

GROUND BEETLES (COLEOPTERA: CARABIDAE) AS BIODIVERSITY
INDICATORS FOR AGE STRUCTURE IN PIEDMONT FORESTS?

By

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ABSTRACT

This study examined the diversity, community composition, and wing state of Carabidae as a function of forest age and identified eighteen species as potential ecological indicators for forest age. Ground beetles (Coleoptera: Carabidae) are typically ground-dwelling, generalist predators. Carabids were collected monthly through pitfall traps from March 2009 through February 2010 from 33 sites representing 5 forest classes approximately 0, 10, 50, 85, and 150 years old. 2,568 individuals were collected, representing 29 genera and 66 species. Carabid species diversity, as measured by six diversity indices, was significantly different between the oldest and youngest forest age classes for some but not all of six diversity indices. Although most carabid species can be considered generalists, occurring in all or most of the forest age classes, carabid species composition still varied significantly across classes. The results of non-metric multidimensional scaling (NMDS) and Detrended Correspondence Analysis (DCA) ordination both show a clear separation of forest age classes in terms of beetle community composition. Eighteen carabid species were identified as potential candidates for ecological indicators of forest age. The proportion of individuals capable of flight decreased with forest age.

INTRODUCTION

Anthropogenic activities such as farming, forestry management, and urbanization have created a patchwork of modified land use. These activities turn may affect biodiversity and the composition of living communities (Niemelä et al. 2000). Land use change prior to 1860 for Piedmont, North Carolina can be classified into three major waves. The first wave was a conversion of natural vegetation to cropland (1860 to 1910); after 1910 there was a second period of forest re-growth from newly abandoned cropland, and finally a wave of high rates of urbanization starting around 1945 and continuing today (Chen et al. 2006). Despite the increase in urbanization, the overall forested area in the South increased from 1910 to 2003 from 35 million ha to 45 million ha (75.6% of all land) due to the reforestation of agricultural land. Fifty percent of harvest for commercial timber in the U.S. takes place in the Southeastern region of the country (Chen et al. 2006). The rapid change of land-use within the southeastern U.S. and in Piedmont NC (Napton 2010) makes this an area of high research interest. A better understanding is required of how human activities affect the biodiversity and community structure of forest biota for forestry management and identify conservation priorities.

Since plants drive succession (Kiovula et al. 2002) an abrupt change in the vegetation (e.g. clear-cutting) will affect not only plant but also forest animal communities. If some species can only survive in mature, undisturbed, continuous forest, the disappearance of mature forest tracts will lead to decreases in biodiversity at the local level at least and possibly on broader geographical scales. An overarching question is whether species assemblages will recover to a pre-disturbance state, or if there are

alternative post-disturbance states? Additionally, what is the timescale and sequence of stages to expect (Niemelä et al. 1993, Kiovula et al. 2002)?

An important question for land managers and for those setting conservation priorities is how to measure faunal diversity in forested areas. While larger, more appreciated fauna such as mammals and birds have traditionally been used as indicator species, much less is known about non-charismatic fauna, especially animals with low vagility (Duelli and Obrist 1998). One aspect of this study is to determine if members of the Family Carabidae (ground beetles) may be potentially useful as an indicator of how forest age affects forest biodiversity and community composition in the Piedmont ecoregion of North Carolina. This study quantifies species distributions of carabid beetles (Coleoptera: Carabidae) for five age-structured forest classes, from newly-cut forests to plots with trees that are approximately 150 years old. Each class was represented by a minimum of 5 replicates. Across the five forest classes we investigated: beetle species diversity, community composition, and wing state (as a proxy of flight ability). Additionally collected species were evaluated as potential ecological indicators of forest age.

While there have been numerous studies focusing on the occurrence of carabid beetles in successional stages in European boreal forests or Northern coniferous dominated forests (e.g. Niemelä et al. 1993, Niemelä et al. 1996, Butterfield 1997, Kiovula et al. 2002, Jukes et al. 2003, Paquin 2008 and more), only a few studies have involved a mixed hardwood forest habitat (Spence et al. 1996; Werner and Raffa 2000, Jennings and Tallamy 2006). In northern temperate zones, mature forests are usually

composed of an assortment of successional patches controlled by natural biological disturbances such as storms, fires, tree falls, landslides (de Warnaffe and Lebrun 2003). Rather than natural biological disturbances, humans have become the main initiator of secondary succession and creation of new habitat types (e.g. clear-cut forests). Vegetational change can also be accompanied by alterations in the animal communities (Koivula et al. 2002).

