levesque and Levesque (1980) found that Elateridae assemblages in Quebec varied across four deciduous forest types (birch, young maple, old maple, and mixed birch-maple). Of the species in common between Levesque and Levesque and my study, all but one were also captured in my hardwood stands, although two species (*C. spinosa* and *C. triundulata*) were more abundant in my softwoods cover types. Four species had at least seven specimens with at least 50% of the specimens in either the birch type (*C. appropinquans*) or the mixed birch-maple type (*C. hieroglyphica, A. collaris*, and *A. stabilis*).

In a previous study (Chapter 1), twelve click beetle species (*A. stabilis*, *C. cruciata*, *C. hieroglyphica*, *C. propola*, *C. triundulata*, *Elathous dicalceatus*, *Fornax canadensis*, *I. obliqua*, *M. castanipes*, *Oxygonus montanus*, *S. brunneus*, and *Sericus viridanus*) were correlated with an increase in hardwood basal area ($p < 0.05$, at least 1 specimen per trap week summed between years). In this study, three of these species (*C. hieroglyphica*, *I. obliqua*, and *M. castanipes*) were associated with specific hardwood species, and four species (*A. stabilis*, *C. hieroglyphica*, *I. obliqua*, and *M. castanipes*) were associated with hardwood cover types. However, one species (*C. triundulata*) was associated with specific softwood species and softwood cover types. One species (*C. propola*) was associated with softwood species and cover types in 2001, but was associated with oaks when this tree species was included in the 2002 study. The other species (*E. dicalceatus*, *F. canadensis*, *O. montanus*, *S. brunneus*, and *S. viridanus*) were either not collected in high enough numbers or were not associated with either hardwood or softwood species or cover types. Therefore, my hypothesis of click beetle species associated with hardwood species was partially supported.

Chapter 3

INFLUENCE OF HARVEST GAPS AND COARSE WOODY MATERIAL ON CLICK BEETLES (COLEOPTERA: ELATERIDAE) IN MAINE'S ACADIAN FOREST

3.1. Abstract

I examined how the species richness, abundance, diversity, and assemblage similarity of click beetles inhabiting coarse woody material (CWM) were affected by gap harvesting and characteristics of the CWM (diameter, degree of decay, and wood type) in Maine's Acadian forest. Species assemblages varied between harvest treatments, canopy conditions, CWM wood type (hardwood vs. softwood), and especially between CWM decay classes and among diameter classes. Size of harvest gap did not influence the species abundance of click beetles across the small range of gap sizes studied (0.01 to 0.21 ha), and there were few differences between the two harvest treatments. Four of the most common species had higher abundances in closed canopy than harvest gaps. Click beetle species richness and species abundance were higher in CWM that had larger diameters and were more decayed. Click beetle diversity was higher in softwood than hardwood CWM.

3.2. Introduction

Maintaining biodiversity in forest ecosystems while meeting economic goals for wood production requires forest management that is based on sound ecological principles. To achieve this goal, it has been recommended that forestry practices emulate patterns of natural disturbances (e.g., insect outbreaks, fire, and windthrow) using harvest arrays, variable retention, rotation schedule, and deadwood maintenance (Franklin and Forman 1987, Franklin 1989, Hansen *et al*. 1991, Hunter 1993, Seymour *et al.* 2002). Although there is a growing body of literature addressing this approach (Haila *et al*. 1994, Bunnell 1995, Jonsell *et al*. 2005), there is still relatively little understanding about the influence of forest management on the majority of forest species (Komonen 2001, Grove 2002a).

The Acadian Forest is considered to be a transitional ecoregion between the boreal forest to the north and the eastern temperate forest to the south (Bailey 1995, Lorimer and White 2003). Large, stand-replacing disturbances in the pre-European settlement forest were unusual, with recurrence intervals of hundreds of years (Lorimer 1977, Seymour, *et al*. 2002, Lorimer and White 2003, Seymour 2005). Disturbances occurred predominantly as small and frequent gaps, resulting in a forest structure dominated by late-successional species in multi-aged stands. Therefore, a silvicultural system modeled after this natural disturbance regime in Acadian forests would include gap creation and the retention of biological legacies, including living retention trees and deadwood (Seymour *et al*. 2002, Franklin *et al*. 1997).

Deadwood, including snags and downed coarse woody material (CWM), supports a wide variety of animals, fungi, and plants and is vital for conserving biodiversity in forests (Speight 1989, Lindenmayer and Franklin 2002). Diameter of the CWM is important; usually larger diameters correspond to greater use or higher species richness and abundance (Gutzwiller and Anderson 1987, Jonsell *et al*. 1998, Kolstrom and Lumatjarvi 2000, Yee *et al*. 2001). Stage of decay also affects species assemblages, as decomposing wood is occupied by a succession of species (Grove 2002a). Tree species or wood type (hardwood or softwood) can affect saproxylic communities, but becomes less important with advancing stages of decay (Jonsell *et al* 1998).

Harvest gaps in the forest canopy can have substantial influence on the forest ecosystem, as forest harvesting often depletes the amount of deadwood through removal of large living trees (potential deadwood), slash disposal, and site preparation (Fridman and Walheim 2000). Harvesting can also alter the distribution of size and decay class through the mechanical crushing of larger pieces in late-stage decay and through the addition of small diameter slash (Freedman *et al*. 1996, Fraver *et al*. 2002. In some intensively managed forests, many deadwood-dependent species are red-listed or considered threatened (Kirby and Drake 1993, Ranius and Jansson 2000, Ehnstrom 2001, Lindenmayer *et al*. 1996), and some species are now extinct (Kirby and Drake 1993).

Insects are the most numerous and diverse group of eukaryotic organisms (Andrewartha and Birch 1984). Although insects mediate many important natural processes within forest ecosystems (Crowson 1981, Wilson 1992), most are poorly understood (Danks and Foottit 1989). Coleoptera is the largest order of insects and includes ~40% of all arthropods (Grove and Stork 2000), and Elateridae (click beetles) is the ninth most species rich family of Coleoptera, with approximately 10,000 described and many undescribed species worldwide. Click beetles are generally regarded as pests in agricultural systems, but many species live in forest soil and CWM without causing any serious damage to living trees. In fact, click beetles have been shown to be important as nutrient cyclers (Wolters 1989), as predators of forest pests (Morris 1951, Yano *et al*. 1984), and as prey for birds and other forest biota (Barron and Walley 1983, Holmes and

Robinson 1988, Heinrich and Bell 1995). Some species of click beetles are considered threatened or endangered (Anon. 1999, Alexander 2003, Zach 2003), but the deficiency of knowledge regarding most species in this family (especially outside Europe) is an impediment to their conservation. Elaterids are an important taxa to study because the family is species rich, numerically abundant, and can be sampled using relatively simple trapping methods. Furthermore, elaterids are useful for forest biodiversity studies because the species have diverse food and habitat preferences.

I hypothesized that creating small canopy gaps modeled after natural disturbance patterns would retain adequate habitat structure for click beetles, thus maintaining elaterid diversity and abundance in managed forests. I tested whether the abundance and composition of click beetles living in CWM were affected by gap harvesting and CWM characteristics, including decay class, diameter, and wood type (softwood or hardwood).

3.3. Methods

3.3.1. Study Site

This study took place in the Penobscot Experimental Forest (Figure C. 1) in east-central Maine (44°50' N, 68°35' W). The dominant tree species in the forest include red (*Picea rubens* Sarg.) and white spruce (*P. glauca* (Moench) Voss), balsam fir (*Abies balsamea* (L.) Mill.), eastern white pine (*Pinus strobus* L.), eastern hemlock (*Tsuga canadensis* (L.) Carr.), northern white cedar (*Thuja occidentalis* L.), red maple (*Acer rubrum* L.), paper (*Betula papyrifera* Marsh.) and gray birch (*B. populifolia* Marsh.), and quaking (*Populus tremuloides* Michx.) and bigtooth aspen (*P. grandidentata* Michx.). The Penobscot Experimental Forest has a complicated history of insect outbreaks and repeated partial cuttings that resulted in multi-cohort stand structures of many species (R. Seymour, unpublished data). Soils range from glacial till ridges with well-drained or sandy loams to flat areas between ridges with poorly to very poorly drained loams and silt loams (Brissette 1996).

Sampling for this study used experimental plots established by the University of Maine's Acadian Forest Ecosystem Research Program, a long-term study comparing two silvicultural systems patterned after the natural disturbance regime of the Acadian forest (Saunders and Wagner 2005). The silvicultural systems include a 10% and 20% expanding-gap harvest system with permanent reserve trees. The 10% harvest treatment removes 10% of the canopy on a 10-year cutting cycle (range: 6.2 to 13.8%, assuming 5 m wide skid trails), with 10% of the basal area permanently reserved. The 20% harvest treatment removes 20% of the canopy on a 10-year cutting cycle (range: 19.5 to 21.3%), with 10 percent of the basal area permanently reserved. A basal area of 30% is retained for one cutting cycle in gaps without sufficient advanced regeneration, and is then reduced to the 10% permanent reserve at the next cycle. Each treatment is replicated three times in 9.4 to 11.3 ha treatment plots using a randomized complete block design. The first harvest for each block was applied in 1996, 1997, or 1998. At the time of this study, vegetation in the gaps had recovered for 3 to 6 years since the harvest.

3.3.2. Field Invertebrate Sampling

I designed two experiments to compare click beetle assemblages in CWM of different characteristics (diameter, type, and decay class). The first experiment compared beetle assemblages in CWM in both the 10% and 20% harvest treatments in 2002. The second experiment examined click beetle assemblages in CWM in the 10% harvest treatment during 2001 and 2002 (Appendix C.3).

To collect click beetles from CWM, I constructed emergence traps of dark mesh tents with clear collecting bottles, containing propylene glycol, located at the approximately 1.0 m high peak (Figure C.2). I fitted the inverted upper collecting bottle with a funnel to catch stronger flying insects; I positioned the lower collecting bottle directly below the upper bottle to capture weaker flying insects that could not maneuver into the funnel. I collected samples from mid-June through mid-September of 2001 and 2002, extracting samples biweekly. Insect samples were stored in 70% ETOH or pinned. Adult click beetle specimens were identified to species by S. L. Thomas and S. LaPlant and incorporated into the University of Maine Insect Collection.

To test the influence of the harvest treatments on click beetles in CWM, I systematically searched all treatment plots for downed logs meeting specific characteristics. These characteristics included harvest treatment (10% or 20%), canopy condition (located in a harvest gap or under the closed canopy in the adjacent unharvested forest matrix), CWM wood type (softwood or hardwood), diameter (small = 14-24 cm, or large = 25+ cm), and two classes of decomposition based on Fraver *et al*. (2002). Only logs in Decay Classes 2 and 4 were selected for my study. Logs identified in Decay Class 2 have "wood that is sound to somewhat rotten; bark may or may not be attached; branch stubs are firmly attached but only larger stubs are present; and log retains round shape and lies on duff." Decay Class 4 logs have "wood that is mostly rotten, "fluffy" when dry and "doughy" when wet; branch stubs are rotted down; bark is detached or absent (except *Betula*); and log is decidedly oval in cross section and usually substantially buried in duff." Therefore, there were 48 and 96 potential trap locations in 2001 (10% harvest treatment only) and 2002 (10% and 20% harvest treatments), respectively (2 harvest treatments x 3 stands x 2 canopy conditions x 2 CWM wood types x 2 decay classes x 2 diameter classes).

An emergence trap that enclosed a 1.0 m length of log was installed over each selected log. For Decay Class 2 logs, the trap mesh was wrapped completely under the log. For Decay Class 4 logs, the mesh was tucked between the leaf litter and the log, without reaching beneath the highly decomposed material.

3.3.3. Analytical Approach

The principal response variables used to describe the click beetle assemblages were species richness (number of species), total abundance (number of individuals), species abundance (number of individuals of the most common species), diversity, and assemblage similarity. I used Jaccard similarity measures, rarefaction, indicator species analysis, general linear models, and non-metric multidimensional scaling to examine the relationships between click beetle assemblages and the different trap location characteristics. For analysis, emergence trap data were grouped in two ways.

First, I compared click beetle assemblages between harvest treatments (10% and 20%) for 2002. These analyses (referred to as Experiment 1) evaluated harvest treatment, canopy condition, diameter, decay class, and wood type (hardwood or softwood). Second, I compared beetle assemblages in the 10% harvest treatment during 2001 and 2002. Due to logistical difficulties, no differentiation was made between softwood and hardwood logs in 2001; therefore, the wood characteristic "type" was not included in the analysis. These analyses (referred to as Experiment 2) evaluated the effect of sample year, canopy condition, diameter, and decay class. In both experiments, the diameter of the smaller and larger ends (one meter apart) of each piece of CWM was averaged, and this average diameter was used for all analyses.

I used cluster analysis of Jaccard percent similarity measures using internet-based software provided by Brzustowski (2002) to compare similarity of species assemblages between pooled samples for the different trap location characteristics. Rarefaction, which takes both richness and abundance into account, was used to measure species diversity. I used PAST (Hammer *et al*. 2001) to calculate the expected number of species derived from random subsamples of the total abundance, comparing species diversity between subsamples of similar sizes (Sanders 1968, Hurlbert 1971). Diversity between two samples was considered significantly different when respective 95% confidence intervals did not overlap. I used a t-test to determine significance between groups of stands for click beetle richness and total abundance.

I assessed the affinity of each species for different trap location characteristics with indicator species analysis (Dufrêne and Legendre 1997) using PC-ORD (McCune and Mefford 1999). This method combines information on the faithfulness (present in all samples of a group) and the exclusiveness (never present in other groups) of a species to a particular group or habitat characteristic. Indicator values range from zero (no indication) to 100 (perfect indication to a group without error). A Monte Carlo *p*-value for each indicator value was determined as the proportion of 1,000 randomized trials with an indicator value equal to or exceeding the observed indicator value. Because the treatment plots had a deficit of large (>35 cm) diameter CWM (Fraver *et al*. 2002), I separated diameter into the following three classes, with different numbers of traps per class for 2001 and 2002, respectively: 14.0 - 24.5 cm (24, 54 traps), 24.6 - 34.5 cm (18, 35 traps), and >34.6 cm (6, 6 traps) and used these size classes for similarity measures, species richness, total abundance, diversity, and indicator species analysis.

I examined the relationships between the individual click beetle species abundances with various trap location characteristics using general linear models (PROC GENMOD, SAS Institute). A negative binomial distribution was used because the data were over-dispersed. Models were generated based on the main effects and their interactions, selecting an optimal model with the second order Akaike Information Criterion (Akaike 1974). Due to insufficient sample size of many species, only the 15 most common click beetle species were included. For Experiment 1, I generated general linear models using harvest treatment, canopy condition, diameter, decay class, wood type, species, and their interactions as main effects. For Experiment 2, I generated general linear models using the variables year, canopy condition, diameter, decay class, species, and their interactions as main effects. In the general linear models, CWM diameter was used as a continuous variable.

To determine whether the size of a harvest gap influenced the abundance of the emerging beetles, I also developed a reduced model based on trap locations only in harvest gaps and using area of the gap as a main effect. For these reduced models, I was concerned that harvest treatment and gap area were colinear, so models were generated excluding either harvest treatment or gap area. Harvest treatment and gap area were not significant for any reduced model (Table C.1).

3.4. Results

3.4.1. Description of taxa

I collected 1,058 click beetles of 60 different species, including two species (*Isorhipis obliqua* Say and *Fornax canadensis* Brown) from Eunemidae, the false click beetles, (Table C.2). *Ctenicera triundulata* Randall, *Ampedus mixtus* Herbst, and *Agriotes stabilis* LeC. were the most common species, representing 20%, 13%, and 5% of the total abundance, respectively. Sixteen species were singletons, and 23 species were represented by only two to nine individuals. Click beetle abundance was higher for the 15 most common species in 2002 than in 2001 ($p = 0.010$, Table 3.1b, Table C.3b, Figure C.3).

3.4.2. Harvest Treatment

In Experiment 1, species richness, total abundance, and diversity did not differ between the 10% and 20% harvest treatments (Table 3.2a). However, assemblage similarity, a measure of the overlap of species between habitats, was only 60%, indicating a difference in species composition between the two harvest treatments. *A. stabilis* was a significant indicator of the 20% harvest treatment (Table 3.3a). The mean abundances of the 15 most common click beetle species were similar between the 10% and 20% harvest treatments ($p = 0.405$, Table 3.1a).

3.4.3. Canopy Condition

In Experiment 1, species richness, total abundance, and diversity were similar between closed canopy and harvest gap conditions (Table 3.2a). *Ctenicera hieroglyphica* Say and *Limonius aeger* LeC. were significant indicators of closed canopy conditions

(Table 3.3a). Assemblage similarity was only 58%. For the fifteen most common click beetle species, individual species responded differently to the canopy conditions (*p* = 0.001); no species were more likely to be found in harvest gaps, but four species (*C. hieroglyphica*, *Ctenicera propola* LeC., *Dalopius* spp Brown, and *L. aeger*) were more abundant in the closed canopy condition (Table 3.1a, Table C.1.3a, Figure 3.1a).

In Experiment 2, total abundance, species richness, and species diversity of click beetles were similar in CWM in harvest gaps and under closed canopy conditions (Table 3.2b), but assemblage similarity was only 61%, suggesting a difference in species composition. No species were found to be indicators of either canopy condition (Table 3.3b). The mean abundance of the 15 most common click beetle species was higher under a closed canopy than in harvest gaps (*p* = 0.014, Table 3.1b, Table C.3b, Figure 3.2).

3.4.4. Coarse Woody Material Characteristics

3.4.4.1. Wood Type

In Experiment 1, species richness and total abundance were similar between hardwood and softwood CWM; however, species diversity was higher in softwood CWM (Table 3.2a, Figure C.4a). No species were indicators of softwood and hardwood logs (Table 3.3a), but assemblage similarity was 64%, indicating a difference in species composition. The mean abundances of the 15 most common click beetle species were similar between the softwood and hardwood CWM (*p* = 0.177, Table 3.1a, Table C.3a).

3.4.4.2. Decay Class

In Experiment 1, species richness and total abundance were 46% and 56% higher in Decay Class 4, respectively, but species diversity was higher in Decay Class 2 (Table 3.2a, Figure C.4b). *C. triundulata* was a significant indicator of Decay Class 4 (Table 3.3a), and the species composition was quite different (56% similarity). The 15 most common click beetle species responded individually to the decay class of CWM ($p <$ 0.001). Three species (*A .semincinctus*, *A. scapullaris*, and *M. castanipes*) were more abundant in the less decayed (Class 2) CWM, and six species (*A. brightwelli*, *Athous orvus* Becker, *C. hieroglyphica*, *C. triundulata*, *Dalopius* spp., and *L. confusus*) were more likely to be found in the more decayed (Class 4) CWM (Table 3.1a, Table C.3a, Figure 3.1b).

In Experiment 2, species richness and total abundance were 20% and 39% higher in Decay Class 4 (more decayed), respectively, but species diversity was similar between the two stages of decay (Table 3.2b). One species (*C. triundulata*) was an indicator of Decay Class 4 (Table 3.3b). The similarity between species assemblages was low (only 57%). The 15 most common click beetle species responded individually to the decay classes ($p < 0.001$), with four species (*Ampedus semicinctus* Randall, *Athous scapullaris* Say, *I. obliqua*, and *Melanotus castanipes* LeC.) being more abundant in less decayed CWM and four species (*Athous brightwelli* Kirby, *C. triundulata*, *Dalopius* spp., and *Limonius confusus* LeC.) being more abundant in more decayed CWM (Table 3.1b, Table C.3b, Figure C.5).

Table 3.1. General linear model results of click beetle species abundance for A) Experiment 1 and B) Experiment 2.

Source	DF	Chi-Square	Pr > ChiSq
A) Experiment 1			
Harvest Treatment	1	0.69	0.405
Site within Harvest Treatment	4	24.72	<0.001
Beetle Species	14	204.06	<0.001
Type (Softwood v. Hardwood)	1	1.83	0.177
Diameter	1	29.8	<0.001
Canopy Condition	1	11.06	0.001
Decay Class	1	11.29	0.001
Beetle Species * Canopy Condition	14	48.19	<0.001
Beetle Species * Decay Class	14	77.29	<0.001
Beetle Species * Decay Class	14	52.62	<0.001
B) Experiment 2			
Year	1	7.21	0.010
Site	2	10.44	0.008
Beetle Species	14	64.91	<0.001
Decay Class	1	0.11	0.608
Canopy Condition	1	0.18	0.014
Diameter	1	2.08	<0.001
Diameter * Canopy Condition	1	13.24	0.008

Table 3.2. Summary of richness (number of species), total abundance (number of individuals), and rarefaction-estimated species diversity of click beetles for A) Experiment 1 (averaged by CWM type) and B) Experiment 2.

Source	Number of Sites[a]	Species Richness	Total Abundance	Diversity[b]
A) Experiment 1				
Harvest Treatment				
10% Removal	48	4.7	7.9	36.9+/-1.0 (355)
20% Removal	48	4.8	9.0	35.0+/-0.1 (355)
Type				
Hardwood	48	4.9	9.3	45.4+/-1.2 (380)
Softwood	48	4.6	7.6	53.8+/-0.4 (380)[d]
Canopy Condition				
Gap	48	4.5	8.0	55.9+/-0.4 (420)
Closed Canopy	48	5.0	8.9	55.1+/-0.9 (420)
Decay Class				
Decay Class 2	48	3.9	6.6	55.9+/-0.3 (360)[d]
Decay Class 4	48	5.6[d]	10.3[d]	43.5+/-1.8 (360)
Diameter Class				
14-24.75cm	54	4.2	6.7	30.3+/-2.1 (110) 39.0+/-1.5 (270)[d]
25-34.75cm	35	4.7	8.5	26.3+/-1.6 (110) 31.0+/-0.2 (270)
35cm +	6	10.0[d]	24.0[d]	17.0+/-0.2 (110)[e]
B) Experiment 2				
Canopy Condition				
Gap	24	7.1	7.1	32.0+/-0.0 (165)
Closed Canopy	24	7.5	7.5	31.8+/-0.4 (165)
Decay Class				
Decay Class 2	24	6.5	6.1	27.0+/-0.0 (135)
Decay Class 4	24	7.8[c]	8.5[d]	26.6+/-1.5 (135)
Diameter Class				
14-24.75cm	24	7.0	5.9	23.1+/-1.8 (75) 27.0+/-1.2 (110)[d]
25-34.75cm	18	6.2	6.8	20.1+/-1.4 (75) 228.+/-0.4 (110)
35cm +	6	10.5[d]	14.8[d]	22.4+/-0.7 (75)

[a]Averaged between CWD wood type traps for Experiment 1, [b]Rarefaction-estimated number of species +/- SD (number of individuals in subsample), [c]Highest class ($p = 0.10$), [d,e]Highest and lowest class ($p = 0.05$).

Table 3.3. Indicator species analysis of click beetle species for A) Experiment 1 and B) Experiment 2 (the total number collected is averaged between softwood and hardwood types). Only significant species (*p* = 0.1) with an IV of at least 25 are shown.

Source	Species	Total number collected	Indicator Value	*p*
A) Experiment 1				
Harvest Treatment				
10% Removal	No species			
20% Removal	*Agriotes stabilis*	35	34.4	0.002
Type				
Hardwood	No species			
Softwood	No species			
Canopy Condition				
Gap	No species			
Closed Canopy	*Ctenicera hieroglyphica*	25	27.1	0.001
	Limonius aeger	24	27.3	0.001
Decay Class				
Decay Class 2	No species			
Decay Class 4	*Ctenicera triundulata*	151	70.7	0.001
Diameter Class				
14-24.75cm	No species			
25-34.75cm	No species			
35cm +	*Agriotes collaris*	8	44.4	0.002
	Ampedus mixtus	121	35.7	0.097
	Athous brightwelli	14	27.8	0.020
	Athous rufifrons	35	64.0	0.001
	Ctenicera hieroglyphica	25	53.0	0.003
	Ctenicera triundulata	151	49.0	0.021
	Dalopius species	33	37.6	0.009
	Limonius aeger	24	39.4	0.013
	Limonius confusus	36	55.5	0.002
B) Experiment 2				
Canopy Condition				
Gap	No species			
Closed Canopy	No species			
Decay Class				
Decay Class 2	No species			
Decay Class 4	*Ctenicera triundulata*	73	51.3	0.024
Diameter Class				
14-24.75cm	No species			
25-34.75cm	No species			
35cm +	*Ampedus mixtus*	46	28.6	0.008

Note: An indicator value approaching 100 denotes the presence of a species and signifies a particular group without error. *P* values were determined using a Monte Carlo test with 1000 permutations and represents the probability of an indicator value greater than or equal to the observed indicator value.

Figure 3.1. Relative abundance of beetle species in Experiment 1 for A) Harvest Gap and Closed Canopy and B) Decay Class 2 and Decay Class 4. Individual species abundances in parentheses.

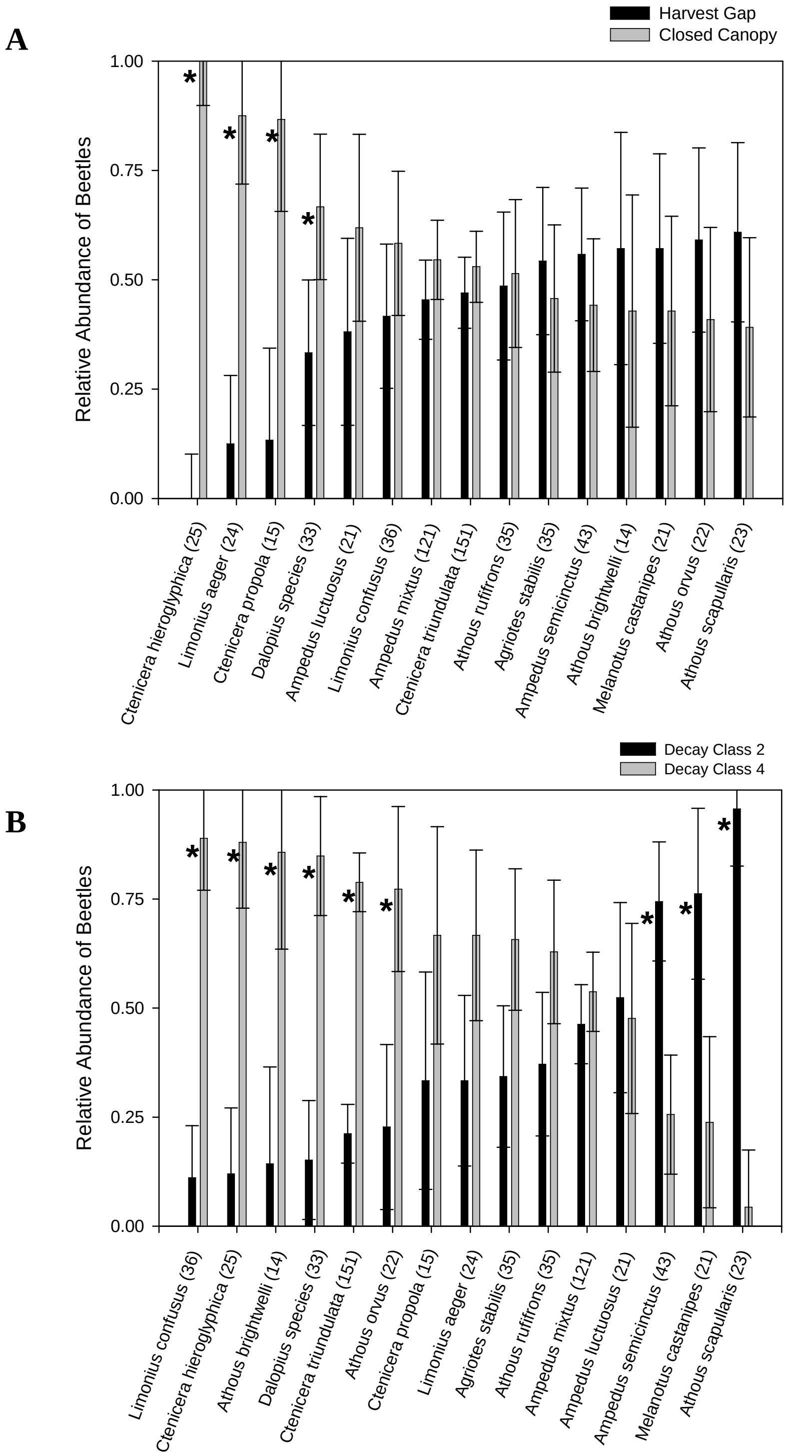
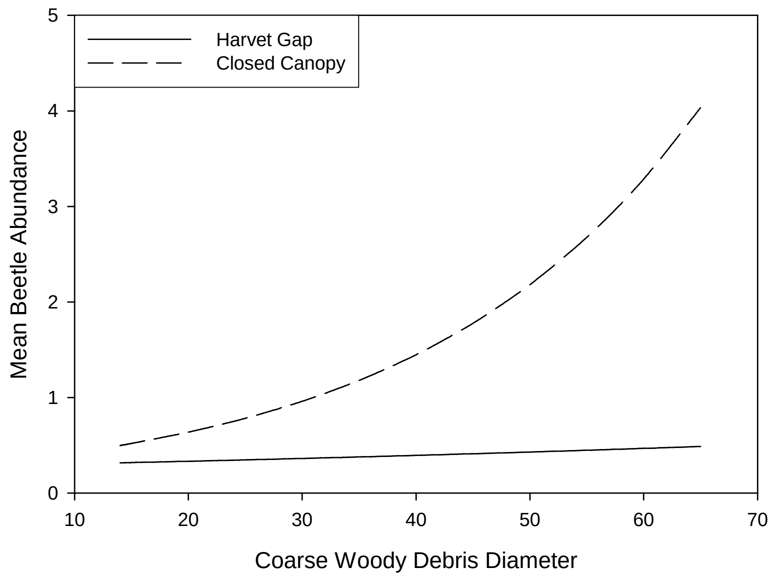


Figure 3.2. General linear model response of the abundance of the most common click beetle species in all trap locations for Experiment 2 with diameter and harvest gap or closed canopy condition.



3.4.4.3. Diameter

In Experiment 1, click beetle species richness was 137% and 115% higher in the large diameter class than in the small and medium diameter classes, respectively (Table 3.2a). Click beetle total abundance was 260% and 183% higher in the large diameter class than in the small and medium diameter classes, respectively. Conversely, species diversity decreased with CWM diameter (Table 3.2a, Figure C.4c). Nine species (*Agriotes collaris* LeC., *A. mixtus*, *A. brightwelli*, *Athous rufifrons* Randall, *C. hieroglyphica*, *C. triundulata*, *Dalopius* spp., *L. aeger*, and *L. confusus*) were indicators of the largest diameter class, while no species were indicators of the two smaller classes (Table 3.3a). The two smaller classes were 67% similar in species assemblage, but the difference between the larger diameter class with the middle and smallest class was greater, at 47% and 46% assemblage similarity, respectively. The mean abundance of the

15 most common click beetle species increased with diameter of the CWM ($p < 0.001$, Table 3.1a, Table C.3a).

In Experiment 2, click beetle species richness was 49% and 70% higher in the large diameter class than in the small and medium diameter classes, respectively (Table 3.2b). Click beetle total abundance was 150% and 117% higher in the large diameter class than in the small and medium diameter classes, respectively. Species diversity was lower in the middle class than in the smallest class (Table 3.2b, Figure C.4d). One species (*A. mixtus*) was an indicator of the largest class, but no species were indicators of the two smaller classes (Table 3.3b). Assemblage similarity among diameter classes was quite low. The two smaller classes were only 59% similar in species assemblage, and the difference between each of these with the larger diameter class was 56% and 49%, respectively. The mean abundance of the 15 most common click beetle species increased more dramatically with CWM diameter under the closed canopy than in harvest gaps ($p < 0.008$, Table 3.1b, Table C.3b, Figure 3.2).

3.5. Discussion

3.5.1. Harvest Gaps

3.5.1.1. Gap Size and Harvest Treatment

I found that size of the harvest gap did not influence click beetle abundance in downed logs, and there were few differences between the 10% and 20% harvest treatments. Species richness, diversity, total abundance, and individual abundances of the most common species were similar, and only *A. stabilis* was an indicator of the 20% harvest treatment. However, there were differences in species composition between the harvest treatments, mostly of uncommon species (fewer than 6 specimens).There are several possible explanations for the general lack of response. First, the range of gaps sizes was relatively limited (0.01 to 0.21 ha). Second, the maximum area of the harvest gaps was relatively small, so that even the largest gaps were still influenced by the surrounding stand. An experiment in a bottomland hardwood forest in South Carolina that created canopy gaps of different sizes (0.13, 0.26, and 0.50 ha) found no differences in the abundance of insect herbivores (Ulyshen *et al.* 2005) or carabid predators (Ulyshen *et al.* 2006). Third, the retention trees that were distributed throughout the harvest gaps further reduced the influence of the canopy openings.

3.5.1.2. Canopy Condition

Many saproxylic species can live in sun-exposed deadwood (Jonsell *et al.* 1998, Lindhe 2004); in fact some species specialize in these environments (Kaila *et al.* 1997). However, other species require or are more abundant in shaded deadwood (Hilszczanski *et al.* 2005), especially species living in later stages of wood decay (Jonsell *et al.* 1998).

The 0.1 and 0.2 ha harvest gaps influenced the click beetles species assemblages. The species composition differed, with 39-42% of the species found exclusively in either harvest gaps or under closed canopy. Four of the most common species were found in greater abundances in CWM under a closed canopy, and two of these species were indicators of closed canopy. None of the most common species had higher abundances in the harvest gaps, and no species were indicators of harvest gaps. However, my results were not as dramatic as those in some studies of sun-exposed deadwood in clearcuts (e.g. Kaila *et al.* 1997). This is not surprising, as the harvest created relatively small gaps for both harvest treatments and retained trees throughout the gaps that reduced sun exposure.

3.5.2. Coarse Woody Material Characteristics

Speight (1989) defines saproxylic insects as those that are “dependent, during some part of their life cycle, upon the dead or dying wood of moribund or dead trees (standing or fallen), or upon wood-inhabiting fungi, or upon the presence of other saproxylics.” Deadwood-dependent beetles outnumber all terrestrial vertebrates by 2-to-1 (Parker 1982, Hunter 1990), and saproxylics comprise a substantial percentage of forest insects (Kohler 2000, Martikainen *et al*. 2000, Siitonen 2001). Saproxylic insects respond to a range of characteristics in deadwood, including those assessed in this study.

3.5.2.1. Wood Type

Recently dead wood is often colonized by insect species with narrow host specificity, but as decomposition advances, there is less host specificity to individual tree species, although there usually remains differentiation in saproxylic species assemblages between hardwood and softwood CWM (Jonsell *et al* 1998, Kolström and Lumatjarvi 2000, and Wikars 2002). However, in this study, we found no difference between hardwood and softwood CWM for most measures of click beetle assemblages. Nevertheless, softwood CWM had higher diversity than hardwood CWM, and beetle assemblage similarity was only 64%, demonstrating a difference in species composition between wood types. These results may be due to our use of CWM in later stages of decay, where host specificity is less likely, and to the possibility that other CWM characteristics were more important in determining species assemblage than wood type.

3.5.2.2. Decay Class

A succession of insect species colonize wood as it decays. Fresh CWM (e.g. Decay Class 1) is inhabited by a distinct fauna that often require fresh phloem or sapwood (Hammond *et al*. 2004). As wood decomposes (Decay Classes 2-4), assisted by suites of fungus species, the species richness of fungivores, scavengers, and predators increases in response to increasing microhabitat diversity (Siitonen 2001). My study reflected this succession. I deliberately avoided the early stage, as Elateridae are not common to fresh deadwood, yet I still observed a difference between the later stages of decay.

In this study, click beetle species richness and total abundance were higher in Decay Class 4, and one species was an indicator of Decay Class 4. Four of the most common click beetle species were more abundant in Decay Class 2, and six of the most common species were more abundant in Decay Class 4. Assemblage similarity was low (56-57%), suggesting a difference in species composition between decay classes. Although few studies have been done on non-pest species, it is assumed that most click beetle species in the later decay classes of CWM are scavengers and predators (Gur'yeva 1978), following the basic trend found by Siitonen (2001). In European forests, where they have been studied more thoroughly, the preponderance of rare and endangered invertebrates are found in the later stages of decomposing wood (Ehnstrom 2001). With lack of availability of CWM and the reduced duration of later stages of decomposition due to CWM crushing during harvest (Freedman *et al.* 1996), North American forests may reflect the same pattern.

3.5.2.3. Diameter

The size of the deadwood is important to most saproxylic species (Appendix C.2). Some species are able to use a wide range of downed CWM sizes, but many species seem to rely on large-sized deadwood. As a result, there are different species assemblages in

CWM of increasing sizes. There is generally a positive relationship between CWM diameter and species richness and abundance (Jonsell *et al*. 1998, Grove 2002a, Hammond *et al*. 2004, but see Araya 1993), and in this study, click beetle species richness and total abundance were higher in the largest diameter class. However, diversity decreased with increasing diameter. Assemblage similarity was low between the largest diameter class and the two smaller classes, indicating difference in species composition. Further, no species were indicators of the smaller diameter logs, but nine species, including *A. mixtus*, were indicators of larger diameter CWM (35+ cm). Hammond *et al*. (2004) also lists *A. mixtus* as an indicator of larger diameter (41+ cm) logs. In Europe, a number of click beetle species that are listed as endangered or vulnerable live in large diameter CWM, snags, or hollow trees (Anon. 1999, Ranius and Jansson 2000, Ranius and Jansson 2002, Zach 2003). However, not all species seem to respond to diameter; Ranius and Jansson (2000) determined that *M. castanipes* abundance in hollow trunks was not correlated with diameter, as was found in my study with downed CWM.

Other factors being equal, larger diameter trees and CWM generally decay more slowly, providing a more stable microclimate that benefits particular invertebrate species (Palm 1959). For example, the endangered click beetle *Limoniscus violaceus* Muller appears to require decaying wood at a certain moisture content to survive (Zach 2003). Larger diameter CWM can also maintain a greater diversity of fungi, including those species that are specific to larger wood pieces (Grove 2002a). Click beetles are commonly assumed to be generalists, presumably increasing in numbers with increased prey items, but there are several species with known prey or habitat requirements. For example, *Elater ferrugineus* is habitually found where its prey, *Dorcus parallelipedus* (Coleoptera: Lucanidae) is active, although it is also known to prey on the threatened scarab beetle (*Osmoderma eremita*) (Svensson *et al*. 2004). Furthermore, several endangered species in Europe are known to have habitat requirements specific to wood decomposed by certain fungus species (Anon. 1999). Although I did not assess the fungi, it is likely some beetle species I collected also respond to specific rot types or prey species that were dependent on particular fungal species or CWM diameters (Appendix C.2).

3.6. Conclusion

The ecological importance of CWM (both snags and downed logs) quantity and quality is becoming well-known. Evidence a number of studies indicate that Elateridae, as with many other saproxylic fauna, utilize a wide variety of CWM characteristics. Based on the work presented here, providing the greatest diversity of habitats for Elateridae should include providing CWM of specific sizes, decay classes, wood types, and overtopping canopy conditions (gaps and closed canopy). Therefore, managing for Elaterid diversity in Acadian Forest stands appears to require addressing the temporal and spatial continuity of CWM characteristics.

EPILOGUE

Summary

The research on Elaterids in the Acadian forest presented in the three preceding chapters had the following objectives:

1. Investigate whether click beetle assemblages and species abundance of flying adults varied with stands that developed following clearcut, shelterwood, and selection harvesting.
2. Determine whether stand conditions (stand structure, vegetation composition, and deadwood conditions) influenced click beetle assemblages and species abundance of flying adults.
3. Assess whether the composition of click beetle assemblages and abundance of individual species emerging from soil were affected by the species composition of overstory and understory vegetation.
4. Examine whether CWM characteristics (stage of decay, diameter, and wood type [softwood or hardwood]) influenced the assemblage and species abundance of emerging adult click beetles.
5. Document the influence of gap harvesting and CWM conditions on the assemblages and species abundance of click beetle adults emerging from soil and CWM.

The first and second objectives were addressed using towers with flight-intercept traps to capture insects at seven different heights in the canopy of forest stands that developed following clearcut, shelterwood, and selection harvesting (Chapter 1).

Abundances of specific species and click beetle assemblage, measured by diversity, richness (numbers of species), overall abundance (numbers of individuals), and assemblage similarity, varied among stands generated by the different harvest methods. Stand characteristics (vegetation structure, composition, deadwood, and relative canopy height) were measured, revealing that click beetle assemblages varied with each stand characteristic, and that, for the stand characteristics, both species richness and species abundance was best predicted by hardwood basal area. Apart from a precursor study associated with this one (Su and Woods 2001), I have found no other studies have captured Elaterids throughout the forest canopy. It was exciting to find that click beetles are commonly found high in the canopy of Acadian forest stands. Relative canopy height also was found to be a better measure of click beetle species richness than harvest treatment and absolute height above the ground.

The third objective was addressed in Chapter 2 where emergence traps placed over the soil were used to capture adult beetles as they emerged in five hardwood (Maple, Birch, Aspen, Blueberry, and Oak) and four softwood (Spruce-Fir-Pine, Pine, Hemlock, and Fern-Hemlock) cover types. Click beetle assemblages varied significantly among vegetation conditions. Although click beetle assemblage overlapped in oak, other hardwood, or coniferous stands, assemblages in oak were less similar to stands with birch, maple, or aspen than these stands were to each other. Assemblages in all hardwood stands were less similar to coniferous stands than they were to one other, with oak stands being the least similar to coniferous stands. Five species of click beetle were more abundant in softwood stands, and nine species were associated with increased presence of specific softwood tree and shrub species. Ten species of click beetle were more abundant in hardwood stands, and ten species were associated with increased amounts of specific hardwood tree and shrub species, including six species associated with oak stands.

Chapter 3 addressed objectives four and five using emergence traps to capture adult beetles as they emerged from either soil or CWM in stands that were treated with two gap-harvesting systems designed based on patterns of natural disturbance in the Acadian forest. Species assemblages varied between harvest treatments, canopy conditions, CWM wood type (hardwood vs. softwood), and especially between CWM decay classes and among diameter classes. There were few differences between the two harvest treatments, and size of harvest gap did not influence the species abundance of click beetles across the small range of gap sizes studied (0.01 to 0.21 ha). Four of the most common species had higher abundances in closed canopy than harvest gaps. Click beetle species richness and species abundance were higher in CWM that had larger diameters and were more decayed. Click beetle diversity was higher in softwood than hardwood CWM.

Strengths and Limitations

In the first study (Chapter 1), pitfall traps, malaise traps, and non-baited intercept traps were hung from towers. Malaise traps are generally less efficient at capturing beetles (but see Ohsawa 2004), so the lack of beetle capture in our study was expected and therefore not discussed. Many Elaterid-specific studies use pitfall traps, primarily in agricultural studies, where species commonly move along the ground. However, some forest studies have also captured Elaterid adults in pitfall traps (e.g., Levesque and

Levesque 1993, Strong *et al*. 2002), so it was surprising to capture no click beetles in our pitfall traps. Non-baited flight intercept traps collect a large number of flying beetles and can be distributed throughout the canopy, so this was a good methodological choice for the first study. However, flight-intercept traps capture adult beetles after they have emerged from their larval habitat, so they tend to measure overall stand abundance rather than abundance from specific sites. These traps were useful for studying the abundance of Elaterids in the canopy rather than only on or near the forest floor. Although the traps were placed up to 11 m into the stands, the traps did not reach to the tops of the canopy in the tallest stands, especially the selection harvest stands. Thus, this study could have been improved had traps been placed fully throughout as well as above the canopy of each stand.

Emergence traps were used in Chapters 2 and 3 because they effectively capture adult beetles as they emerge from their larval habitat. As a result, emergence traps are excellent for measuring beetle relationships with site-specific conditions. The Chapter 2 study was originally designed to include nutrient testing of samples of the top soil layers. Several studies have suggested or concluded that soil nutrients and/or mineral soil type are important determinants of Elaterid habitats (David *et al*. 1993, Ponge *et al*. 1997, Saetre *et al*. 1999, Scheu *et al*. 2003). Including a nutrient dimension of this study would have improved this study by providing a link from vegetation composition to the soil inhabitants.