Since it is impossible to gauge all anthropogenic impacts on the total biota, even in a small geographic area (Duelli and Obrist 1998, 2003), bioindicator taxa are often used to assess impacts of land-use change (Niemelä et al. 2000). Although a variety of organisms have served as indicator taxa, insects may best be suited to play this role (Duelli and Obrist 1998). Insects make up 80 percent of all described species and may consist of 97 percent of all species richness around the world (Lucky et al. 2002). Within Class Insecta, the largest order is Coleoptera (beetles), with the Family Carabidae comprising at least 40,000 described species (Lövei and Sutherland 1996). Carabids are holometabolous insects (i.e. have complete metamorphosis), generally reaching the adult stage in less than a year. Most species live for less than one year, reproducing only once; however, some species can survive for up to four years (Lövei and Sutherland 1996). Carabids are ecologically important as generalist invertebrate predators (Larsen et al. 2002), with a few species being phytophagous or having specialized feeding preferences (Thiele 1977; Lövei and Sutherland 1996). Carabidae are found in all environments except the driest portion of deserts. They are not randomly distributed but instead are broadly structured by geography, climate, and historical factors. Carabid distribution is

generally patchy and aggregated, reflecting microclimatic variations (Thiele 1977, Niemelä and Spence 1994, Lövei and Sutherland 1996).

Piedmont Forests

Most Piedmont North Carolina forests have developed from what were formerly cultivated fields. Many agricultural fields were abandoned when economic conditions turned less favorable and when soil fertility decreased in the area (Oosting 1942; Christensen and Peet 1984; Peet and Christensen 1987). Following the abandonment old fields are dominated by herbs, hardwood, and pine seedlings. Pine seedlings are more numerous than hardwoods. Dominating pines in this area are *Pinus virginiana* and *Pinus echinata* (Christensen and Peet 1984; Peet and Christensen 1980, 1987). The rapidly growing pines are able to form a closed canopy above other seedlings approximately 5-15 years post abandonment. From 70 to 100 years the light requiring pines will start to die out and young hardwoods are able to fill the canopy gaps. More mature forests of Piedmont are uneven aged, hardwood deciduous forest, characterized by *Quercus*, *Caraya*, and *Populus* species (Peet and Christensen 1980, 1987; Christensen and Peet 1984). Abandonment since the mid 1800's has left the forests Piedmont, NC a mosaic of varying successional ages (Christensen and Peet 1984). The primary management approach has been passive ownership, with occasional forest management (via various logging regimes).

Diversity and Community Structure

Previous studies on the affect of forest succession or management practices have revealed a few common trends for the diversity and composition of ground beetles. Species richness and abundance tend to increase after an anthropogenic clear-cutting

event (Niemelä et al. 1993; Spence et al. 1996; Niemelä 1997; Butterfield 1997; Kiovula et al. 2002; de Warnaffe and Lebrun 2004) probably due to the relatively high number of carabid species which prefer the drier, open areas of grasslands and similar habitats. Open habitats, such as clear-cut sites, will usually be drier and subject to more extreme changes in temperature in comparison to more mature forested areas (Niemelä 1993; Niemelä et al. 2007). Following a clear-cut three common stages have been reported in the literature: (1) colonization by open habitat species, followed by (2) initial decline of forest generalist species which may or may not recover with succession, and (3) loss of forest specialist species (Niemelä 1993, 1997; Niemelä et al. 1993, 1994, 2007; Werner and Raffa 2000). Although studies have shown an increase in carabid diversity after clearing forested land, the negative long term effect on mature forest-associated species is of concern (Niemelä et al. 1993; Spence et al. 1996; Werner and Raffa 2000; Niemelä et al. 2007).

Subsequent to a clear-cut, a major transition point occurs in terms of carabid species composition, at least for the well-studied northern boreal forests of northern Europe, when the forest canopy closes. Canopy closure initiates a change in forest floor conditions, creating a corresponding response in the arthropod species assemblage. At this point there is a drastic reduction in numbers of species requiring open habitat condition and species requiring more mature forested conditions increase and become dominant (Niemelä et al. 1996, 2007; Kiovula et al. 2002). Although literature support is lacking, canopy closure may also be a critical stage for ground dwelling invertebrates in the Piedmont NC deciduous forests. In Piedmont NC forests a pine dominated canopy

forms approximately 5-15 years post abandonment (Peet and Christensen 1980; Christensen and Peet 1984).