The study presented in Chapter 3 was limited in two ways. First, only the two harvest treatments were compared. The study could have been improved if it had included the untreated control stands with natural gaps in the comparison, either by using stands from all three (controls and two harvest treatments) or at least comparing the control stands to stands of one harvest treatment. In this way, it would have been possible to more effectively test differences between the harvest methods and the untreated control plots. Second, the study was limited by the results of the harvest treatments. For example, the number of logs (CWM) of the correct combination of characteristics was quite low in each stand. It was difficult to find large diameter logs with specific combinations of characteristics (softwood or hardwood, decay class 2 or 4, in the gap or in the forest matrix). Decay classes 2 and 4 were chosen because they were most easily distinguished from one another. However, CWM pieces in decay class 3 were most common, thus limiting opportunities for trap placement. This limitation may change as the long-term study progresses, since trees are being retained in harvest gaps. Some of these retention trees will become snags and downed logs, increasing the number of possible trap sites, as well as providing a wider and more consistent diameter range of the various downed log types. It was possible to wrap the emergence traps fully around the decay class 2 logs, but for the decay class 4 logs the edges of the traps were placed beneath the leaf litter, leaving the connection in place with the soil. This design was appropriate for restricting intrusion from epigeal insects, but may not have fully separated the decay class 4 logs from the surrounding soil, so measurement of click beetle populations in the soil may have been affected by the presence of nearby CWM (Chershire 1988, Marra and Edmonds 1998, Jabin *et al*. 2004). However, the sites selected in for traps in this study deliberately avoided locations with nearby CWM, thus limiting any effect of CWM on the soil traps.

Conservation and Forest Management Implications

Results and observations from this study have several implications for maintaining biodiversity in managed forests. First, was the apparent importance of vegetative composition in forest stands. Click beetle richness and overall abundance were higher in stands dominated by deciduous trees, and many click beetle species were associated with specific species of hardwood trees. Other species of click beetle had higher abundances in coniferous stands, even in stands that were almost pure pine or pure spruce-fir-pine with little to no moss or understory. Click beetle assemblages also varied among stands dominated by different hardwood species (e.g., oak or maple) or stands dominated by different softwood species (e.g., hemlock or pine). Therefore, maintaining Elaterid diversity at the landscape level appears to require that a wide array of stands dominated by different deciduous and/or coniferous species should be maintained.

Second was the importance of structural diversity in forest stands. In the first study, click beetle richness, total abundance, and diversity increased with stand structural diversity. In the third study, the small size of the harvest gaps and the increased structure provided by the retention trees in harvest gaps appeared to help mitigate negative effects of harvest gaps. Therefore, incorporating structural diversity into silvicultural practices at the stand level, even in traditional methods like clearcut, shelterwood, and selection harvest systems, may help maintain Elaterid diversity (e.g., Vanha-Majamaa and Jalonen 2001).

Third was the importance of deadwood (both snags and downed logs) quantity and quality, including type (hardwood or softwood), diameter, and stage of decay. Deadwood-dependent beetles outnumber all terrestrial vertebrates by 2-to-1 (Parker

1982), and saproxylics (fauna dependent on deadwood) comprise a substantial proportion of forest insects. Differences in click beetle assemblages in softwood and hardwood logs were found in this study. Other studies have found considerable differentiation in saproxylic species assemblages between deadwood types (Jonsell *et al.* 1998, Kolstrom and Lumatjarvi 2000, Wikars 2002, and Jonsell *et al.* 2004). As wood decomposes, assisted by a wide array of fungal species, the species richness of fungivores, scavengers, and predators increases in response to increasing microhabitat diversity (Siitonen 2001). Several Elaterid species were found in this study to be nearly exclusive to either Decay Classes 2 (less decomposed) or 4 (more decomposed) logs. In European forests, where invertebrates have been studied more thoroughly, the preponderance of rare and endangered invertebrates are found in the later stages of decomposing wood (Ehnstrom 2001). With the loss of later stages of decomposition due to harvest crushing (Freedman *et al.* 1996), North American forests may reflect the same pattern of rare and endangered species. Although some saproxylic species are able to use a wide range of deadwood diameters, many species rely on large diameter pieces. Thus, there is generally a positive relationship between deadwood diameter and species richness and abundance (Jonsell *et al.* 1998, Grove 2002a, Hammond *et al.* 2004, but see Araya 1993). As a result, there are different species assemblages in deadwood of increasing sizes. Results for click beetles from this study corroborated findings of these other studies; moreover, as diameter size class increased, the abundance of logs in the forest stands decreased (Fraver *et al.* 2002). Forest managers are beginning to consider deadwood retention as part of their silvicultural objectives by permanently retaining large trees in stands so that they can eventually become deadwood (Seymour 2005), and by deliberately creating snags or high stumps (Kaila *et al*. 1997, Jacobs 2005, Lilja *et al*. 2005). These modifications addressing the diversity and continuity of deadwood may help to sustain biodiversity in managed forests.

Future Directions

Results from the studies presented in this dissertation suggest several potential directions for future research. First, a greater understanding about the importance of leaf litter and soil nutrients and mineral soil type on forest-dwelling Elateridae is needed. One approach could involve selecting several sites with similar forest cover types but different soil types (e.g., Ponge *et al*. 2003), but to identify specimens to species to better understand the preferences of individual species rather than simply summing abundance for the family. Second, it would be helpful to use rearing studies that determine the food preferences and length of the larval stage for different Elaterid species. Third, it would be interesting to better understand the click beetle species dispersion, including how far they disperse from their emergence point and how the females choose egg-laying sites (especially for CWM). One study released several hundred marked specimens of one species in an island field (Yamamura *et al*. 2003), however this was a pest species, easily accessible and relatively easily recaptured. In a forest system, telemetry would be more expensive but perhaps more beneficial (see Ranius 2006). Fourth, deadwood should be studied more intensely. For example, many studies have noted the impact of different fungal species on the invertebrate populations. Although there are no known species-specific fungal associations with click beetles, it may be that rot type (brown or white) may play a role in habitat preferences. Deadwood creation could also be studied. Logs of specific diameters could be introduced to forest stands (or specific trees in the stand cut) to address a wider and more continuous size range. Snags could be created by girdling to compare snag and CWM, natural snag and girdled snags, or snag diameter, decay class, and type (softwood and hardwood).

Context of Faith in Natural Resource Conservation

There are many contexts in which conservation of natural resources takes place. A person's or group's faith can have a major impact on how they perceive the importance of biodiversity and the need to preserve it. In recognition of this, the journal Conservation Biology recently published a series of articles on the context of Christian faith in conservation (Cobb 2005, Flood 2005, Henderson 2005, Johns 2005a, Johns 2005b, Orr 2005a, Orr 2005b, Stuart *et al*. 2005, Van Dyke 2005). I find it interesting that that the major differences among the articles were in how the Christian church, especially the portion in the United States, has responded to conservation philosophy, not in how the Bible describes the need for conservation. No matter what people believe about possible differences between the Bible and science, we cannot deny that the Bible teaches specifically and copiously on the requirement of humans to care for the whole creation. Here I discuss only one small theme in the ecology of faith-- "till and keep."

One of the most important verses in the Bible that describes our relationship with God in the context of conservation is Genesis 2:15.

> *The LORD God took the man and put him in the garden of Eden to* ***till*** *it and* ***keep*** *it.* (NRSV)

The two verbs used (till and keep) help us to understand what actions God desires for us in the context of our interaction with the rest of the creation. The first word, till (*abad*) is a common agricultural term for working the soil, referring to the use of our natural resources. The idea here is that we are permitted to till the ground to provide for our needs. But we are only to till in the context of second word, "keep" (*shamar*). This word means to protect, attend to, watch, preserve, and save, or to hedge about as with thorns (Strong 1990). The picture is given of a thorn hedge growing around that which you wish to protect.

This word was exemplified well by something I experienced in Kenya. Each family's *boma* (enclosure often containing several homes) was surrounded by a thick, living fence of plants with massive thorns; some species (like *Euphorbia candelabrum*) contained a milky, extremely toxic latex that can blind or burn the skin. Shepherds kept their animals in the fenced area each night to protect them from wild animals and thieves. Every time I read this verse, I picture those thick, thorny fences. That is the kind of protection God asks us to give to the rest of the creation.

The following are two of many verses that can help us to understand the word "keep/*shamar*." The first passage is the well-known story of the building of an ark to save species from the coming flood. God commands Noah:

> *You are to bring into the ark two of all living creatures, male and female, to* ***keep them alive*** *with you. Two of every kind of bird, of every kind of animal and of every kind of creature that moves along the ground will come to you to be* ***kept alive****. You are to take every kind of food that is to be eaten and store it away as food for you and for them.* (Genesis 6:19-21, TNIV)

The second passage is a blessing that God gave to the high priest of Israel for the purpose of blessing the followers of God. Even today, it is often used in many Christian churches at the end of the community gathering to bless the people as they leave.

> *The LORD bless you and* ***keep*** *you; the LORD make his face shine on you and be gracious to you; the LORD turn his face toward you and give you peace.*
> (Numbers 6:24-26, TNIV)

I find both of these passages instructional in our understanding of the word "keep/*shamar*." In the first passage, God makes sure that the people and all the other species are protected from the flood, but also note God's extra instructions to make sure Noah also provided whatever food they needed to survive. In the second passage, "keep/*shamar*" is used to describe the kind of protection we wish God to provide for us. When we connect these passages, we conclude a more profound understanding of our role in *keeping*. As much as Christians desire God to keep us, protect us, watch over us, sustain us, provide for us, and preserve us in times of need, this is what God expects us to do for the entire creation. This is our role as keepers of the earth.

Therefore, one role of Christians is to make sure that our human wants do not supercede the needs of the rest of the creation. We are permitted to use the natural resources of the earth, but only in a way in which we can still protect and care for the rest of the creation. When we do so, we are obeying God, our Creator and Keeper.

There are many other Scripture passages addressing conservation- game regulation (Deuteronomy 22:6-7), taxonomic naming (Genesis 2:19-20), leaving agricultural land fallow (Leviticus 25:2-5), clean water (Ezekiel 34:18), sprawl (Isaiah

5:8), praise of animals of no use to humans (Job 41:1-12), the proper role of those with power (Matthew 20:20-28, John 13), and God’s love and care for, delight in, and blessing on all of the creation (e.g. Genesis 1:22, Genesis 9:9-17, Job 39:13-18, John 3:16-18).

For me, these passages apply directly to our work in conservation and forest management. My primary research interest is the question of how to use our forest resources to meet our human needs (and perhaps our wants) while still caring for (keeping) all the other species that depend on the forest ecosystem. My faith did not affect my experimental design, my analyses, or my findings in this thesis. But it does affect my desire to care for this creation and to help people better understand- and perhaps even love- these tiny, amazing creatures that we have named click beetles.

> *God made the wildlife of the earth ... and all crawling things of the soil...*
> *God saw that it was good.* (Genesis 1:25, trans. E. Fox 1997).

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Appendix A

Figures and Tables from Chapter 1

Table A. 1. Click beetle abundance per trap week for all species, stands, and years.

	1997													1998												
Species	c22	c8	s12	s20	s25	s26	s52	w2	w21	w23	w29	w7a	w7b	c22	c8	s12	s20	s25	s26	s52	w2	w21	w23	w29	w7a	w7b
Agriotella bigeminata	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	0.00	0.00	0.00	0.00	0.00	0.00	0.25	0.00	0.00
Agriotes collaris	0.00	0.00	0.00	0.00	0.00	0.50	0.00	0.13	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.25	0.50	0.00	0.13	0.13	0.00	0.00	0.00	0.00
Agriotes fucosus	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	0.00	0.00	0.00	0.00	0.00	0.25	0.00	0.00	0.00	0.00	0.00	0.00
Agriotes limosus	0.00	0.00	0.13	0.13	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	0.13	0.00	0.00	0.00	0.00	0.00	0.25	0.00
Agriotes stabilis	0.75	1.75	1.75	1.00	3.13	3.25	0.88	0.13	1.00	0.63	1.25	3.38	2.13	0.83	1.60	1.00	0.54	3.13	2.38	1.75	0.13	0.68	0.13	0.25	2.50	0.13
Ampedus apicatus	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.13	0.00	0.00	0.00	0.13	0.29	0.20	0.13	0.00	0.00	0.25	0.13	0.00	0.00	0.25	0.00	0.00	0.00
Ampedus luctuosus	0.00	0.13	0.00	0.00	0.00	0.00	0.00	0.00	0.13	0.00	0.00	0.50	0.00	0.25	0.00	0.38	0.93	0.13	0.50	0.00	0.38	0.89	0.00	1.13	0.00	0.00
Ampedus mixtus	0.13	0.50	0.63	0.00	0.38	0.00	0.88	1.38	0.00	0.88	0.13	0.88	0.38	0.75	0.20	1.00	0.79	0.50	1.50	0.88	2.21	0.75	0.50	0.75	0.63	2.15
Ampedus melsheimeri	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	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Ampedus molestus	0.13	0.13	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	0.13	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Ampedus nigricollis	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	0.00	0.00	0.00	0.00	0.00	0.00	0.13	0.00	0.00
Ampedus near melantoides	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.13	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.13	0.00	0.00	0.00	0.00	0.00	0.13
Ampedus near mixtus	0.00	0.00	0.13	0.00	0.00	0.00	0.00	0.00	0.25	0.00	0.00	0.13	0.00	0.00	0.00	1.00	0.00	0.38	0.13	0.00	0.13	0.14	0.00	0.00	0.00	0.33
Ampedus pullus	0.13	0.13	0.00	0.38	0.00	0.25	0.00	0.00	0.38	1.00	0.13	1.50	2.25	0.67	0.00	0.38	0.25	0.00	0.38	0.00	0.13	0.13	0.00	2.50	1.00	1.40
Ampedus sellatus	0.00	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	0.00	0.13	0.13	0.00	0.00	0.00	0.25	0.00	0.00
Ampedus semicinctus	0.00	0.00	0.13	0.00	0.13	0.88	2.00	0.13	0.38	0.00	0.00	0.13	0.13	0.46	0.13	0.75	0.89	0.00	1.50	1.25	0.96	0.64	0.00	1.00	0.13	0.25
Ampedus species C	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	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Ampedus species E	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	0.00	0.00	0.13	0.00	0.00	0.00	0.00	0.00	0.00
Athous brightwelli	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	0.00	0.13	0.00	0.00	0.13	0.00	0.00	0.00	0.00
Athous cucullatus	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	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Athous orvus	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	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.13	0.00
Athous rufifrons	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	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Cardiophorus gagates	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	0.00	0.00	0.00	0.00	0.00	0.00	0.13	0.00	0.00
Ctenicera appropinquans	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.13	0.25	0.13	0.25	0.00	0.00	0.13	0.00	0.14	0.00	0.00	0.00	0.00	0.00	0.00	0.50	0.13	0.13
Ctenicera arata	0.13	0.00	0.00	0.13	0.00	0.13	0.13	0.00	0.13	0.13	0.13	0.00	0.00	0.00	0.00	0.63	0.00	0.00	0.63	0.00	0.00	0.64	0.25	0.50	0.13	0.13
Ctenicera cruciata	0.13	0.00	0.00	0.00	0.63	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.13	0.53	0.13	0.00	0.13	1.00	0.38	0.13	0.00	0.00	0.13	0.13	0.00
Ctenicera fulvipes	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	0.00	0.00	0.00	0.13	0.25	0.00	0.00	0.00	0.13	0.13	0.00
Ctenicera hamata	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	0.00	0.00	0.00	0.25	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Ctenicera hieroglyphica	0.25	0.13	0.00	0.00	0.00	0.00	0.38	0.38	0.00	0.00	0.00	0.00	0.00	0.00	0.20	0.13	0.00	0.25	0.00	1.38	0.25	0.29	0.00	0.13	0.13	0.20
Ctenicera insidiosa	0.00	0.13	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	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
Ctenicera mediana	0.13	0.00	0.00	0.13	0.00	0.00	0.00	0.50	0.00	0.00	1.88	0.13	0.25	0.00	0.00	0.00	0.00	0.13	0.00	0.50	0.75	0.00	0.00	2.13	0.25	0.00
Ctenicera nitidula	0.00	0.00	0.13	0.00	0.00	0.00	0.00	0.00	0.38	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.25	0.00	0.00	0.00	0.00	0.14	0.00	0.00	0.13	0.00
Ctenicera propola	0.00	0.13	1.38	0.50	0.75	0.25	0.13	0.00	0.00	0.00	0.38	0.25	0.00	0.13	0.00	1.25	0.00	0.13	0.00	0.63	0.00	0.00	0.00	0.00	0.00	0.00
Ctenicera resplendens	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.13	0.00	0.13	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.25	0.00	0.00	0.00	0.00
Ctenicera rufopleuralis	0.13	0.00	0.00	0.00	0.00	0.00	0.00	0.25	0.38	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.13	0.00	0.00	0.13	0.27	0.63	0.00	0.25	0.00
Ctenicera spinosa	0.00	0.38	0.00	0.38	0.13	0.25	0.00	0.00	0.00	0.00	0.13	0.25	0.50	0.13	0.00	0.00	0.00	0.13	0.13	0.00	0.00	0.00	0.00	0.25	0.00	0.25
Ctenicera tarsalis	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	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Ctenicera triundulata	0.63	1.63	9.13	11.63	11.75	10.75	2.63	1.75	7.00	9.13	5.00	4.00	1.63	3.17	0.50	4.63	10.79	3.38	14.50	6.25	1.75	18.96	3.13	13.13	21.13	12.28
Dalopius species	0.00	0.00	0.50	0.50	0.00	0.50	0.25	0.38	0.25	0.13	0.00	0.13	0.50	0.17	0.33	0.50	0.79	0.00	0.63	0.88	0.75	0.27	0.25	0.13	0.00	2.30
Danosoma brevicornis	0.13	0.13	0.25	0.63	0.25	0.00	0.00	0.25	0.13	0.00	0.50	0.13	1.38	0.00	0.00	0.00	0.29	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Danosoma obtectus	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	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Denticollis denticornis	0.00	0.13	0.13	0.00	0.13	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.13	0.00	0.00	0.00	0.00	0.00	0.00
Drasterius debilis	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	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Elathous dicalceatus	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	0.00	0.25	0.25	0.00	0.00	0.00	0.13	0.00	0.25	0.00
Fornax canadensis	0.00	0.00	0.00	0.00	0.13	0.00	0.38	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.25	0.14	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.13
Isoriphis obliqua	0.00	0.00	0.00	0.00	0.63	0.25	0.25	0.00	0.13	0.13	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	0.00
Lacon auroratus	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	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Limonius aeger	0.00	0.13	0.13	0.50	0.00	0.00	0.00	0.00	0.38	0.25	0.00	0.00	0.00	0.00	0.00	0.25	0.00	0.25	0.25	0.00	0.00	1.14	0.75	0.00	0.00	0.00
Limonius confusus	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	0.00	0.00	0.00	0.00	0.00	0.13	0.00	0.14	0.00	0.00	0.00	0.00
Melanotus castanipes	0.13	0.00	0.13	0.88	0.25	0.75	0.38	0.13	0.25	0.25	0.13	0.75	0.38	0.13	0.00	0.38	0.39	0.63	1.00	0.25	0.25	0.00	0.25	0.38	0.13	0.00
Melanotus hyslopi	0.13	0.00	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	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Melanotus sagitarius	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.13	0.00	0.00	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
Melanotus similis	0.13	0.00	0.00	0.00	0.38	0.00	0.00	0.00	0.00	0.00	0.13	0.25	0.00	0.13	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.13	0.00	0.13	0.00	0.13
Melanotus species	0.00	0.00	0.00	0.00	0.25	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	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Microhypnus striatulus	0.00	0.00	0.00	0.00	0.13	0.00	0.00	0.00	0.13	0.00	0.00	0.00	0.00	0.17	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Oxygonus montanus	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	0.00	0.00	0.38	1.25	1.88	0.00	0.00	0.00	0.00	0.00	0.00
Oxygonus obesus	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	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Sericus brunneus	0.00	0.13	3.25	0.38	0.00	0.38	0.13	0.00	0.00	0.00	0.13	0.25	0.88	0.17	0.00	4.25	0.64	0.50	0.25	0.25	0.00	0.13	0.00	0.63	0.63	1.90
Sericus honesticus	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	0.00	0.00	0.00	0.00	0.13	0.00	0.25	0.00	0.00	0.00	0.00	0.00	0.00
Sericus viridanus	0.13	0.00	0.00	0.13	0.00	0.13	0.13	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.75	0.14	0.00	0.00	0.25	0.00	0.00	0.00	0.00	0.00	0.00

Table A.2. Click beetle richness and total abundance (per trap week) by year and total between years.

	Richness			Abundance		
Site	1997	1998	Total	1997	1998	Total
c22	15	15	23	3.1	7.5	15.3
c8	14	10	20	5.5	3.9	13.2
s12	15	18	23	17.9	17.8	20.8
s20	15	14	21	17.4	17.0	18.5
s25	16	20	29	19.1	11.0	21.8
s26	15	23	27	18.5	27.8	24.0
s52	20	22	28	9.8	18.0	23.1
w2	11	14	15	5.4	8.0	12.6
w21	20	19	27	11.9	25.8	21.2
w23	12	10	15	13.1	6.3	12.8
w29	17	21	27	10.5	24.5	22.3
w7a	17	18	25	13.1	28.0	20.5
w7b	13	15	20	10.6	21.8	18.3

Table A.3. Summary of significant responses of click beetle species richness to general linear models.

Source	Response
a) Site model including harvest treatments	
Harvest Treatment	Selection > Clearcut
Site within harvest treatment	w23 < w21 and w29
b) Site model including environmental variables	
Hardwood Basal Area	Increased with hardwood basal area
c) Height model including harvest treatments	
Site within harvest treatment	w23 < w21 and w29
	s20 < s12, s26, s52
Height	Decreased with height
Harvest Treatment	Selection > Shelterwod > Clearcut
d) Height model including environmental variables	
Relative Canopy Height	Decreased with relative canopy height

Table A.4. Summary of significant responses of click beetle species abundance to general linear models.

Source	Response
a) Site model including harvest treatments	
Year	1997 > 1998
Harvest Treatment	Selection and Shelterwod > Clearcut
b) Site model including environmental variables	
Year	1997 > 1998
Hardwood Basal Area * Species	Increased with hardwood basal area
	Ampedus semicinctus
	Ctenicera hieroglyphica
	Oxygonus montanus
c) Height model including harvest treatments	
Year	1997 > 1998
Species	Varied among species
Harvest Treatment	Selection > Shelterwod > Clearcut
Trap Height*Treatment	Increased with height
	Selection
	Decreased with height
	Clearcut
	Shelterwood
d) Height model including environmental variables	
Year	1997 > 1998
Species	Varied among species
Relative Canopy Height	Decreased with relative canopy height

Figure A.1. Click beetle responses to harvest treatment for A) species richness at the stand scale and B) species abundance at the trap height scale.

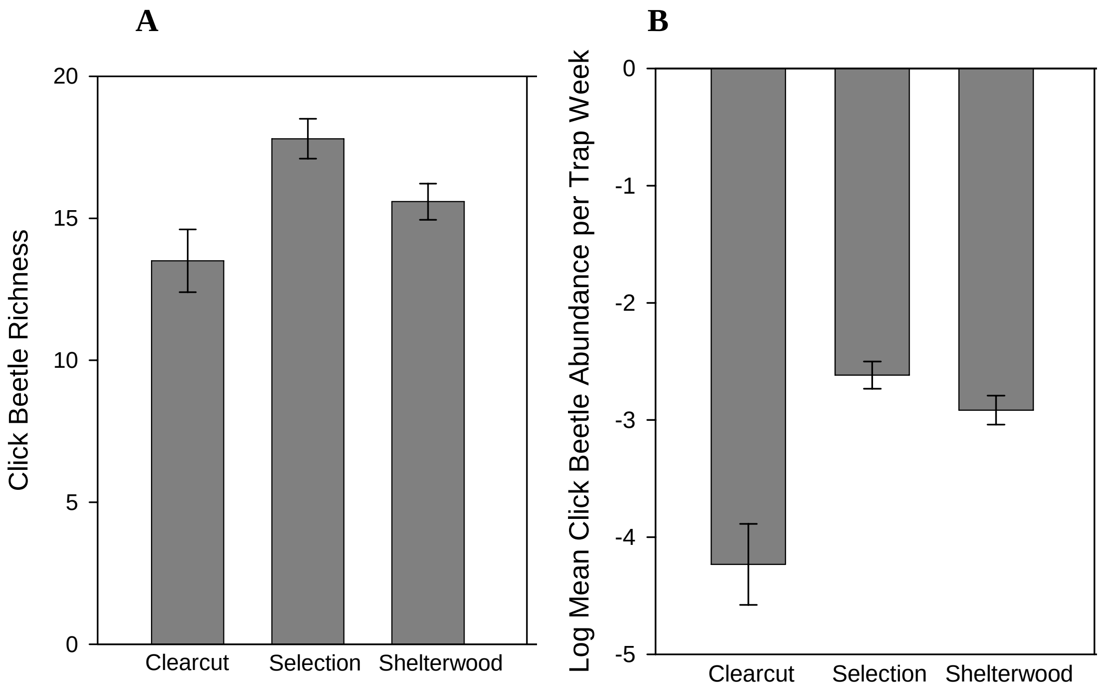


Figure A.2. Click beetle responses for trap height scale models. A) Species richness response to trap height, B) species richness response to relative canopy height, C) species abundance response to height for each harvest treatment, D) species abundance response to relative canopy height, E) species richness response to hardwood basal area, and F) species abundance response to hardwood basal area.

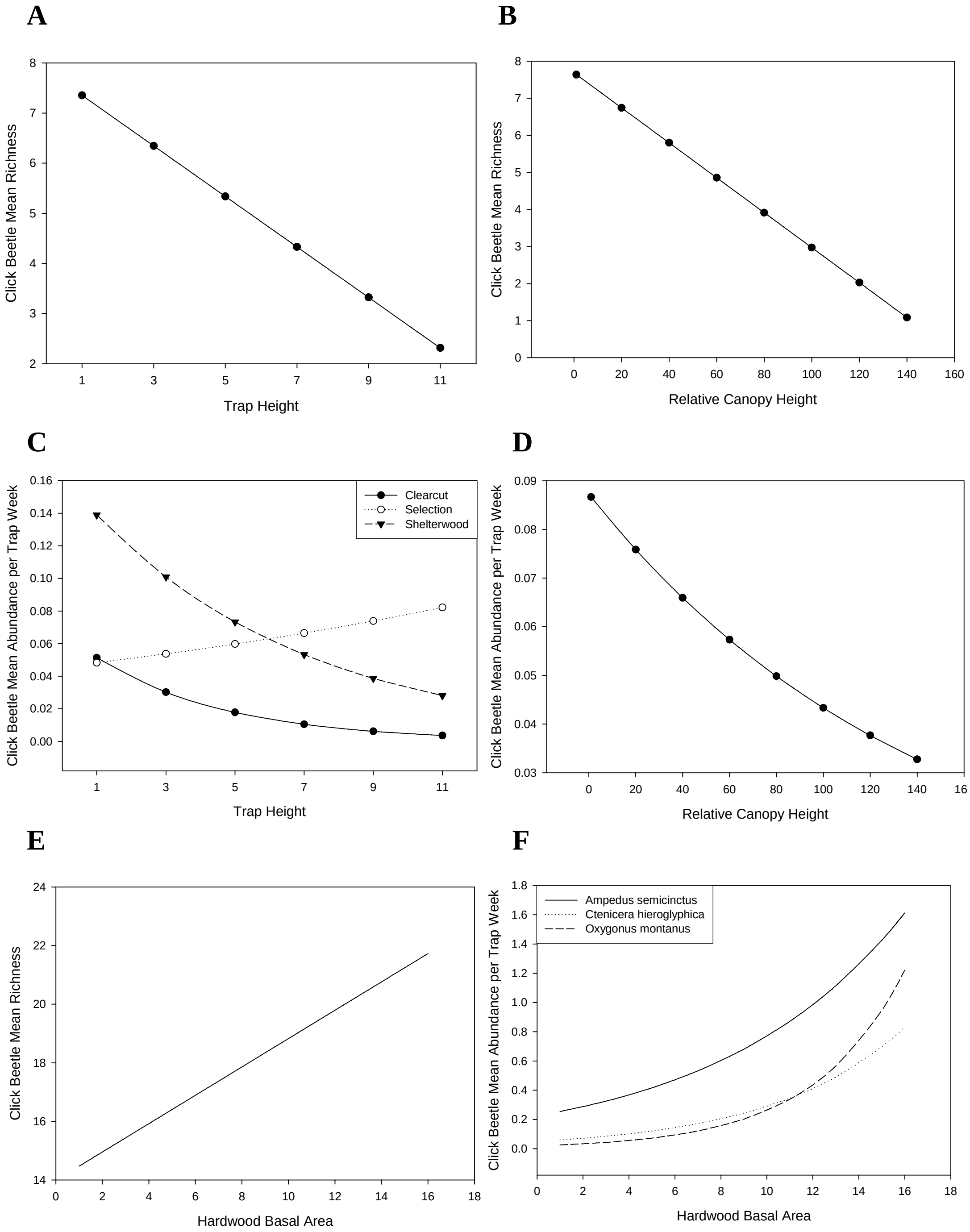


Table A.5. AIC comparisons between Stand and Height models for click beetle species richness and species abundance.

Source	Parameters	AICc	Δ AIC
A) Richness Stand Model			
Year, Treatment, Site within Treatment	44	-99.3	0.0
Year, Hardwood Basal Area	3	61.8	161.1
Year, Snag Class 2 Basal Area	3	63.5	162.8
Year, Snag Class 4 Basal Area	3	64.8	164.1
Year, Vegetation Structural Diversity	3	65.3	164.5
B) Richness Height Model			
Year, Relative Canopy Height	3	307.4	0.0
Year, Height, Treatment, Stand within Treatment	45	360.4	53.0
C) Abundance Stand Model			
Year, Species, Hardwood Basal Area, Species*Hardwood Basal Area	35	-49.5	0.0
Year, Species, Total Basal Area, Species*Total Basal Area	35	-48.2	1.3
Year, Species, Treatment, Site within Treatment	47	33.8	83.3
Year, Species, CWD Class 2	19	286.1	335.6
Year, Species, CWD Classes 2-4	19	289.4	338.9
D) Abundance Height Model			
Year, Species, Relative Canopy Height	19	1390.1	0.0
Year, Species, Relative Canopy Height, Species*Relative Canopy Height	35	1412.4	22.3
Year, Species, Height, Treatment, Site within Treatment, Treatment*Height	64	1570.7	180.6
Year, Species, Height, Treatment, Site within Treatment	61	1586.2	196.1
Year, Species, Height, Treatment, Site within Treatment, Species*Height, Treatment*Height	80	1640.6	250.5
Year, Species, Height, Treatment, Site within Treatment, Species*Height	77	1644.4	254.3
Year, Species, Height, Treatment, Site within Treatment, Species*Height, Treatment*Height, Species*Treatment*Height	128	2858.2	1468.1

Appendix B

Appendix B. 1. Figures and Tables from Chapter 2

Figure B.1. Soil insect emergence trap, showing the base pegged and the upper and lower collecting bottles fixed to the pole inside the tent. For clarity the pole ropes and the weights along the tent edges are not shown.

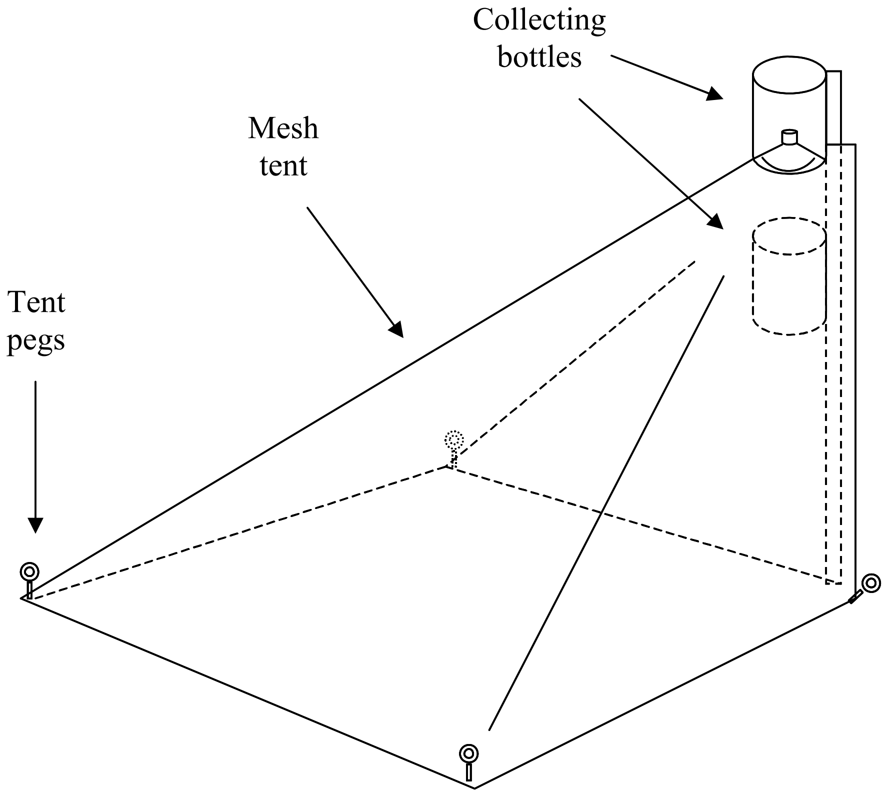


Table B.1. Total canopy width (m/ha) per stand of shrub and small tree species for A) 2001 and B) 2002.

Site	*Abies balsamea* Balsam Fir	*Acer rubrum* Red Maple	*Betula papyrifera* White Birch	*Kalmia angustifolia* Sheep Laurel	*Lonicera canadensis* American Fly Honeysuckle	*Osmunda claytoniana* Interrupted Fern	*Picea rubra* Red Spruce	*Pinus strobus* White Pine	*Populus* species Aspen species	*Prunus serotina* Black Cherry	*Quercus rubra* Red Oak	*Tsuga canadensis* Eastern Hemlock	*Vaccinium angusifolium* Early Low Blueberry	*Viburnum lantanoides* Hobblebush
A) 2001														
asp22	133	0	1,035	80	0	0	0	0	1,618	424	0	0	27	0
bir08	398	0	2,759	0	0	0	0	0	0	849	0	0	0	0
bir22	0	0	7,029	371	0	0	0	0	0	0	0	0	159	0
inf12	80	981	0	0	0	2,228	0	0	0	212	0	0	0	159
inf20	0	0	0	0	0	1,671	106	0	0	0	0	0	0	318
map25	318	6,897	0	0	0	0	186	0	0	0	0	1,525	0	80
map26	0	17,454	0	0	0	0	186	398	0	0	0	1,035	0	0
spr21	637	0	0	0	0	0	0	0	0	0	0	0	0	0
spr23	1,592	0	0	0	0	0	4,032	531	265	0	0	239	0	0
hem12	1,340	0	0	0	0	0	172	0	0	0	0	2,202	0	0
hem20	0	0	0	0	0	0	0	0	0	0	0	0	0	0
blu08	0	610	875	0	0	0	0	0	398	531	0	398	1,499	0
blu22	0	796	1,194	318	0	0	0	0	0	0	0	0	1,923	0
B) 2002														
asp02	411	902	6,870	0	93	0	610	0	0	0	239	0	0	0
asp22	212	1,857	2,135	0	0	0	0	0	5,623	1,061	0	0	0	0
bir22	1,220	584	9,059	0	531	0	0	0	0	2,600	0	0	265	0
bir08	0	597	6,472	0	53	0	0	0	0	0	0	0	504	0
oak04	212	902	0	0	0	0	0	0	0	0	66	0	623	0
oak05	0	0	0	0	0	0	0	0	0	0	239	398	0	0
pin06	0	119	0	0	0	0	0	0	0	1,950	0	0	0	0
pin07	0	0	0	0	0	0	0	0	66	0	27	0	0	0
spr21	637	0	0	0	0	0	0	0	0	0	0	0	0	0
spr23	4,112	0	0	0	0	0	2,971	0	265	0	0	955	0	0
hem12	576	0	0	0	0	0	584	0	0	0	0	1,247	0	0
hem20	1,021	0	1,419	0	544	0	769	0	0	0	0	13	0	0

Table B.2. Click beetle species abundance (total number of individuals within each stand) for each cover type in 2001 and 2002.

	2001													2002											
	Blueberry		Aspen	Birch		Maple		Spruce-Fir-Pine		Hemlock		Fern-Hemlock		Aspen		Birch		Oak		Pine		Spruce-Fir-Pine		Hemlock	
Species	blu22	blu08	asp22	bir22	bir8	map25	map26	spr21	spr23	hem12	hem20	inf12	inf20	asp2	asp22	bir22	bir8	oak04	oak05	pin06	pin07	spr21	spr23	hem12	hem20
Agriotes arcanus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
Agriotes collaris	0	1	0	0	1	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0
Agriotes evansi	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0
Agriotes fucosus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	0	0	0	0	0	0
Agriotes limosus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
Agriotes quebecensis	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0
Agriotes stabilis	5	1	5	5	3	5	1	8	1	7	8	2	3	5	6	8	15	6	1	0	0	2	1	6	13
Ampedus mixtus	0	2	0	0	1	1	2	0	1	3	0	1	1	0	0	0	0	0	0	1	0	0	0	0	1
Amedus near melanotoides	0	0	0	0	0	0	0	0	0	1	2	1	0	3	0	0	0	4	0	0	0	0	0	1	0
Amedus pullus	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Ampedus semicinctus	0	0	0	0	0	1	0	0	0	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0
Ampedus species C	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	2	1	0	0	0	0	0	0
Athous acanthus	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Athous brightwelli	4	1	3	3	0	3	4	0	0	0	2	0	0	0	1	0	0	0	0	0	0	0	0	0	0
Athous orvus	0	0	0	4	0	0	4	0	0	0	0	0	0	0	2	3	1	0	2	0	1	0	0	0	1
Athous protervus	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	0	0	0	0	0	0	1	0	0
Athous rufifrons	0	0	0	0	0	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	0
Ctenicera appropinquans	0	0	2	1	0	0	0	0	0	0	0	0	0	3	0	1	2	0	0	0	0	0	0	0	1
Ctenicera arata	0	0	0	0	0	0	0	1	0	1	0	5	1	0	0	0	1	2	1	0	0	0	0	1	0
Ctenicera cruciata	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	0	0	0	0	0	0
Ctenicera cylindriformis	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	3	0	0	0	0	0	0	0
Ctenicera fulvipes	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0
Ctenicera hieroglyphica	1	0	0	0	0	0	1	0	0	0	1	0	0	6	1	5	1	18	1	0	2	1	0	0	0
Ctenicera mediana	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0
Ctenicera nitidula	0	0	0	0	1	0	0	1	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	1	1
Ctenicera propola	0	0	1	0	1	5	0	0	0	7	4	3	1	0	1	1	0	1	0	1	1	0	0	4	12
Ctenicera rufopleuralis	0	0	0	0	1	0	1	0	0	0	0	0	1	0	2	1	1	3	1	1	1	0	1	0	1
Ctenicera spinosa	1	0	0	0	0	0	1	1	0	0	0	0	1	0	0	0	0	1	0	2	0	1	0	0	1
Ctenicera triundulata	5	7	1	4	22	9	20	10	12	43	46	33	36	7	0	1	21	3	4	14	14	8	10	16	21
Dalopius species	0	1	0	4	38	0	44	0	0	0	15	9	21	3	8	14	16	3	1	1	1	0	0	0	13
Denticollis denticornis	0	0	0	0	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Hadromorphus inflatus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0
Hemicrepidius memnoius	0	0	0	0	0	3	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	1	0
Isoriphis obliqua	0	0	1	1	0	2	2	0	0	0	0	0	0	0	1	0	1	0	1	0	0	0	0	0	0
Lacon brevicornis	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Limonius aeger	0	0	1	0	1	2	0	0	9	1	2	1	0	2	0	0	3	2	0	1	5	1	3	1	4
Melanotus canadensis	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	0	0	0	0	0	0
Melanotus castanipes	0	1	1	0	0	0	0	0	0	0	0	0	0	1	0	0	1	2	4	0	0	0	0	0	0
Melanotus similis	1	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0
Oxygonus obesus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0
Sericus brunneus	1	2	0	2	0	0	0	0	0	3	2	2	0	0	0	0	0	0	0	0	0	0	0	0	1

Appendix B.2. NMS v. CCA

Two ordination analyses were used to examine the relation between click beetle species abundance and the vegetation community. I used non-metric multidimensional scaling (NMS; Kruskal 1964) to determine the strongest gradients in the click beetle assemblage structure among cover types and to associate click beetle species with particular vegetation species. Canonical correspondence analysis (CCA, Ter Braak 1986) was used to determine the amount of the variation in the click beetle assemblage that could be accounted for by vegetation variables. To exclude bias provided by including rare species (Jongman *et al*. 1995), I included only the 20 and 17 most common species for 2001 and 2002, respectively, in the analyses. A cube root transformation was used to reduce dominance of the most abundant species (McCune & Grace 2002).

NMS is an iterative ordination method based on ranked distances between sample units. This method searches for low stress, measured by the relationship between the ranked distances in the original multidimensional space and the reduced dimensions produced by the ordination. NMS is an effective ordination method for community data; it is robust to a large proportion of zero values and does not assume normality (Clarke 1993, McCune and Grace 2002). I used PC-ORD (McCune and Mefford 1999) with random starting configurations and the quantitative version of the Sorensen distance measure; the run with the lowest stress was used for the final analysis. In a previous NMS analysis on the stands in common between sample years, I examined the relative position of the species and found little difference between years. In order to use all of the stands, however, I analyzed the two years separately. For each year, six axes were assessed and three axes were selected. I presented results for only the two axes that had significant Monte Carlo test results ($p < 0.05$). The 2001 ordination final stress was 5.96, and the two axes were 93.6% orthogonal and explained 19.5% and 63.9% of the variation in the click beetle assemblage structure. The 2002 ordination final stress was 6.11, and the two axes were 99.9% orthogonal and explained 29.5% and 41.7% of the variation in the click beetle assemblage structure. I subsequently performed Pearson and Kendall correlations between the ordination axes with the beetle species and the vegetation species, and joint-plotted the vegetation species. A high correlation between a vegetation species and an NMS axis indicated a strong association between that vegetation species with the click beetle species associated with the axis. I overlaid polygons encircling the stands of major vegetation types.

CCA conducts an ordination that is constrained by the environmental variables in that CCA regresses the click beetle species onto the environmental variables and then ordinates the results. The eigenvalues are estimates of "inertia," or the total variance in the species data set. The interset correlations indicate the influence of the environmental variables in structuring the ordination. CANOCO version 4.5A (Ter Braak 2003) was used to employ automatic forward selection to determine the most important vegetation species and the order of their inclusion in the model based on the conditional effects (the variance each vegetation species explained after selecting the most important variables). I subsequently carried out an automatic CCA to determine the statistical significance of each model. Monte Carlo analysis was performed using 1,000 permutations to test each CCA model at a significance level of alpha = 0.05. For each year, models were based on the following vegetation categories: "understory only" (including shrubs, small trees, and ferns), "overstory only," and "mixed understory and overstory." The results from the

CCA showed that no multicollinearity was detected in any of the models. For both the 2001 and 2002 collections, no significant ($p < 0.05$) CCA model including only overstory tree species was found. CCA models including both overstory and understory vegetation and those including only understory vegetation were similar in significance, ordination, and amount of variance explained. For each model the CCA stand ordination plots were very similar to the NMS ordination plots; they are presented here.

Figure B.2. CCA ordination plots based on 17 click beetle species from 2001. Monte Carlo test results, eigenvalues, and percent variation explained in Table B.1. Length of vectors indicates the strength of the correlation. Symbols (A and C) code for site type (square = dominated by other hardwoods, diamond = dominated by softwoods.) Beetle and plant species' abbreviations (B and D) based on Table B.2. (A and B) Understory species only; (C and D) Understory and overstory species included.