European forest succession studies (Niemelä et al. 1993; Niemelä 1997; Butterfield 1997; Kiovula et al. 2002), suggest that species richness, diversity, and abundance of carabid beetles have not been as sensitive to the forest successional cycle as species assemblage and that the structure of the community may be affected by changes in species diversity as well as species assemblages changes (Butterfield 1997).

Wing State

One advantage of ground beetles as an environmental indicator is the low relative dispersal ability of certain species due to hind wing atrophy (Erwin 1979). Flightlessness and flight dimorphism has evolved repeatedly within the Carabidae lineage (Darlington 1943; Lövei and Sutherland 1996). In many carabid species, the presence or absence of wings is inherited through single gene by a dominant or recessive Mendelian genetic pattern (Liebherr 1988). Carabids are primarily ground dwelling beetle species which originally used fully functional wings as a primary means of dispersal (Lövei and Sutherland 1996). Flight and the associated morphological structures (i.e. wing and muscle development) are energetically costly, so if they are no longer beneficial there is rapid selection against these structures (Darlington 1943). Hence wingless individuals are able to put more energy towards reproduction and body development (Kavanaugh 1985; Wagner and Liebherr 1992). The occurrence of winged and non-winged species is not random; it can be linked with locality as well as habitat type (Darlington 1943). A lack of dispersal power can directly be related to the stability of the habitat. As environmental stability and time since colonization increases, the proportion of

macropterous (flight enabled) individuals (Darlington 1943; Liebherr 1988; Lövei and Sutherland 1996) correspondingly decreases. Apterous (wingless) or brachypterous (small winged) forms are generally more numerous in homogenous, stable habitats. Abiotic and biotic conditions of environmentally stable habitats allow for the success of viable populations over multiple generations (Darlington 1943). On a broad geographical scale there is a greater number of flightless carabid species in the temperate areas of the world than in the tropics (Erwin 1979).

Wing state is a combination of morphological, behavioral, and physiological components all of which are significant in terms of the ecology and evolution of carabid beetles (Darlington 1943; Wagner and Liebherr 1992). Forest carabid species are indicators of larger, mature woodlands and are typically apterous or brachypterous. In northern European forests, higher numbers of open-habitat, macropterous species have been found in smaller forest fragments (Desender et al. 1999). Macropterous species tend to favor unstable, early successional habitats (Gutiérrez and Menéndez 1997). The incidence of reduced or non-winged species, with limited dispersal ability, has been positively correlated with persistent, stable continuous habitats (Kavanaugh 1985; Wagner and Liebherr 1992; Lövei and Sutherland 1996; Gutiérrez and Menéndez 1997). As the forest age structure increases, increasing stability, the number of poorly dispersing carabids is predicted to increase.

Ecological Indicators

In terms of habitats many carabid species are generalists while other species are highly selective, requiring a particular habitat in order to survive and reproduce. Variation in the distribution among different habitat types suggests that there are species-

specific adaptations for microhabitat affinities and/or environmental conditions (Larsen et al. 2003). The results of Niemelä and Spence (1994), who observed differences in catch size among pitfall traps at various forested sites, support the influence of microhabitat factors on carabid distributions. However, explanation for disparities in small scale distributions needs to be investigated further (Niemelä and Spence 1994). Specialist species with specific habitat preferences are of particular interest due to their sensitivity to habitat change (Larsen et al. 2003). A general pattern to the reassembly of species compositions along forest age gradients have been reported (Niemelä et al. 1993; Larsen et al. 2003; Paquin 2008). These changes in assemblages suggest that responsive species can be categorized into distinct classes according to their affinity for a particular forest age. Identifying indicator species for forest age would allow for the inference of habitat type or microhabitat conditions by the presence or absence of certain carabid species. Although there is some information for species of European and North American forests (Erwin 1981; Niemelä et al. 1993; Niemelä and Spence 1994; Koivula 2001; Larochelle and Larivière 2003; Larsen et al. 2003; Niemelä et al. 2007), more information is needed on the habitat preference and/or forest specialty grouping (i.e. generalist/specialist) for carabid beetles. Little information is available for carabids occurring southern forests such as those of Piedmont North Carolina. This data would be useful not only for broader estimates of biodiversity, but also for environmental and ecological conservation purposes (Koivula 2001; Larsen et al. 2003). Protection of high diversity areas does not provide for the security of rare or spatially restricted species which may occur in less diverse areas. These species may not be in the most diverse areas but contribute to regional (gamma) diversity (Dufrêne and Legendre 1997).