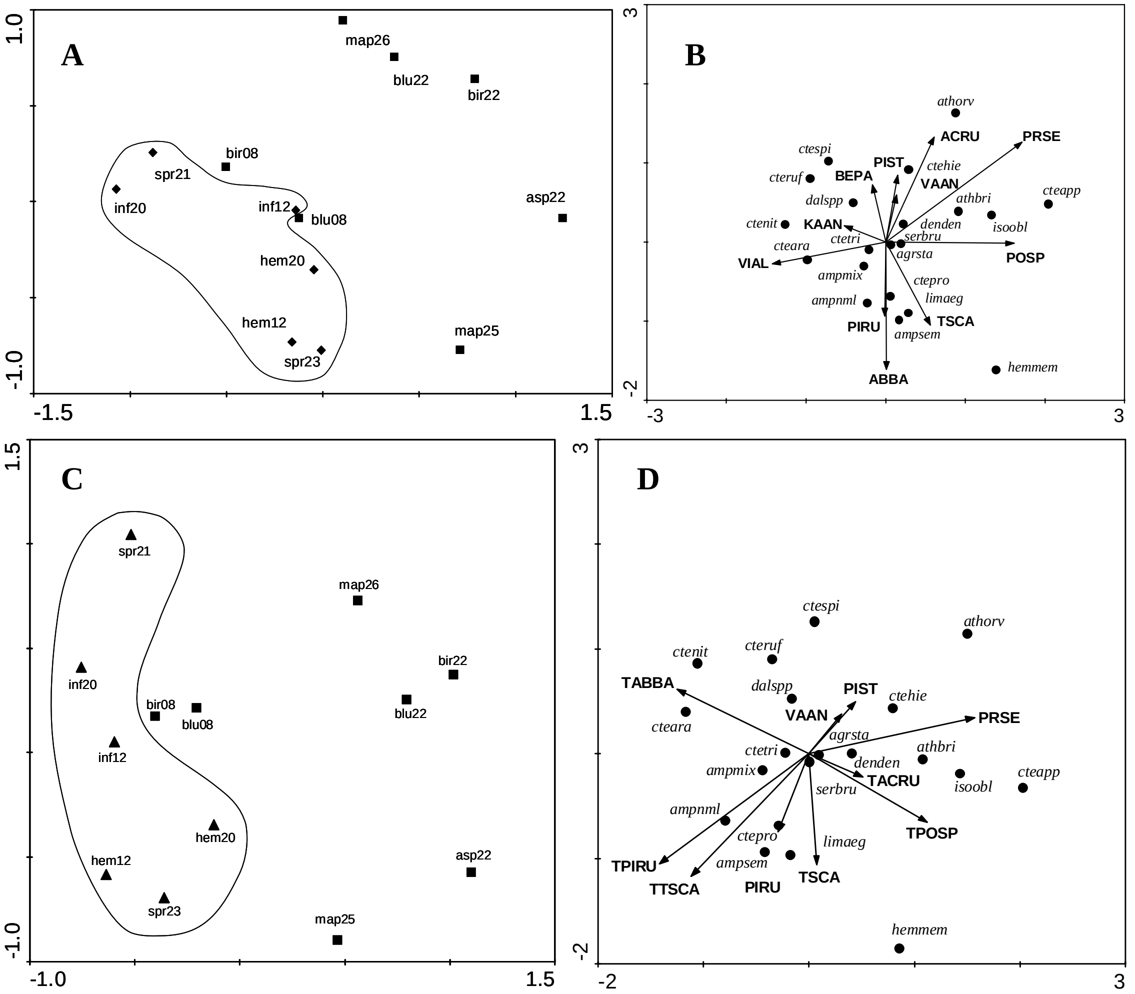


Figure B.3. CCA ordination plots based on 20 click beetle species from 2002. Monte Carlo test results, eigenvalues, and percent variation explained in Table B.1. Length of vectors indicates the strength of the correlation. Symbols (A and C) code for site type (triangle = dominated by oak, square = dominated by other hardwoods, diamond = dominated by softwoods.) Beetle and plant species' abbreviations (B and D) based on Table B.2. (A and B) Understory species only; (C and D) Understory and overstory species included.

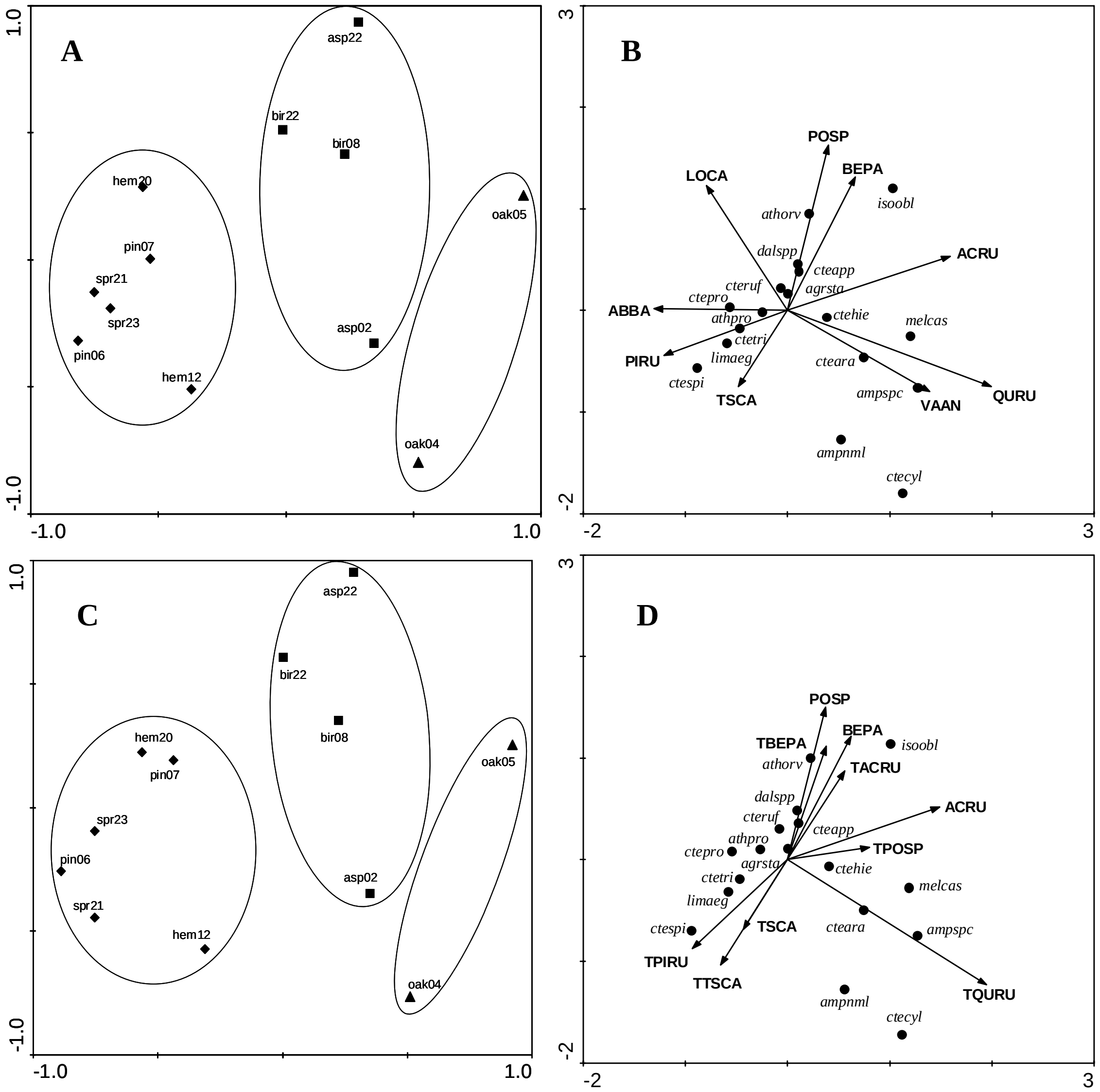


Table B.3. Results of Canonical Correspondence Analysis for 2001 and 2002 click beetle abundances with tree and shrub species.

Source (Montel Carlo Test Results)	Axis 1	Axis 2	Axis 3	Axis 4
2001 Shrubs (F-ratio: 1.837; P-value 0.046)				
Eigenvalues (Total: 1.223; Canonical: 1.166)	0.26	0.23	0.18	0.13
Cumulative percentage variance of species data	21.0	40.1	54.6	65.4
2001 Shrubs & Trees (F-ratio: 1.783; P-value 0.022)				
Eigenvalues (Total: 1.223; Canonical: 1.1)	0.28	0.23	0.18	0.13
Cumulative percentage variance of species data	22.8	41.4	55.9	66.4
2002 Shrubs (F-ratio: 2.141; P-value 0.0100)				
Eigenvalues (Total: 0.902; Canonical: 0.817)	0.22	0.20	0.13	0.09
Cumulative percentage variance of species data	24.3	46.0	60.9	70.5
2002 Shrubs & Trees (F-ratio: 2.896; P-value 0.004)				
Eigenvalues (Total: 0.902; Canonical: 0.872)	0.22	0.20	0.13	0.09
Cumulative percentage variance of species data	24.5	46.8	60.8	70.6

Table B.4. Inter-set correlations for two axes of four Canonical Correspondence Analyses for Shrubs only or Shrubs & Trees for 2001 and 2002. Empty spaces indicate species not included in analysis.

Species	Abbre-viation	2001		2002	
		Axis 1	Axis 2	Axis 1	Axis 2
Shrubs					
Balsam Fir	ABBA	0.00	-0.50	-0.42	0.00
Red Maple	ACRU	0.19	0.42	0.51	0.17
Paper Birch	BEPA	-0.05	0.23	0.21	0.41
Sheep Laurel	KAAN	-0.17	0.06		
American Fly Honesuckle	LOCA			-0.26	0.39
Red Spruce	PIRU	-0.00	-0.29	-0.39	-0.14
White Pine	PIST	0.05	0.26		
Aspen species	POSP	0.52	-0.01	0.13	0.51
Black Cherry	PRSE	0.55	0.39		
Red Oak	QURU			0.64	-0.23
Eastern Hemlock	TSCA	0.18	-0.33	-0.16	-0.23
Early Low Blueberry	VAAN	0.04	0.19	0.45	-0.25
Hobblebush	VIAL	-0.46	-0.09		
Shrubs & Trees					
Balsam Fir	TABBA	-0.49	0.23		
Red Maple	TACRU	0.20	-0.08	0.19	0.30
Paper Birch	TBEPA			0.13	0.38
Red Spruce	TPIRU	-0.55	-0.39	-0.32	-0.30
Aspen species	TPOSP	0.44	-0.24	0.28	0.04
Red Oak	TQURU			0.67	-0.42
Eastern Hemlock	TTSCA	-0.44	-0.43	-0.23	-0.35
Red Maple	ACRU			0.51	0.18
Paper Birch	BEPA			0.21	0.42
Red Spruce	PIRU	-0.11	-0.28		
White Pine	PIST	0.17	0.19		
Aspen species	POSP			0.13	0.51
Black Cherry	PRSE	0.61	0.13		
Eastern Hemlock	TSCA	0.03	-0.39	-0.15	-0.23
Early Low Blueberry	VAAN	0.12	0.14		

Appendix B.3. Variation in click beetle assemblages

B.3.1. Distant hemlock trees did not influence Maple Cover Type

In 2001, vegetation at the two maple stands near the traps (within 5 m) was dominated by many smaller-diameter maple trees; however, a few large diameter hemlock trees at 5 to 12 m from the traps were included by the 10-factor prism and therefore dominate the overall basal area for these two stands. To determine whether these distant hemlocks influenced the results, I compared the assemblages in the Maple cover type to the assemblages in the Hemlock cover type. I contrasted the relative abundances of the click beetle species in the Maple and Hemlock cover types, using 95% confidence intervals as described in the methods. The elaterid species associated with Maple were associated with all the hardwood cover types combined, and the elaterid species associated with Hemlock were associated with all the softwood cover types combined. The assemblage similarity for Maple was most similar to other hardwood cover types compared to the softwood cover types, except for Blueberry (very different because they had so little overstory) and the 2001 Aspen (different because there was only one stand). The NMS ordinations also placed the stands in the Maple cover type closer to the other hardwood stands than to the softwood stands. Therefore, I believe the distant hemlocks did not have a significant influence on click beetle assemblages in the Maple cover type.

B.3.2. Possible Small-scale Heterogeneity

I sampled sites within cover types that were sometimes near sites within another cover type. For example, the hemlock sites sampled in 2001 were located near the fern-hemlock sites. Therefore, I examined the differences between the Hemlock and Fern-Hemlock cover types. Overall click beetle species richness, species abundance, and assemblage similarity were similar between these two cover types, although diversity was higher in the Fern-Hemlock than the Hemlock cover type. Three species (*Ctenicera triundulata*, *Dalopius* spp., and *Sericus brunneus*) had similar abundances between the Hemlock and Fern-Hemlock cover types, but *Agriotes stabilis*, *Athous brightwelli*, and *Limonius aeger* had lower abundances in Fern-Hemlock than Hemlock. These results indicated that although Hemlock was preferred over other softwood cover types for several species, the areas dominated by ferns within those stands were likely not as favorable for three species of click beetles. (In contrast, Hendrix (1980) and Balick *et al.* (1978) identified one Elaterid as a fern herbivore and one as a fern associate). This small-scale heterogeneity suggested that click beetle communities may have responded to fine scale differences in forest vegetation. As a result, these small-scale responses to vegetation serve to increase the overall diversity of Elaterid species in the region.

Other studies have found small-scale heterogeneity within forest stands. Apigian *et al* (2006) studied litter-inhabiting beetles, including 22 species of Elateridae, in a Sierran mixed-conifer forest and determined that the beetle assemblages were heterogeneous across smaller (~60 m) and larger (100’s of meters) spatial scales. Niemelä *et al.* (1996) found that in the boreal forest, assemblages of beetles in the family Carabidae can be heterogeneous even at scales as narrow as 10-15 m; this may be due to micro-habitat preferences for specific types of ground cover. However, I detected only minor differences between Hemlock and Fern-Hemlock cover types.

B.3.3. Vegetation species explain majority of variation in click beetle assemblages

Results from the CCA suggest that the understory layer is a better predictor of the click beetle assemblages than the overstory layer. However, this is obfuscated by the influence of the overstory on the understory species. Why are the click beetle assemblages seemingly responding to the vegetation species? Although relatively little is known about these click beetle species, there are several possibilities. First, a direct relationship may exist where the click beetle larvae may feed on the roots of specific plant species. Click beetle larvae are well known as pests in agricultural systems, and species found in forests can survive on vegetative matter (Fox 1961). However, this is not a strong possibility. Most soil-dwelling species are predaceous or omnivorous (Johnson 2002), and those that are primarily herbivorous feed on a wide array of plant species (C. Pilcher, P. Johnson, pers. communication). Second, an indirect relationship may exist with click beetles responding to prey types that are specific to vegetation species. Some click beetle species are known to be effective predators of wood borers (Craighead 1950 and Woodruff 2004), and many species in our study are known to feed on pests of forest trees (Tostowaryk 1972 and Morris 1951). However, these species were not specific to their prey items (sometimes feeding on vegetable matter), and even species responding to specialized chemical cues from their preferred prey also feed on other species (Svensson *et al*. 2004).

Third, an indirect relationship may exist with click beetles responding to the soil conditions (e.g. soil type, nutrients, temperature, and moisture) influenced by or correlated with the vegetation community. To a certain extent the mineral soil layer influences the plant communities (Jenny 1980). Click beetle assemblages are known to change across certain mineral soil types, despite similarities in soil moisture and dominant vegetation (Penev 1992). However, our vegetation treatments were not correlated with the soil mineral types. The leaf litter can influence the click beetle assemblages; several species are considered to be saprophagous on dead leaves (Zacharuk 1963, Wolters 1989, and David *et al*. 1993), and even carnivorous larvae will shift to become detritivorous or saprophagous in the absence of prey (Balduf 1935). Because of this, Saetre *et al*. (1999) and Scheu *et al*. (2003) interpreted the changes in click beetle assemblages across different forest stands as responses to nutrient input from leaf fall. Additionally, Ponge *et al*. (1997) and David *et al*. (1993) found that Elaterid larvae abundance increased with the shift from dystrophic mull to dysmoder, with a corresponding increase in acidity and decrease in iron, calcium, magnesium. Trees and shrubs also influence the temperature and moisture of the soil (Phillips and Shure 1990 and Kapos 1989), both of which greatly impact the presence and movement of click beetles (Lees 1943a&b, Zacharuk 1962, and LaFrance 1968). This is a complex relationship; soil conditions affect the plant communities, plant communities affect the soil conditions, both soil conditions and plant communities seem to affect click beetle assemblages, and click beetles influence the nutrients available to plants (Wolters 1989). We believe that the interaction between the vegetation and soil conditions is most likely driving the results of our study (see Figure B.4 and Table B.5 for mineral soil information on our sites).

Figure B.4. NMS ordination plots based on Figures 2.7 and 2.8 with mineral soil type overlays. (A) 2001 ordination of 17 click beetle species. Symbols code for site type (square = hardwoods, diamond = softwoods). (B) 2002 ordination of 20 click beetle species. Symbols code for site type (triangle = oak, square = other hardwoods, diamond = softwoods).

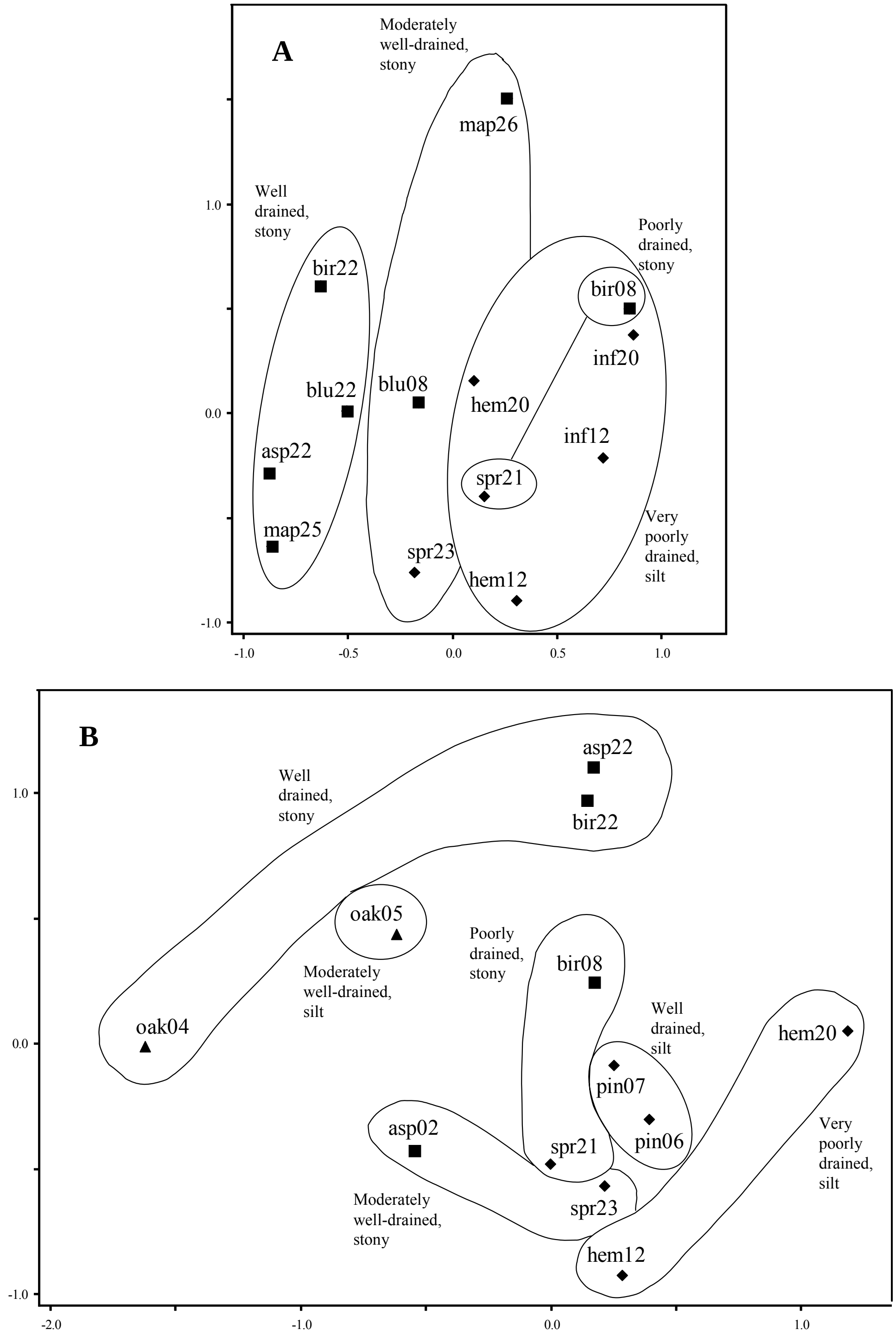


Table B.5. Mineral Soil Types for each 2001 and 2001 site.

Grouping	Soil Type	% Slope	Parent Material	Comp	2001	2002
Well-Drained Soils	Plaisted very stony loam	5 to 15	Deep till	c22	asp22	asp22
Well-Drained Soils	Plaisted very stony loam	5 to 15	Deep till	c22	bir22	bir22
Well-Drained Soils	Plaisted very stony loam	5 to 15	Deep till	c22	blu22	
Well-Drained Soils	Plaisted very stony loam	5 to 15	Deep till	c25	map25	
Well-Drained Soils	Plaisted very stony loam	5 to 15	Deep till	oak04		oak04
Well-Drained Soils	Suffield silt loam	2 to 8	Lacustrine	pin06		pin06
Well-Drained Soils	Suffield silt loam	2 to 8	Lacustrine	pin07		pin07
Moderately Well-Drained to Somewhat Poorly-Drained Soils	Buxton silt loam	0 to 2	Lacustrine	oak05		oak05
Moderately Well-Drained to Somewhat Poorly-Drained Soils	Howland very stony loam = Dixmont stony loam	0 to 8	Deep till	c02/c03		asp02
Moderately Well-Drained to Somewhat Poorly-Drained Soils	Howland very stony loam = Dixmont stony loam	0 to 8	Deep till	c08blu	blu08	
Moderately Well-Drained to Somewhat Poorly-Drained Soils	Howland very stony loam = Dixmont stony loam	8 to 15	Deep till	c23	spr23	spr23
Moderately Well-Drained to Somewhat Poorly-Drained Soils	Howland very stony loam = Dixmont stony loam	8 to 15	Deep till	c26	map26	
Poorly Drained and Very Poorly Drained Soils: Mostly Stony	Monarda and Burnham very stony silt loams	0 to 8	Deep till	c21	spr21	spr21
Poorly Drained and Very Poorly Drained Soils: Mostly Stony	Monarda and Burnham very stony silt loams	0 to 8	Deep till	c08bir	bir08	bir08
Very Poorly Drained Soils: Mostly Stone-Free	Biddeford silt loam	0 to 3	Lacustrine	c12	hem12	hem12
Very Poorly Drained Soils: Mostly Stone-Free	Biddeford silt loam	0 to 3	Lacustrine	c20	hem20	hem20
Very Poorly Drained Soils: Mostly Stone-Free	Biddeford silt loam	0 to 3	Lacustrine	c20	inf12	
Very Poorly Drained Soils: Mostly Stone-Free	Biddeford silt loam	0 to 3	Lacustrine	c20	inf20	

Appendix C

Appendix C.1. Figures and Tables from Chapter 3.