Several studies involving carabids as biodiversity indicators for forest conservation purposes have been conducted in Europe and/or in conifer dominated forests (e.g. Butterfield et al. 1995, Kiovula et al. 2002, de Warnaffe and Lebrun 2004, Paquin 2008, and others) but only a few studies conducted in deciduous forests of the eastern portion of the United States (e.g. Larsen et al. 2003, Jennings and Tallamy 2006). Desender et al. (1999) compared the beetle diversity and species composition of historical (around 500 AD) carabid remains in Flanders to beetle diversity in the present era. The extreme change in community composition and the loss of stenotypic species indicates that human settlement has had a serious effect on woodlands and carabid species composition. The study, which included changes for 1500 years in Flanders woodlands, cannot be directly compared to the historical data for Piedmont NC which has been agriculturalized for only the last 200 years (although aboriginal land management practices may have had a similar effect on landscape composition pre-European settlement).

However, there can be at least some cross-comparison between the European studies and the effects of land change in the southeastern U.S. As mentioned previously, a majority of carabid studies in forest ecosystems has been conducted in coniferous dominated forests, which in terms of forest succession, vary significantly with the deciduous forests of the southeastern U. S. Even within the same geographical location Butterfield et al. (1995) demonstrated that the carabid fauna of European coniferous plantations differed from deciduous woodlands, suggesting that the deciduous forests of the southeastern United States may show different trends in carabid diversity and community structure compared to the relatively well-studied European sites.

Invertebrates have not commonly been used as bioindicators despite their high contribution to species diversity (Niemelä 1997; Duelli and Obrist 2003). A working definition of a bioindicator is a species or a group of species which indicates biotic or abiotic factors of an environment, represent change in habitat, community, ecosystems, and the response of other taxa (McGeoch 1998; Rainio and Niemelä 2003). McGeoch (1998) divides bioindicators into three distinctive categories: environmental, ecological, and biodiversity. The main differentiation is environmental and ecological indicators detect changes in habitat surroundings, whereas, biodiversity indicators should reflect the diversity of other biota in a given area (McGeoch 1998; Rainio and Niemelä 2003).

Rainio and Niemelä (2003) reviewed the literature for support of using carabid beetles as environmental and ecological indicator species, but were unable to make a solid conclusion for the use of carabids as biodiversity indicators. However, their study did suggest that carabids met several broad bioindicator requirements. As a group, Carabidae have some species with specializations for particular habitat conditions and could potentially be used as bioindicators (Thiele 1977; Koivula 2001; Rainio and Niemelä 2003). Although different habitat types will almost always contain species assemblages consisting of both generalist and specialist species, specialist species are more useful as bioindicator candidates (Niemelä et al. 2000; Rainio and Niemelä 2003). Specific species of ground beetles have been used to indicate temperature and moisture gradients, and their community assemblages have been directly related to habitat type, ground vegetation and litter (Niemelä et al. 1993; Niemelä and Spence 1994; Butterfield et al. 1995; Koivula 2001; Rainio and Niemelä 2003). Carabid species and community assemblages have been shown to respond to several different types of habitat

change (e.g. fragmentation, clear-cutting). Many carabid species have also been shown to exhibit early responses to different environmental stressors, suggesting that they are potentially useful as environmental indicators. Previous studies have suggested they may serve as biodiversity indicators meaning they may represent how other invertebrates and other biota will respond to habitat change (Butterfield et al 1995; Lövei and Sutherland 1996). For example, the response of carabid beetles to habitat change has paralleled that of spiders, although the underlying factor for change is thought to be different (Niemelä et al. 1996; Niemelä 1997; Rainio and Niemelä 2003). Additional studies have shown the response to habitat loss and isolation by carabids correlates to that of butterflies and ants (Punttila et al. 1991; Rainio and Niemelä 2003). In contrast, Niemelä et al. (1996) found that carabid responses did not parallel those of ants along a forest succession gradient. In summary, although the evidence remains inconclusive as to the similarity in response to environmental changes between carabid beetles and other ground dwelling invertebrate species (Rainio and Niemelä 2003), carabids have proven useful in biodiversity studies since they are easy to collect, are present at high numbers (allowing greater statistical power), are globally widespread, are relatively abundant, and are taxonomically and ecologically relatively well studied (Koivula et al. 2002). This study aims to identify carabid species which exhibit a response to forest age structure in the Piedmont NC as possible biodiversity indicators species.

MATERIALS AND METHODS

Study Sites

Thirty-three sites, selected to represent five forest classes, were sampled. All sites are located within Stokes, Surry, or Forsyth counties in the Piedmont region of North Carolina (Table 1, Figure 1a). Twenty nine sites are located within the Pilot Mountain State Park (PMSP) boundaries. These sites are located in either of the two larger continuous sections of the park (Mountain or Yadkin River sections) or along the six mile Yadkin River Corridor Trail which connects the larger sections.

The sites represent the following five categories: recently cut forest (n = 6 sites), 10 year old forest (n = 6 sites), 50 year old forest (n = 7 sites), 85 year forest (n = 9 sites), and 150 year forest (n = 5 sites). The 150 year old category was limited to five replicates due to the difficulty of finding mature forests in the region. The highest number of replicate (n = 9) replicates is for 85 year forest, with some sites consisting of smaller fragments while other sites were in much larger forest tracts. The fragmentation component to this study will be addressed in a later paper.

The 0-1 year old sites are within a 160 acre plot which was logged in December 2008; most the tract was clear-cut with a few trees left standing in riparian zones (which is legally dictated). That plot is located approximately 23 km east of the nearest Pilot Mountain State Park sites but at the same altitude and with the same North Carolina Geological Survey (NCGS) soil type (i.e., Metagraywacke and Muscovite – Biotite Schist (CZma²)) (Brown 1985). The age of the forest pre-logging was approximately 75-85

years of age, as determined by tree ring counts on four trees within the plot. The oldest age class (approximately 150 year old forest) sites were forest fragments located within the city limits of Winston-Salem at Bethabara Park, at Wake Forest University campus, and one site situated on a bluff above Muddy Creek Floodplain. These sites were located approximately 23 km from the recently logged sites and 29 km from the farthest site at PMSP and at slightly lower elevations (Table 1). The soil type for the five 150 year old forest sites was Biotite Gneiss and Schist (CZba) (Brown 1985). Elevation among all study sites ranged from 850-1166 m. See Table 1 for additional site information (i.e. elevation, largest tree species, circumference measurements, etc.).

Sampling

Sampling commenced in March 2009 and continued through February 2010, allowing for a one year study to account for seasonal variation (Rainio and Niemelä 2003). Pitfall trapping which has been shown to be useful for studies comparing species richness and activity/abundance levels of larger (>5 mm) beetles (Thiele 1977, Butterfield 1997, Werner and Raffa 2000, de Warnaffe 2004, etc.). Pitfall traps consisted of a plastic drinking cup (Solo brand, with a 12 cm diameter at the mouth), positioned flush with the ground. A dense foam plastic cover was loosely placed over each trap and fixed to the ground using nails, in order to keep, rain and other debris out of the trap, yet provide sufficient room for beetles to gain access to the trap. Each cup contained a non-toxic propylene glycol or antifreeze as a preservative. In order to test for microhabitat heterogeneity, alpha diversity, (which will be addressed in a later paper) pitfall traps at each study site were divided into two groups (6 A cups and 6 B cups) located approximately 10 m apart for a total of 12 traps at each site (Figure 1b). Pitfall traps at

each microsite (A or B) were arranged in two side-by-side triangles, comprised of 6 traps each. Carabids were collected from each trap monthly throughout the year long study. The by-catch from each study site was also collected and preserved in 95% ethanol. By-catch analysis provides the possibility to produce comparable data for other taxa along this forest age gradient. Individuals were identified to the species level using a morphological key (Ciegler 2000) and by comparing selected individuals with specimens housed at the Smithsonian National Museum of Natural History.

A correction factor was used to modify the raw count of individuals to provide the equivalent number of beetles obtained as if there were 182.5 trap nights per month for each of the six cups at A and B microsites. The number of trap nights per month was calculated by multiplying the number of nights in a year (365) by the number of traps at the A or B site (6), and then dividing that value by the twelve months to account for all months (12) (i.e. an average of 30.416 nights per month times 6 traps = 182.5 trap nights). This corrected for variations in collection times and when pitfall traps were disturbed (i.e. overturned) at each site.

Abundance

To correct for large variances within and among study sites the mean abundance for each forest age classification was natural log transformed ($\ln+1$). After verifying the assumption of homoscedasticity via F_{\max} tests, a single factor analysis of variance (AVOVA) test was utilized to determine if the mean abundance values were statistically different among sites from different forest ages. If statistically significant differences were found, a Tukey comparison of means test was used to examine the differences among the means (Hampton and Havel 2006).