Figure C.1. The Acadian Forest Ecosystem Research Program stands within the Penobscot Experimental Forest near Bradley, Maine, USA.

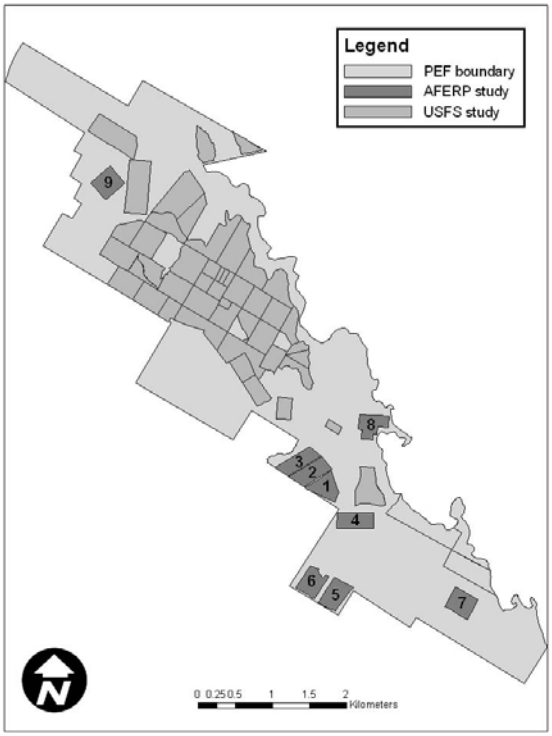


Figure C.2. Coarse woody material insect emergence trap, showing the upper and lower collecting bottles fixed to pole inside the tent.

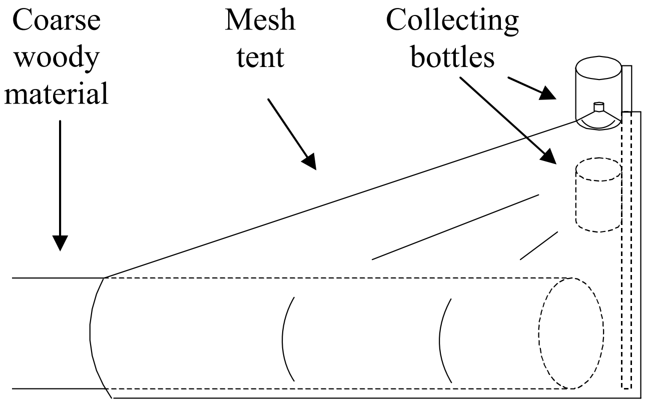


Table C.1. General linear model results of click beetle species abundance in trap locations in gaps only for A) Experiment 1 and B) Experiment 2.

Source	DF	Chi-Square	Pr > ChiSq
A) Experiment 1			
Year	1	2.85	0.091
Site	2	2.96	0.227
Beetle Species	14	56.99	<0.001
Decay Class	1	1.60	0.206
Diameter	1	2.22	0.136
Area of Gap	1	0.03	0.861
B) Experiment 2			
Harvest Treatment	1	0.00	0.951
Site within Harvest Treatment	4	2.50	0.645
Beetle Species	14	97.60	<0.001
Type	1	0.74	0.389
Decay Class	1	3.37	0.067
Diameter	1	6.78	0.009
Area of Gap	1	0.24	0.623

Table C.2. Abundance of the most common click beetle species by harvest treatment (10% or 20%), canopy condition (harvest gap or closed canopy), and decay class (DC2 or DC4) for CWM samples in 2001 (averaged between CWM types) and 2002 (summed between CWM types).

	2001 10% Harvest Treatment				2002 10% Harvest Treatment				2002 20% Harvest Treatment			
	Gap		Closed		Gap		Closed		Gap		Closed	
Species	DC2	DC4	DC2	DC4	DC2	DC4	DC2	DC4	DC2	DC4	DC2	DC4
Agriotes collaris	0.0	0.0	0.0	0.0	0.0	1.0	1.0	3.0	0.0	0.0	1.0	2.0
Agriotes stabilis	2.0	4.0	1.0	3.5	1.0	3.0	1.0	1.0	7.0	8.0	3.0	11.0
Ampedus apicatus	0.0	0.0	0.0	0.0	0.0	0.0	1.0	0.0	0.0	0.0	0.0	0.0
Ampedus deletus	0.0	0.5	0.0	0.5	0.0	1.0	2.0	1.0	0.0	0.0	0.0	0.0
Ampedus laurentinus	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	1.0	0.0	0.0	0.0
Ampedus luctuosus	0.0	1.0	0.5	0.0	2.0	5.0	7.0	2.0	1.0	0.0	1.0	3.0
Ampedus mixtus	0.5	1.5	2.0	5.5	11.0	13.0	27.0	22.0	14.0	17.0	4.0	13.0
Ampedus molestus	0.0	0.0	0.0	0.0	1.0	0.0	0.0	0.0	8.0	0.0	0.0	0.0
Ampedus near impolitus	0.0	0.0	0.0	0.5	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Ampedus near melsheimeri	0.0	1.5	0.5	0.5	0.0	5.0	1.0	3.0	0.0	1.0	2.0	3.0
Ampedus near mixtus	0.5	0.5	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Ampedus near protervus	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	1.0	0.0
Ampedus near semicinctus	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	1.0
Ampedus nigricollis	0.0	0.0	0.0	0.0	2.0	0.0	0.0	0.0	4.0	0.0	0.0	0.0
Ampedus pedalis	0.0	0.0	0.0	0.0	1.0	0.0	4.0	0.0	0.0	0.0	0.0	0.0
Ampedus pullus	0.0	0.0	0.0	0.0	0.0	0.0	1.0	0.0	1.0	2.0	0.0	0.0
Ampedus semicinctus	0.5	1.0	3.0	0.0	13.0	0.0	2.0	1.0	11.0	0.0	6.0	10.0
Ampedus specc	0.0	0.0	0.0	1.0	0.0	2.0	1.0	1.0	1.0	9.0	0.0	1.0
Athous acanthus	0.0	0.0	0.0	0.5	0.0	1.0	0.0	0.0	0.0	1.0	1.0	0.0
Athous brightwelli	0.5	2.5	2.0	6.0	0.0	1.0	0.0	0.0	1.0	6.0	1.0	5.0
Athous cucullatus	0.0	0.0	0.0	0.0	0.0	2.0	0.0	0.0	2.0	4.0	0.0	1.0
Athous orvus	1.0	0.5	0.5	0.5	3.0	10.0	2.0	7.0	0.0	0.0	0.0	0.0
Athous productus	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	2.0
Athous rufifrons	1.0	3.5	0.5	0.5	1.0	7.0	6.0	8.0	5.0	4.0	1.0	3.0
Athous scapularis	1.0	0.0	1.5	0.0	11.0	1.0	6.0	0.0	2.0	0.0	3.0	0.0
Ctenicera appropinquans	0.0	0.5	0.5	0.5	1.0	1.0	0.0	0.0	2.0	1.0	0.0	1.0
Ctenicera arata	0.0	0.0	1.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	3.0
Ctenicera cruciata	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	1.0	1.0	0.0	0.0
Ctenicera fulvipes	0.0	0.0	0.0	0.5	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Ctenicera hamata	0.0	0.0	0.0	0.0	0.0	2.0	0.0	2.0	0.0	1.0	0.0	0.0
Ctenicera hieroglyphica	0.0	0.0	1.0	0.5	0.0	0.0	3.0	9.0	0.0	0.0	0.0	13.0
Ctenicera insidiosa	1.0	0.0	0.5	0.5	0.0	0.0	1.0	1.0	0.0	0.0	0.0	2.0
Ctenicera lobatus	0.0	0.0	0.0	0.0	0.0	1.0	1.0	0.0	0.0	0.0	0.0	0.0
Ctenicera nigricollis	1.5	0.5	1.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Ctenicera propola	0.0	0.5	0.5	0.0	0.0	1.0	1.0	1.0	1.0	0.0	3.0	8.0
Ctenicera resplendens	0.0	0.0	0.0	0.0	0.0	0.0	0.0	1.0	0.0	0.0	0.0	0.0
Ctenicera rufopleuralis	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	1.0
Ctenicera spinosa	0.0	0.0	0.5	0.0	0.0	1.0	0.0	2.0	0.0	1.0	1.0	2.0
Ctenicera sulcicollis	0.0	0.0	0.0	0.0	0.0	0.0	1.0	0.0	0.0	0.0	0.0	0.0
Ctenicera tarsalis	0.0	0.0	0.0	0.0	0.0	0.0	0.0	1.0	0.0	0.0	0.0	0.0

Table C.2. Continued.

	2001 10% Harvest Treatment				2002 10% Harvest Treatment				2002 20% Harvest Treatment			
	Gap		Closed		Gap		Closed		Gap		Closed	
Species	DC2	DC4	DC2	DC4	DC2	DC4	DC2	DC4	DC2	DC4	DC2	DC4
Ctenicera triundulata	5.0	10.5	9.5	6.0	7.0	36.0	11.0	28.0	8.0	20.0	6.0	35.0
Dalopius species	1.0	4.5	1.5	2.0	1.0	8.0	3.0	7.0	1.0	1.0	0.0	12.0
Denticollis denticornis	0.5	1.0	0.0	1.5	0.0	0.0	4.0	0.0	1.0	2.0	1.0	0.0
Drasterius debilis	0.0	0.0	0.0	0.0	0.0	0.0	2.0	0.0	1.0	0.0	0.0	0.0
Fornax canadensis	0.0	0.0	0.0	0.0	7.0	0.0	0.0	0.0	4.0	0.0	0.0	0.0
Hemicrepidius memnonius	0.0	0.5	0.0	0.5	0.0	1.0	1.0	0.0	1.0	2.0	0.0	0.0
Hypolithus striatulus	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	1.0	0.0
Isoriphis obliqua	8.0	0.5	1.0	1.0	3.0	0.0	1.0	1.0	2.0	0.0	3.0	1.0
Lacon aurorata	0.0	0.5	0.5	0.0	0.0	1.0	2.0	0.0	2.0	0.0	0.0	0.0
Lacon brevicornis	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	7.0	0.0	0.0	0.0
Lacon obtecta	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	1.0	0.0	0.0	0.0
Limonius aeger	2.5	0.5	1.0	1.0	0.0	2.0	4.0	8.0	0.0	1.0	4.0	5.0
Limonius confusus	0.0	2.0	0.0	1.5	1.0	10.0	0.0	9.0	2.0	2.0	1.0	11.0
Limonius stigma	0.0	0.0	0.5	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Megapenthes species A	0.0	0.0	0.0	0.0	0.0	0.0	1.0	0.0	0.0	0.0	0.0	0.0
Megapenthes stigmosus	0.0	0.0	0.0	0.0	0.0	0.0	0.0	1.0	0.0	0.0	0.0	0.0
Melanotus castanipes	2.5	0.0	1.0	0.5	5.0	1.0	4.0	2.0	5.0	1.0	2.0	1.0
Oxygonus montanus	0.0	0.0	0.0	0.0	0.0	0.0	1.0	0.0	0.0	0.0	0.0	0.0
Sericus brunneus	0.0	0.5	0.0	0.0	0.0	1.0	0.0	0.0	0.0	0.0	0.0	0.0
Sericus viridanus	0.0	0.0	0.0	0.5	0.0	5.0	0.0	3.0	0.0	0.0	0.0	1.0

Table C.3. Summary of significant responses to general linear models of the abundance of the most common click beetle species in all trap locations. A) Experiment 1 (10% harvest treatment, 2001 & 2002) and B) Experiment 2 (10% and 20% harvest treatments, 2002). Species listed are significant to category.

Source	Response	
A) Experiment 1		
Diameter	Increase with diameter	
Canopy Condition	Closed Canopy > Harvest Gap	
	Higher abundance in Closed Canopy	Higher abundance in Harvest Gap
	Ctenicera hieroglyphica	No species
	Ctenicera propola	
	Dalopius species	
	Limonius aeger	
Decay Class	Higher abundance in Decay Class 2	Higher abundance in Decay Class 4
	Ampedus semicinctus	*Athous brightwelli*
	Athous scapullaris	*Athous orvus*
	Melanotus castanipes	*Ctenicera hieroglyphica*
		Ctenicera triundulata
		Dalopius species
		Limonius confusus
B) Experiment 2		
Year	2002 > 2001	
Canopy Condition	Closed Canopy > Gap	
Diameter	Steeper slope for Closed Canopy than Gap	
Decay Class	Higher abundance in Decay Class 2	Higher abundance in Decay Class 4
	Ampedus semicinctus	*Athous brightwelli*
	Athous scapullaris	*Ctenicera triundulata*
	Isoriphis obliqua	*Dalopius species*
	Melanotus castanipes	*Limonius confusus*

Figure C.3. General linear model response of the abundance of the most common click beetle species in all trap locations for Experiment 1 by year.

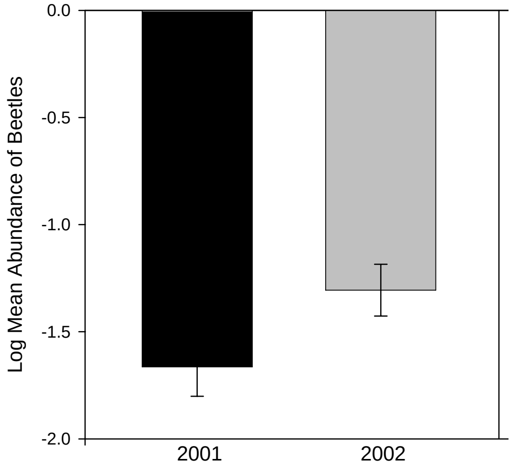


Figure C.4. Rarefaction estimates of beetle species diversity in Experiments 1(A-C) and 2 (D) for A) hardwood and softwood CWM, B) CWM decay classes, C) three diameter classes of CWM, and D) three diameter classes of CWM. Note the different scales.

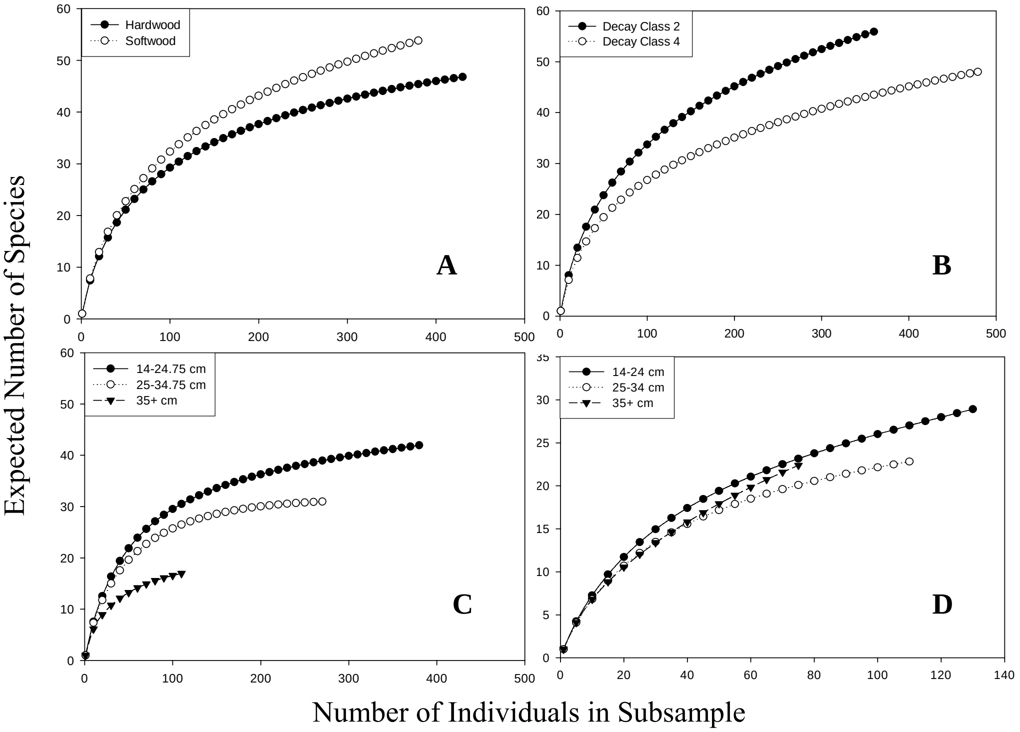


Figure C.5. Relative abundance of beetle species in Decay Class 2 and Decay Class 4 for Experiment 1.

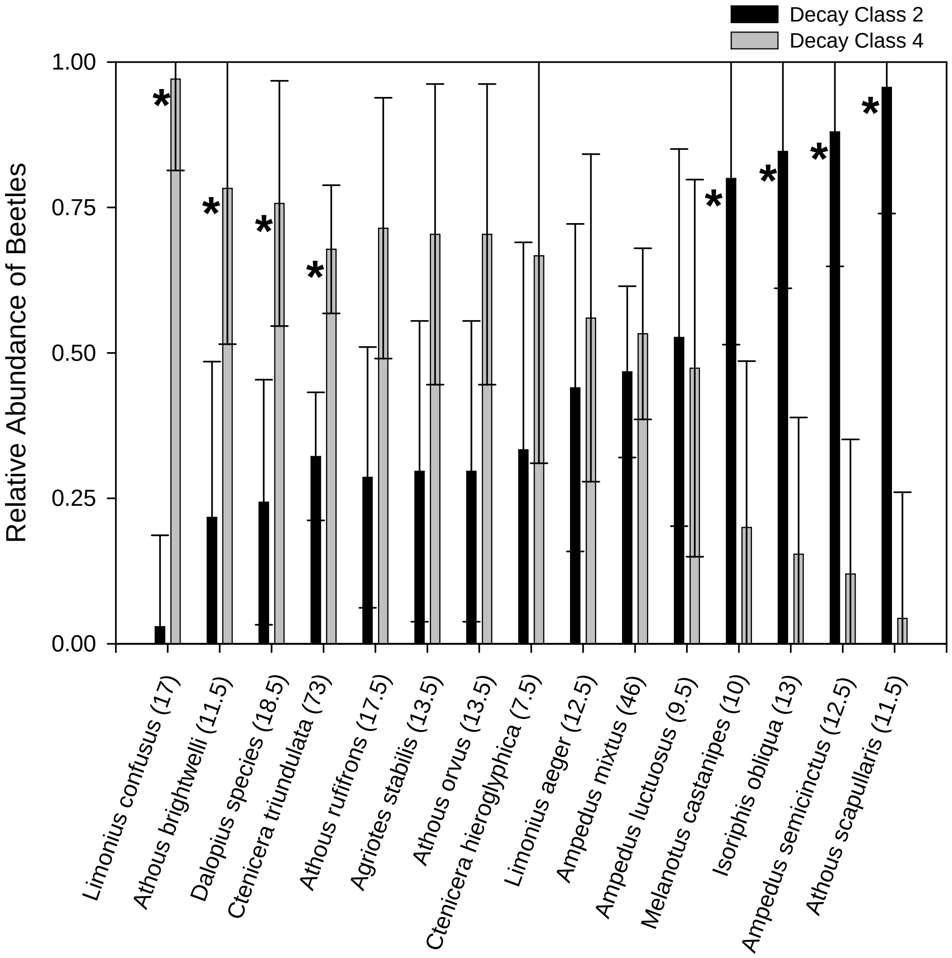
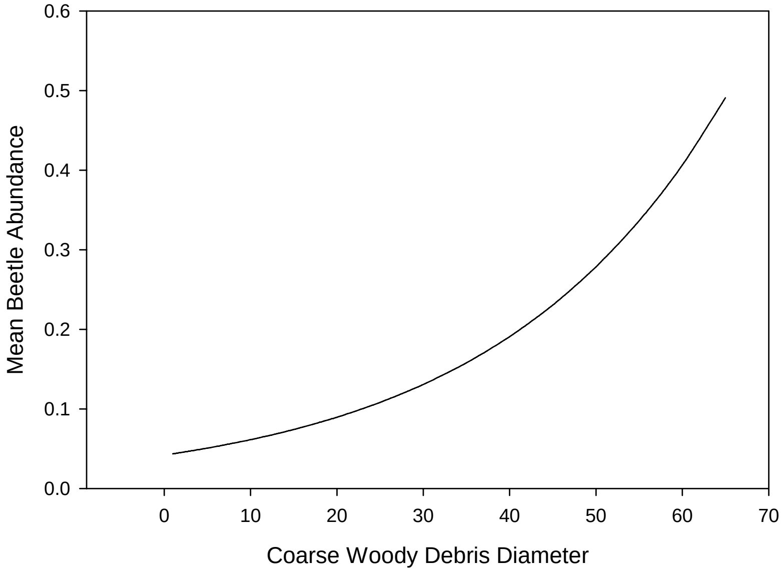


Figure C.6. Beetle abundance for Experiment 2 with diameter of the CWM.



Appendix C.2. Diameter v. Volume of CWM.

Because the length of the CWM is equal in all traps, it can be argued that the beetles are responding to volume of the log rather than to diameter of the log. In other words, the abundance of some species may increase because there may be more habitat in the larger-diameter logs, not because there is a special characteristic of the larger-diameter CWM pieces in and of themselves. (For example, larger logs have a greater diversity of fungus, which affects the general insect community and may directly or indirectly affect the click beetle community). In order to address this point, I summed a portion of the smaller pieces of CWM and compared these “summed-CWM” to the larger pieces of CWM for the 2002 data.

The CWM pieces had previously (see the chapter body) been separated by diameter into three size classes- small (14-24.75 cm), medium (25-34.75 cm), and large (35+ cm). There were only six pieces in the large size class. For each large CWM piece, I selected all the pieces in the small size class with the same type, decay class, and canopy condition. Of this portion of those small pieces, I randomly selected pieces until the summed diameter equaled (within 0.5 cm) the diameter of the large CWM piece. In some cases, there were not enough pieces in the portion, so I included pieces from the opposite type (hardwood or softwood) in the pool. In some cases the addition of one more piece would make the summed diameter much too high; in this case I used half, three-quarters, or (in one case) two-fifths of a piece. For each of these summed pieces, the abundances of each click beetle species were summed; in the case of the fractions of logs, the abundances were multiplied by the fraction.

This created six "summed-CWM" in the small size class, six "summed-CWM" in the medium size class, and the six original pieces in the large size class. I then used this data for indicator species analysis and general linear models.

Indicator species analysis revealed four species as significant indicators ($p = 0.1$; Indicator Value > 24). *Athous orvus* (12.0 specimens; IV = 61.1, $p = 0.0260$) and *Ctenicera triundulata* (75.0 specimens, IV = 54.4, $p = 0.0550$) were indicators of the small size class. *Athous cucullatus* (2.8 specimens, IV = 50.0, $p = 0.0630$) was an indicator of the medium size class, and *Agriotes collaris* (4.0 specimens, IV = 50.0, $p = 0.0850$) was an indicator of the large size class. However, the low numbers of specimens for *A. cucullatus* and *A. collaris* calls these two results into question.

I examined the relationships between the total abundance of click beetles with the CWM characteristics through general linear models (PROC GENMOD, SAS Institute). I employed a negative binomial distribution because the data were over-dispersed. I generated models based on the main effects and their interactions, selecting an optimal model with the second order Akaike Information Criterion (Akaike 1974). Main effects included size (the small, medium, and large categories), type, decay class, and canopy condition. In all models, size was not significant ($p > 0.05$, Table C.2.1, Table C.2.2a). I also examined the relationship of each individual species with CWM size through general linear models (PROC GENMOD, SAS Institute), employing a negative binomial distribution. Only *Athous orvus* returned a significant response to size ($p = 0.006$, Table C.2.2b), with more species in the small size class than in the large size class ($p = 0.033$).

Therefore, there were no major differences among the size classes in total abundance or the abundance or indicator value of any species save *A. orvus* and *C. triundulata*, both of which were associated with the small size class. These results indicated that the above argument was correct; the beetles are responding to volume of the log rather than to diameter of the log. However, an appropriate interpretation of the results is difficult because of the confounded nature of the experiment. In fact, it may be inappropriate to address the argument in this way.

First, there were only six "summed-CWM" or actual pieces used for each category, and the results might be due to a lack of power. Second, my original experiment was not set up to ask this question. Third, there is a fundamental difference in large and small logs, so adding together small logs to equal the same amount of wood volume is in some senses inappropriate. Equal volume of wood does not necessarily mean equal wood quality or habitat. For example, the smaller wood pieces have a greater bark or surface to volume ratio. Another example is wood decomposition. We destroyed some logs in order to search through the logs for click beetle larvae. We found that click beetles were not using the very hard, un-decomposed wood (unpublished data). Therefore, there is more to "habitat" than simply volume of the log. By definition, decay class 2 logs have a greater amount of hard, un-decomposed wood than decay class 4 logs. Furthermore, hardwood and softwood logs tend to decompose differently, further complicating an estimate of usable habitat. Fourth, larger logs last longer in the forest, and therefore these larger logs contribute to habitat continuity differently than smaller logs. These logs are therefore important whether or not the hold a greater number of animals per unit volume than small logs.

Table C.4. AIC Comparisons of models comparing total abundance of all 44 click beetle species between the three size categories using the summed CWM method. Size was non-significant ($p > 0.05$) for all models.

Source	Parameters	AICc	Difference
Size	1	-1640.7	0.0
Size, Canopy Condition	5	-1620.5	20.2
Size, Canopy Condition, Type, Decay Class	7	-1607.2	33.5
Size, Canopy Condition, Type	7	-1607.1	33.6
Size, Canopy Condition, Decay Class	7	-1606.5	34.2
Size, Canopy Condition, Size*Canopy Condition	11	-1568.3	72.4
Size, Canopy Condition, Type, Decay Class, Size*Canopy Condition	13	-1514.0	126.7
Size, Canopy Condition, Type, Size*Canopy Condition	13	-1513.9	126.8
Size, Canopy Condition, Decay Class, Size*Canopy Condition	13	-1513.5	127.2

Table C.5. Results of individual general linear models for Experiment 2 "summed-CWM," where logs in small and medium size categories were summed together to add up to the same diameter as each log in the large size class and size category is the only term in the model. A) Total abundance of all 44 species summed together. B) Species run with individual models. Note: [a]Total abundance not separated by species. [b]Model did not converge.

	Number of Individuals				
Species	Small	Medium	Large	Total	*P* value
A) Total Abundance					
44 species	147.00	90.00	144.00	381.00	0.274[a]
B) Individual Species					
Agriotes stabilis	7.00	4.50	2.00	13.50	0.134
Ampedus mixtus	22.00	16.75	32.00	70.75	0.660
Ampedus semicinctus	5.00	1.00	4.00	10.00	0.596
Athous orvus	11.00	0.00	1.00	12.00	0.006
Athous rufifrons	5.00	4.75	11.00	20.75	0.374
Ctenicera hieroglyphica	7.00	2.75	8.00	17.75	0.447
Ctenicera triundulata	41.00	17.30	17.00	75.30	0.066
Dalopius species	9.00	2.50	9.00	20.50	0.233
Limonius aeger	8.00	3.15	4.00	15.15	-[b]
Limonius confusus	7.00	1.50	14.00	22.50	0.084

Appendix C.3. Experiment 3: Soil

This is to be read in conjunction with Chapter 3. Introduction, methods, and discussion points are not repeated here if redundant with Chapter 3.

C.3.1. Abstract

I compared click beetle abundance and species composition in soil in a field experiment using two harvest treatments that created canopy gaps patterned after the natural disturbance regime of the Acadian forest in central Maine, USA. Size of harvest gap did not influence the species abundance of click beetles across the small range of gap sizes studied (0.01 to 0.21 ha). Abundance of the most common species was higher in the closed canopy than in the harvest gaps. Overall abundance was slightly higher in the smaller gap harvest treatment and was influenced by tree species composition, especially fir, pine, hemlock, maple, and birch. Although click beetle species richness was similar between the harvest treatments and between the canopy conditions, there were different assemblages of species between each. I concluded that the abundance and composition of click beetles were affected by gap harvesting.

C.3.2. Introduction

I examined whether the abundance and composition of click beetles living in soil were influenced by gap harvesting. Harvest gaps in the forest canopy can have substantial influence on the forest ecosystem. Harvesting alters stand structure and removes biomass on which many species depend (Grove 2002b, Fraver *et al*. 2002). Canopy gaps often support more diverse and productive herbaceous and woody plant communities (Busing and White 1997, Schofield 2003, Schumann *et al*. 2003) due to increased sunlight and unique microsite conditions (Poulson and Platt 1989). In turn, these changes affect populations of forest birds (Bisson and Stutchbury 2000, Guenette and Villard 2005), amphibians (Harpole and Hass 1999, Knapp *et al* 2003), and invertebrates (Basset *et al*. 2001, Peñaloza and Farji-Brener 2003, Gorham *et al*. 2002). Properly interpreting gap dynamics is essential to developing appropriate silvicultural guidelines for the Acadian forest (Seymour, *et al*. 2002, Lorimer and White 2003).

C.3.3. Methods

C.3.3.1. Field Invertebrate Sampling

To test the influence of the harvest treatments on click beetles in soil, during 2002, I selected areas of ground with no substantial CWM within one meter and employed emergence traps that covered one square meter of soil (Figure B.1). Twenty-four traps were used to collect from selected areas in the three treatment plots within each harvest treatment (10% or 20%) and distributed between canopy conditions (harvest gap or closed canopy). In each of the treatment plots I used two replications of each combination of harvest treatment-canopy condition. I used a 10-factor prism to determine the basal area of each tree species around each trap.

C.3.3.2. Analytical Approach

I compared beetle assemblages in soil in both harvest treatments (10% and 20%) for 2002, evaluating harvest treatment and canopy condition in my analyses. Hereafter this third approach is referred to as “Experiment 3.” I measured assemblages and used ISA and rarefaction as in Chapter 3. For the general linear models, I generated models of the eight most common species; the main effects were harvest treatment, canopy condition, and species. A reduced model was developed as in Chapter 3, based on trap locations only in harvest gaps and using area of the gap as a main effect.

Because click beetle larvae in the soil may be influenced by vegetation composition, for Experiment 3 I examined relationships between click beetle species abundance and the vegetation community by ordinating trap locations in click beetle species-space with non-metric multidimensional scaling (NMS; Kruskal 1964) using PC-ORD (McCune and Mefford 1999). NMS is an iterative ordination method based on ranked distances between sample units; it searches for low stress, measured by the relationship between the ranked distances in the original multidimensional space and the reduced dimensions produced by the ordination. NMS is an effective ordination method for community data; it does not assume normality and is robust to a large proportion of zero values (Clarke 1993, McCune and Grace 2002). I summed the click beetle samples between replicated traps and used all 26 species collected from soil traps. I used the quantitative version of the Sorensen distance measure and random starting configurations; the run with the lowest stress was used for the final analysis. I assessed the dimensionality of six axes and selected three axes with a final stress of 4.7. All three axes had significant Monte Carlo test results; however, I presented results for only the two axes that described the most variation. Subsequently, I performed Pearson and Kendall Correlations between the ordination axes with the beetle species and the tree basal area gradients and joint-plotted the environmental variables. A high correlation between any vegetation variable and an NMS axis indicated a persuasive association between that variable with the beetle species associated with the axis. I overlaid a polygon encircling the closed canopy trap locations.

In order to compare the CWM and soil habitats, I also analyzed all the data from 2002 (CWM and soil) comparing assemblage measurements and indicator species in decay class2 and 4 and soil. I ordinated trap locations in click beetle species-space with NMS using PC-ORD (McCune and Mefford 1999) based on the 60 click beetle species in the 2002 CWM and soil traps. I used the quantitative version of the Sorensen distance measure and a starting configuration based on a previously run medium autopilot mode; the run with the lowest stress was used for the final analysis. I assessed the dimensionality of six axes and selected three axes with a final stress of 21.85. This stress is tending toward high in Clark's (1993) "rules of thumb," but this ordination has high sample size, and stress tends to increase with sample size.

C.3.4. Results

C.3.4.1. Description of Taxa

I collected 267 click beetles of 26 different species, including one species (*Isoriphis obliqua*) from Eunemidae, the false click beetles, (Table C.6). *Ctenicera triundulata*, *Agriotes stabilis*, and *Limonius aegis* were the most common species, representing 30%, 30%, and 7% of the total abundance, respectively. Eight species were singletons, and 12 species were represented by only two to nine individuals.

C.3.4.2. Harvest Treatment

Four more species were found in the 20% harvest treatment than in the 10% harvest treatment (Table C.7a), but total abundance was 43% higher in the 10% harvest treatment. Beetle assemblages showed 62% similarity between the two harvest treatments. No species were found to be significant indicators, and species diversity was not different for the harvest treatments. There was no difference between harvest treatments (*p* = 0.304) for the abundance of the eight most common species (Table C.8a).

C.3.4.3. Canopy Condition

Total richness was similar for the canopy conditions, no species were found to be significant indicators, and species diversity was not different for the canopy conditions (Table C.7a). However, the total abundance was 143% higher in the closed canopy than in the harvested gaps. There was high turnover in species assemblage (46% similarity) between canopy conditions.

Mean click beetle abundance was also higher in the closed canopy condition than the harvest gaps ($p < 0.001$) for the eight most common species (Table C.8a, Figure C.7). In the reduced model, including only the trap locations in the harvest gaps, beetle abundance did not change in response to area of the gap (Table C.8b).

The NMS ordination on all species (Table C.9, Table C.10, Figure C.8) separated trap locations by canopy condition (Figure C.8a), and most species' centroids were clustered close to the centroids of the closed canopy sites (Figure C.8b). White pine was negatively correlated with the horizontal axis, with relatively higher basal area in the harvest gaps than in the closed canopy trap locations. Balsam fir, red maple, white birch, and eastern hemlock were positively correlated with the horizontal axis, and balsam fir was negatively correlated with the vertical axis. The ordination represented 90.0% of the variation in the click beetle community, with 45.9% depicted by the horizontal axis and 44.1% by the vertical axis. The axes were 99.9% orthogonal.

C.3.4.4. CWM and Soil

The overall number of click beetles caught in 2002 also varied between the CWM decay classes and soil (Figure C.9). Richness per trap decreased from less decayed CWM to more decayed CWM by 6% and then to soil by 38%, and species diversity also decreased with increased decomposition to soil (Figure C.10). Decay Class 4, however, had the highest abundance per trap, being 53% higher than Decay Class 2 and 81% higher than soil. Indicator species analysis results depend on the number of habitat types included, so adding the soil trap locations modified some of the results for the CWM decay classes. Three species were indicators of less decayed CWM, three of more decayed CWM, and seven of soil (Table C.11). *Ctenicera triundulata* had been found to be an indicator of Decay Class 4 in the CWM analysis (Table 3.3), but it was an indicator of soil when soil trap locations were added to the analysis (Table C.11). The two CWM classes were 56% similar in species assemblage, as mentioned above. There was even greater turnover between each of these with soil, at 43% and 37% similarity for Decay Class 4 and 2, respectively.

Despite possible stress problems, the general trends of the sites in the NMS ordination are evident, with Decay Class 4 mixed between Soil and Decay Class 2. All axes had significant Monte Carlo test results. Axes 1, 2, and 3 accounted for 29.2%, 19.3%, and 20.0% of the variation in the data, respectively, for a total of 68.5% (Figure C.11).

C.3.5. Discussion

C.3.5.1. Canopy Condition

Many studies have shown a change in insect species richness or abundance following a forest disturbance; some species are attracted to disturbance patches, while others can be reduced or eliminated (Schowalter 1985). Often these species are herbivores responding to the greater abundance of herbaceous plants (Gorham *et al*. 2002, Peñaloza and Farji-Brener 2003, Ulyshen *et al.* 2005) or predators and parasitoids responding to prey items, vegetation structure, light intensity, temperature, or soil moisture (Shelly 1988, Marra and Edmonds 2005, Valladares *et al*. 2006, Hilszczanski *et al*. 2005). Although such findings have yet to be demonstrated for the species in my study, many elaterid species have demonstrated similar sensitivity to variables affected by harvesting, such as light intensity, temperature and moisture (Fulton 1928, Campbell 1937, Lees 1943a&b, Falconer 1945, Jones 1951, LaFrance 1968, Blennow *et al*. 2002), food preference (Zacharuk 1963, Svensson *et al.* 2004), climate (Penev 1992), vegetation structure (Thomas, chapter 1), soil type (Wolters 1989, David *et al.* 1993, Strbac 1997) and land use (Lefko *et al.* 1998). Several studies have shown a decrease in elaterid abundance following forest harvesting (Theenhaus and Schaefer 1995, Marra and Edmonds 1998, Siira-Pietikainen *et al.* 2003).

The 0.1 and 0.2 ha harvest gaps influenced the assemblage of click beetles in my study. Although species richness and diversity between closed canopy conditions and harvest gaps were similar, the species assemblage differed. Abundance was much higher under closed canopy conditions. The NMS clustered most species within the closed canopy trap locations; of the seven species located outside the closed canopy cluster, only

Athous cucullatus had more than three individuals. *A. cucullatus* is known to live in non-forest habitat, having been found in prairie (Paiero *et al.* 2006) and old field habitats (Evans 1989).

The NMS ordination indicated that basal area of three coniferous tree species (fir, pine, and hemlock) and two hardwood species (red maple and white birch) influenced the composition of the click beetle assemblages. This result may simply reflect the dominance of coniferous trees across my study locations and the relatively higher basal area of white pine in the harvest gaps than in the closed canopy. However, other studies have also found an influence of tree species on elaterid assemblages. For example, Scheu *et al*. (2003) determined that elaterids were more strongly affected by tree species than stand age (30 yr. or 120 yr.), with greater abundance in spruce stands than in either mixed or beech stands. Saetre *et al*. (1999) also found a difference among tree species, but found greater abundance in the mixed stands (birch-spruce) than in pure spruce stands. Saetre *et al*. proposed that the presence of birch leaf litter greatly influenced the composition of soil fauna by regulating soil moisture and through general food inputs, which in turn affected higher trophic levels.

C.3.5.2. Gap Size

See chapter for discussion.

C.3.5.3. Harvest Treatment

Harvest treatment did not have a large influence on species richness

Species richness did not differ between harvest treatments, but there were differences in abundance and assemblage. Four more species were found in the 20% harvest treatment than in the 10% harvest treatment, but total abundance was 43% higher in the 10% harvest treatment. Beetle assemblages showed 62% similarity between the two harvest treatments. No species were found to be significant indicators, and species diversity was not different for the harvest treatments.

C.3.5.4. CWM and Soil

A few studies have examined the effect of CWM on soil invertebrate assemblages. Jabin *et al*. (2004) investigated the density of soil macro-arthropods in a forest, finding approximately twice as many individuals near to CWM (within 10 cm) as they found distant to CWM (further than 500 cm). Furthermore, this difference was more pronounced in the edge zone between the oak-beech forest and meadows. Marra and Edmonds (1998) also found that distance to CWM influenced arthropod density, although soil depth was more influential for most species. Of the two click beetle species they observed, soil depth did not influence density, but one species had higher densities more distant to CWM (100-110 cm) than close to CWM (0-10 cm). Chershire (1988) observed that the elaterid *Melanotus similis*, considered a pest of row crops in agricultural systems, was also common in forest systems. Many larvae were collected from decomposing CWM, but the majority was collected in soil adjacent to CWM.

In my studies, comparisons of the 2002 collections of both soil and CWM identified three indicators of Decay Class 2 CWM, three of Decay Class 4 CWM, and seven for soil. When only the CWM information was included in the analysis, *Ctenicera triundulata* was determined to be an indicator of Decay Class 4, but in this mixed analysis of soil and CWM, it was an indicator of soil. This result suggests that some species of click beetles, although found in logs of the later stages of decomposition, are more likely to be found in soil. These species may move freely between the two habitats, but concentrate in the soil. For my soil traps, I did not measure distance to CWM; it may be that these species are influenced by the presence of nearby CWM. Those species that did not switch between habitats likely have early- or late-stage decomposing CWM as their primary habitat.

Table C.6. Abundance click beetle species by harvest treatment (10% or 20%) and canopy condition (harvest gap or closed canopy) for soil samples in 2002.

	10%		20%		
Species	Gap	Closed	Gap	Closed	Total
Agriotes collaris	1	4	0	2	7
Agriotes fucosus	1	0	0	0	1
Agriotes limosus	0	0	1	0	1
Agriotes stabilis	4	19	13	43	79
Ampedus mixtus	1	0	0	0	1
Ampedus nigricollis	0	0	0	1	1
Ampedus near melantoides	0	4	0	1	5
Ampedus semicinctus	0	1	0	1	2
Athous brightwelli	1	2	2	0	5
Athous cucullatus	2	2	2	2	8
Ctenicera appropinquans	0	0	3	0	3
Ctenicera arata	0	0	0	1	1
Ctenicera cruciata	0	1	1	0	2
Ctenicera fulvipes	1	0	1	0	2
Ctenicera hieroglyphica	2	3	1	4	10
Ctenicera propola	0	3	4	9	16
Ctenicera spinosa	0	0	1	0	1
Ctenicera triundulata	13	19	9	39	80
Dalopius species	3	6	1	3	13
Elathous dicalceatus	0	1	0	0	1
Isorhipis obliqua	0	1	0	1	2
Limonius aeger	6	7	1	4	18
Limonius confusus	0	1	0	1	2
Liotrichus vulneratus	0	0	0	1	1
Melanotus castanipes	0	0	1	1	2
Sericus viridanus	1	0	1	1	3

Table C.7. Summary of richness (number of species), total abundance (number of individuals), and rarefaction-estimated species diversity of click beetles for A) Experiment 3 (no significant differences in diversity) and B) Experiments 2 and 3 (all three categories significantly different, see Figure C.12).

Source	Number of Sites	Species Richness	Total Abundance	Diversity[a]
A) Experiment 3				
Harvest Treatment				
10% Removal	12	19	157	19.0+/-0.0 (110)
20% Removal	12	23	110	19.3+/-1.6 (110)
Canopy Condition				
Gap	12	18	78	17.7+/-0.5 (75)
Closed Canopy	12	20	189	14.0+/-1.6 (75)
B) Experiments 2 and 3				
CWD or Soil				
Decay Class 2	48	45	317	49.8+/-2.1 (260)[b]
Decay Class 4	48	42	484	38.7+/-2.3 (260)
Soil	24	26	267	25.8+/-0.4 (260)[c]

[a] Rarefaction-estimated number of species +/- SD (number of individuals in subsample), [b,c] Highest and lowest diversity ($p = 0.05$).

Table C.8. General linear model results of click beetle species abundance for Experiment 3 for A) the full model of all trap locations and B) the reduced model of only traps in the harvest gaps.

Source	DF	Chi-Square	Pr > ChiSq
A) All trap locations			
Harvest Treatment	1	0.14	0.304
Site within Harvest Treatment	4	11.94	0.065
Beetle Species	7	83.02	<0.001
Canopy Condition	1	21.71	<0.001
B) Harvest Gap traps only			
Harvest Treatment	1	0.10	0.749
Site within Harvest Treatment	4	6.40	0.171
Beetle Species	7	29.75	<0.001
Area of Gap	1	0.03	0.860

Figure C.7. Abundance of click beetles in 2002 Harvest Gap and Closed Canopy soil traps

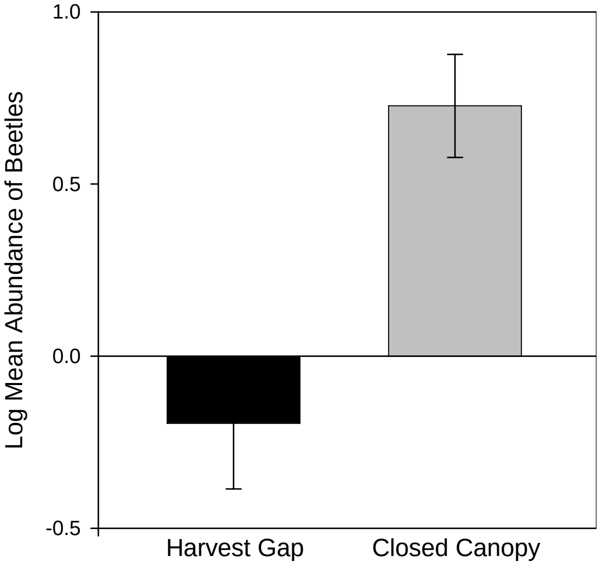


Table C.9. Basal area (m^2 / ha) of tree species for soil emergence trap locations in harvest gaps and closed canopy with significant NMS correlations.

Trap Location	Balsam Fir	White Pine	Eastern Hemlock	Red Maple	White Birch
10% Gap Site 2	0.0	0.0	8.0	1.1	2.3
10% Closed Site 2	0.0	0.0	20.7	4.6	1.1
10% Gap Site 5	0.0	13.8	1.1	0.0	0.0
10% Closed Site 5	0.0	8.0	17.2	3.4	8.0
10% Gap Site 7	1.1	1.1	2.3	2.3	4.6
10% Closed Site 7	1.1	5.7	5.7	12.6	2.3
20% Gap Site 1	0.0	0.0	3.4	1.1	5.7
20% Closed Site 1	0.0	0.0	20.7	5.7	2.3
20% Gap Site 6	1.1	2.3	0.0	5.7	1.1
20% Closed Site 6	8.0	1.1	4.6	3.4	3.4
20% Gap Site 9	0.0	2.3	0.0	1.1	0.0
20% Closed Site 9	6.9	1.1	5.7	5.7	0.0

Figure C.8. NMS ordination plots based on the 26 click beetle species in the 2002 soil traps. The vertical axis accounts for 45.9% of the variation in the data, and the horizontal axis accounts for 44.1%. Only significant correlation vectors (r^2 or *tau* at least $p < 0.1$) are shown. Length of vectors indicates the strength of the correlation. (A) Symbols code for site type: triangle = Harvest Gap; square = Closed Canopy (encircled). (B) Beetle and tree species' abbreviations based on Table 3.8.Note different scales.

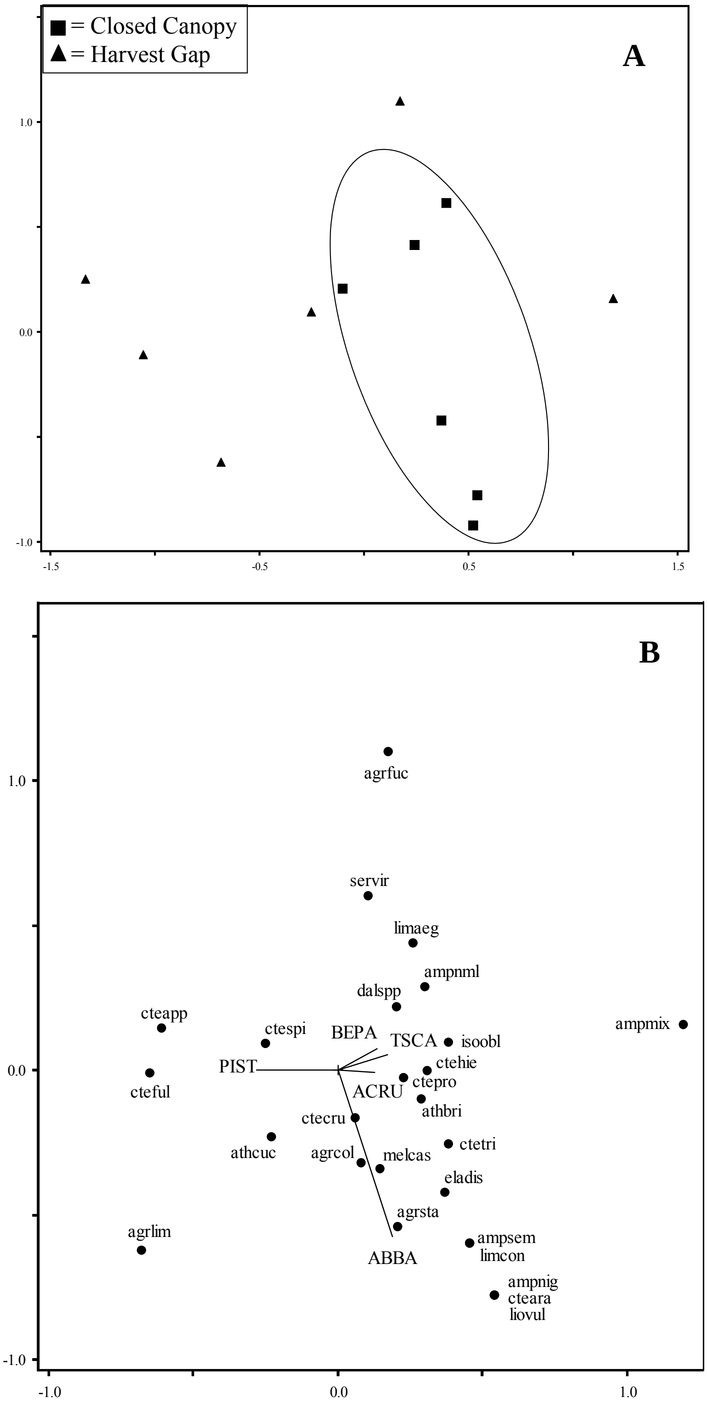


Table C.10. Pearson and Kendall correlations of click beetle species and tree species basal area with site locations along two NMS ordination axes. The vertical and horizontal axes explain 45.9% and 44.1% of the variation in the click beetle community structure, respectively. Note: Only the tree species with significant correlations with one or both ordination axes are shown. *, ($p < 0.1$); **, ($p < 0.05$); ***, ($p < 0.001$)

Source	Abbreviation	Horizontal Axis		Vertical Axis	
		r	*tau*	r	*tau*
Click Beetle Species					
Agriotes collaris	agrcol	0.08	0.10	-0.43	-0.40**
Agriotes fucosus	agrfuc	0.07	-0.04	0.58**	0.41**
Agriotes limosus	agrlim	-0.30	-0.26	-0.33	-0.26
Agriotes stabilis	agrsta	0.25	-0.05	-0.80***	-0.73***
Ampedus mixtus	ampmix	0.52**	0.41**	0.08	0.04
Ampedus nigricollis	ampnig	0.23	0.33*	-0.41	-0.33*
Amedus near melanotoides	ampnml	0.21	0.16	0.24	0.25
Ampedus semicinctus	ampsem	0.29	0.33*	-0.47*	-0.39**
Athous brightwelli	athbri	0.23	0.16	-0.10	-0.16
Athous cucullatus	athcuc	-0.36	-0.25	-0.42	-0.40**
Ctenicera appropinquans	cteapp	-0.37	-0.40**	0.11	0.08
Ctenicera arata	cteara	0.23	0.33*	-0.41	-0.33*
Ctenicera cruciata	ctecru	0.04	-0.06	-0.13	-0.17
Ctenicera fulvipes	cteful	-0.42	-0.39**	-0.01	-0.11
Ctenicera hieroglyphica	ctehie	0.46*	0.38**	0.00	0.02
Ctenicera propola	ctepro	0.24	0.23	-0.03	-0.23
Ctenicera spinosa	ctespi	-0.11	-0.19	0.05	-0.04
Ctenicera triundulata	ctetri	0.70***	0.77***	-0.57**	-0.33*
Dalopius species	dalspp	0.17	-0.02	0.23	0.38**
Elathous discalceatus	eladis	0.16	0.11	-0.22	-0.19
Isoriphis obliqua	isoobl	0.25	0.22	0.08	0.11
Limonius aeger	limaeg	0.32	0.26	0.66***	0.53***
Limonius confusus	limcon	0.29	0.33*	-0.47*	-0.39**
Liotrichus vulneratus	liovul	0.23	0.33*	-0.41	-0.33*
Melanotus castanipes	melcas	0.09	0.11	-0.27	-0.28*
Sericus viridanus	servir	0.09	-0.02	0.61***	0.45***
Tree Species					
Balsam Fir	ABBA	0.15	0.46**	0.46***	-0.46**
Red Maple	ACRU	0.10	0.27*	0.01	-0.11
White Birch	BEPA	0.11	0.27*	0.06	0.18
White Pine	PIST	0.23*	-0.26	0.00	-0.07
Eastern Hemlock	TSCA	0.14	0.30*	0.04	0.17

Figure C.9. Abundance per trap for all 60 click beetle species in the 2002 CWM and soil traps. (A&B) Decay Class 2 x Decay Class 4; (B) without *Ctenicera triundulata*, *Ampedus mixtus*, or *Ampedus semicinctus*; (C&D) Decay Class 2 x Soil; (D) without *C. triundulata*, *A. mixtus*, *A. semicinctus*, or *Agriotes stabilis*; (E&F) Decay Class 4 x Soil; (F) without *C. triundulata*, *A. mixtus*, or *A. stabilis*.

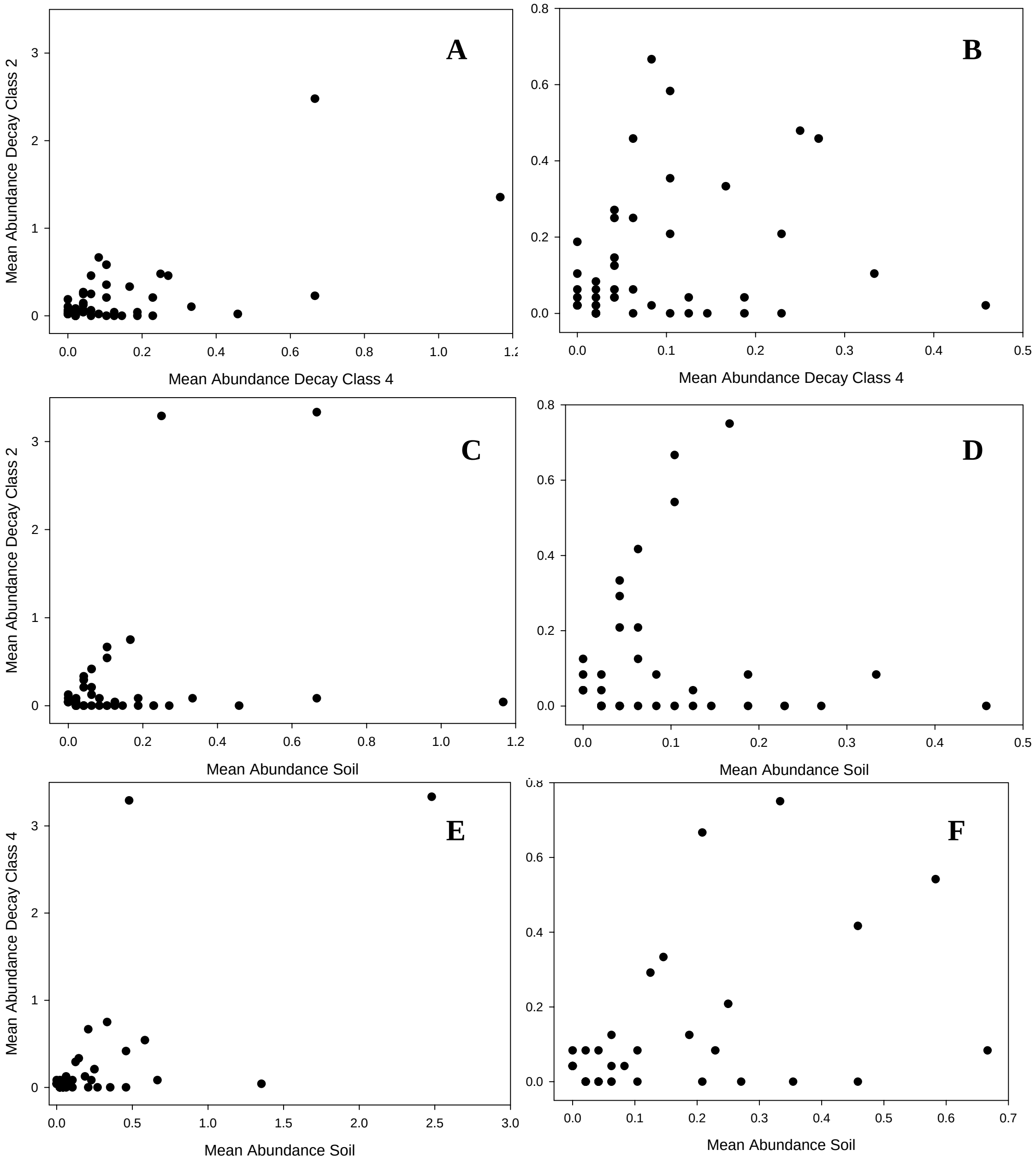


Table C.11. Indicator species analysis of click beetle species for CWM decay classes and soil in Experiments 2 and 3.

Source	Species	Total number collected	Indicator Value	*p*
Decay Class 2	*Ampedus semicinctus*	45	21.2	0.029
	Athous scapullaris	23	17.9	0.003
	Melanotus castanipes	23	18.6	0.030
Decay Class 4	*Ampedus mixtus*	122	34.1	0.008
	Athous rufifrons	35	20.2	0.025
	Limonius confusus	38	20.5	0.007
Soil	*Agriotes collaris*	15	18.5	0.008
	Agriotes stabilis	114	61.2	0.001
	Athous cucullatus	17	18.6	0.011
	Ctenicera hieroglyphica	35	16.5	0.060
	Ctenicera propola	31	22.6	0.007
	Ctenicera triundulata	231	46.8	0.001
	Limonius aeger	42	22.4	0.013

Note: An indicator value approaching 100 denotes the presence of a species and signifies a particular group without error. *P* values were determined using a Monte Carlo test with 1000 permutations and represents the probability of an indicator value greater than or equal to the observed indicator value.

Figure C.10. Rarefaction estimates of beetle species diversity for CWM decay classes and soil in Experiments 2 and 3.

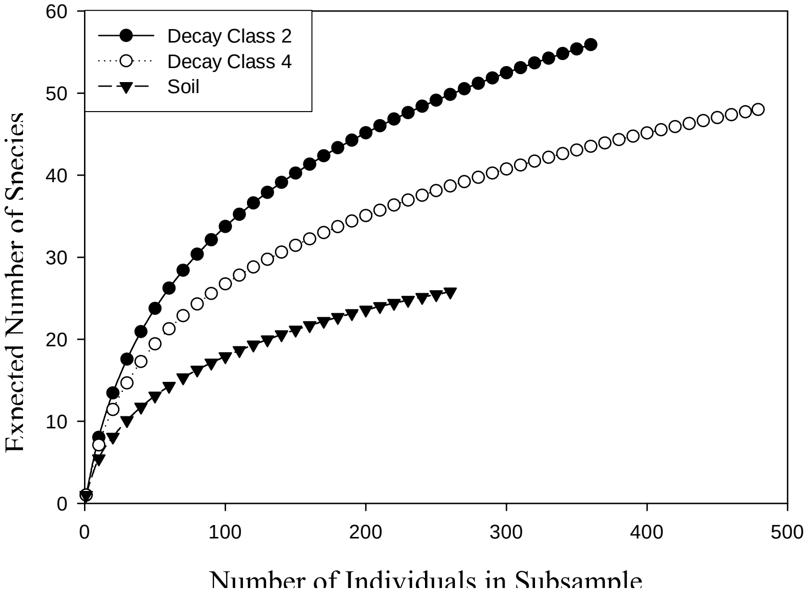
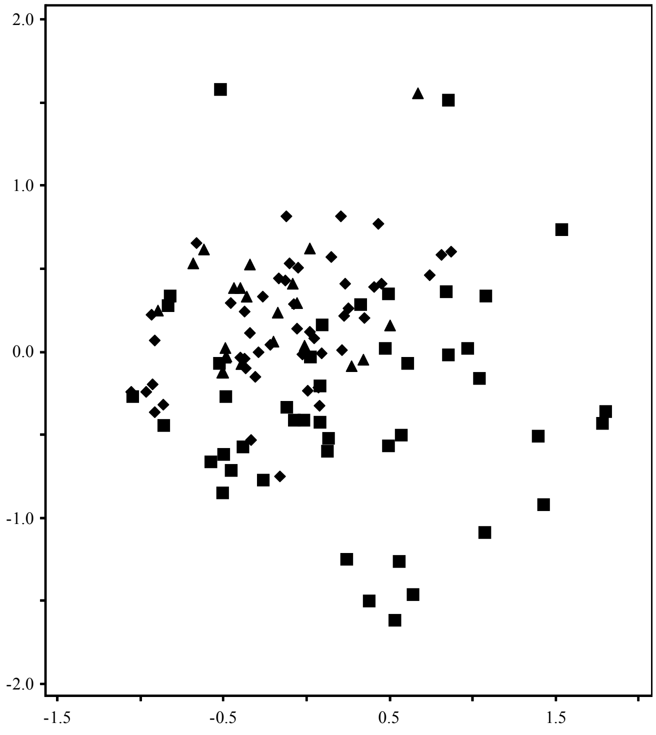
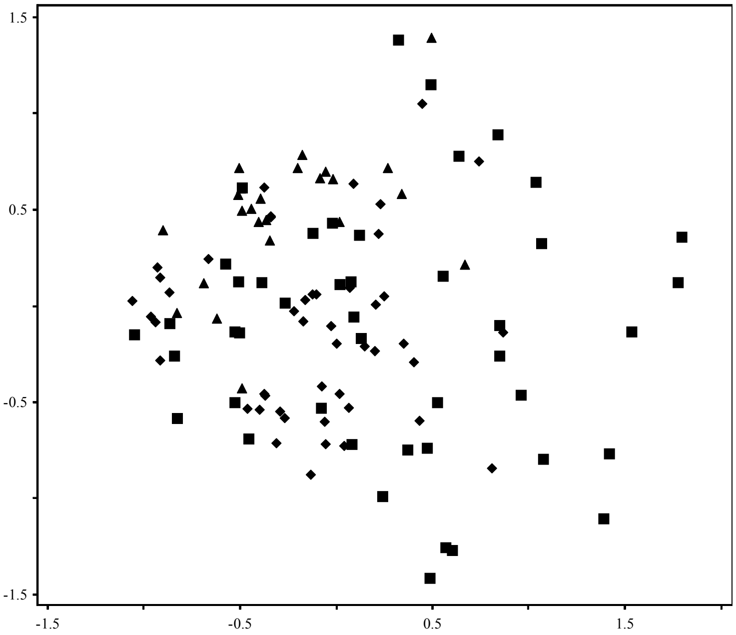


Figure C.11. NMS ordination plots based on the 60 click beetle species in the 2002 CWM and soil traps. We used PC-ORD (McCune and Mefford 1999) with the quantitative version of the Sorensen distance measure and a starting configuration based on a previously run medium autopilot mode; the run with the lowest stress was used for the final analysis. We assessed the dimensionality of six axes and selected three axes with a final stress of 21.85. This stress is tending toward high in Clark's (1993) "rules of thumb," but this ordination has high sample size, and stress tends to increase with sample size. Despite this, the general picture of the sites is evident, with Decay Class 4 mixed between Soil and Decay Class 2. All axes had significant Monte Carlo test results. Axes 1, 2, and 3 account for 29.2%, 19.3%, and 20.0% of the variation in the data, respectively, for a total of 68.5%. The axes were 99.4-99.8% orthogonal. Symbols code for site type: triangle = Soil, diamond = Decay Class 4, and square = Decay Class 2.

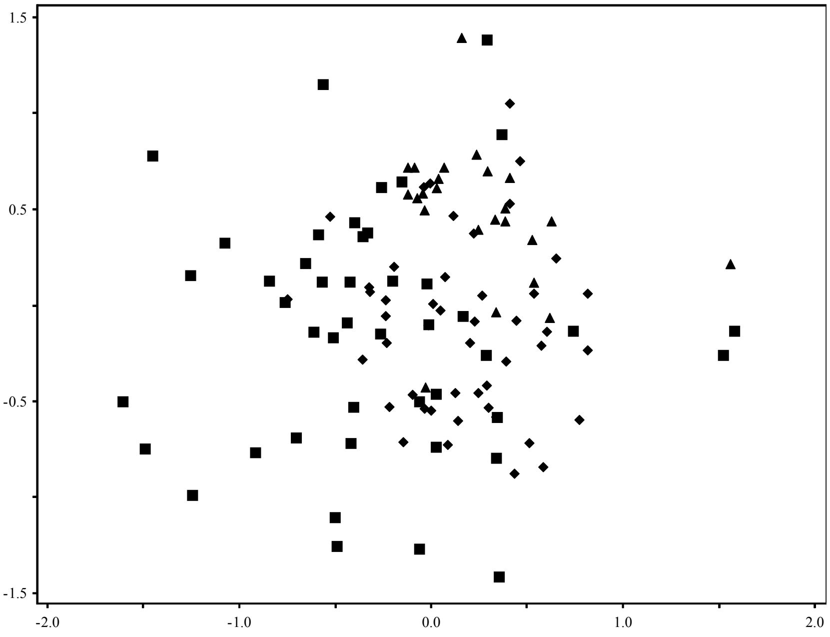


A. Axes 1 x 2

Figure C.11. Continued.



B. Axes 1 x 3



C. Axes 2 x 3.

BIOGRAPHY OF THE AUTHOR

Shelly L. Thomas was born in Danville, Pennsylvania, and graduated from Wellsboro High School, Wellsboro, Pennsylvania (home of the Pennsylvania Grand Canyon). She attended Eastern University near Philadelphia and graduated *Magna Cum Laude* in 1995 with a Bachelor's degree in Biology. During her undergraduate career, she earned her Naturalist Certificate from Au Sable Environmental Institute in Michigan, where she developed a passion for creation care, beetles, and teaching. Shelly worked with staphylinid beetles in California and with burying beetles at the Apostle Islands National Lakeshore in Wisconsin. She taught environmental education in Michigan and developed an environmental education program in Kenya, on the shores of Lake Victoria.

Shelly then entered the Ecology and Environmental Studies graduate program, concentrating in Conservation Biology, at The University of Maine. She taught for two years in the Milford, Maine eighth grade science class through the NSF GK-12 program. As part of this program she worked in the Arabuko-Sokoke Forest in Kenya with A Rocha International. She presented her research at many Society for Conservation Biology and Entomological Society of America conferences. Shelly was Small Group Director at Pathway Wesleyan Church, where she helped organize the Growth Ring Ministry, trained leaders, and led small groups. She taught on Biblical equality between women and men at Emmanuel Wesleyan Seminary in Swaziland through World Hope Canada. Shelly enjoys the beauty of Maine, hiking, paddling, rock-climbing, camping, and playing with friends. She is a candidate for the Doctor of Philosophy degree in Ecology and Environmental Science from The University of Maine in May, 2007.