Diversity

Six indices were calculated to compare the carabid beetle diversity among forest age classes.

1.) Species Richness (S). The mean species richness within each age class was determined. This index is simply a count of the number of species (S) in a given area. Differences in richness among age classes were tested through single-factor ANOVAs followed by Tukey's comparison of means tests.

EstimateS v8.2.0 was used to predict richness value for each of the forest succession classes via ACE (Abundance-based Coverage Estimator). ACE is a richness estimate that uses the study data to provide a predicted species count with additional sampling effort (Colewell 2009).

2.) Shannon Diversity Index (H'). The Shannon diversity index is calculated as:

$$H' = -\sum_{i=1}^s p_i \ln p_i$$

where p_i stands as the proportion of the sample comprised of species i , and \ln is the natural logarithm. It takes into account the species richness and the equality of abundance among the number of species (evenness) (Smith and Smith 2006). Unique species, as well as increased evenness among species abundance, leads to an increase in this index (Liebherr and Mahar 1979).

3.) Shannon's Evenness. This diversity index focuses on the relative abundances of species. Evenness of a community refers to the number of individuals collected of the various species present in a community. As the evenness index in a given area increases, the abundances of species become more similar (Liebherr and Mahar 1979). This measure is integrated into the Shannon diversity index as well.

4.) Simpson's Diversity Index (D): This index is a measure of dominance and is strongly influenced by the most commonly collected species (Liebherr and Mahar 1979; Werner and Raffa 2000). The equation for D is:

$$\sum_{i=1}^S \frac{n_i(n_i - 1)}{N(N - 1)}$$

where n_i is the number of individuals belonging to a species and N is the total number of individuals collected. It is often expressed as (1-D), for ease of interpretation, so that the higher value indicates a more diverse the community (Werner and Raffa 2000; Colewell 2009).

5.) Fisher's Alpha. This diversity measure is independent of sample size independence, which is beneficial for studies comparing communities where the numbers of collected specimens differ. Fisher alpha is calculated as:

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

where species is represented by S, number of individuals is N, and α is the constant, Fisher's alpha (Fisher et al. 1943; Devarus and Gras 2010). This constant is characteristic of the overall community, not the sample, and has a positive relationship with the number of species. Fisher's alpha is a log-based series, widely used in ecology to approximate the distribution of the species abundance from a sample within a community (Devarus and Gras 2010). Fisher's alpha values were calculated by the program EstimateS v8.2.0, with a total of 50 randomizations conducted for each forest age group.

6.) Dominance. Dominance is the proportion of individuals of the most commonly collected species within a community. It was estimated by dividing the total

individuals for the most common species by the total number of individuals collected within each age group. Similar to species richness it is sensitive to sample size. A dominance value indicates the contribution of one species to the overall catch in a given area.

All six diversity indices were calculated for each study site, with mean and 95% confidence interval calculated for each forest age class. Single factor ANOVA was used to determine if the means of five of the diversity measures were statistically different among forest age classes. If significant statistical differences were found, Tukey's comparisons of means tests were conducted to detect significant differences among the age classes (Hampton and Havel 2006). Due to the uncorrectable heteroscedasticity for Simpson's values a Games and Howell test for unplanned comparison of means (Games and Howell 1976; Sokal and Rohlf 1995) was conducted, in place of an ANOVA test, to detect differences between age classes. This test is more powerful than non-parametric comparison tests and also involves comparison of means (Sokal and Rohlf 1995). Pearson correlation and regression analyses among the means of all six diversity indices with the increase in forest age were conducted via Microsoft Excel.

Species accumulation curves were computed using EstimateS (v8.2.0) software. The corrected abundance data for each site was subjected to 50 randomizations in EstimateS, with species number (referred to as Sobs Mao Tau) plotted against the number of individuals for each of the five age classes. This technique calculates the rate at which species are being accumulated as sampling effort increases i.e., individuals collected (Smith and Smith 2006). To compare differences in the rate of species accumulation

among forest age classes, a Chi-square goodness-of-fit test (χ^2) was computed at selected points along the sampling curve.

Community Structure

Rarity. Species were classified in terms of commonness based the contribution of their abundance to the overall carabid beetle catch for this study. Several forms of rarity are discussed in ecological studies. In terms of this study, rarity refers to local population size (abundance) as measured through pitfall trapping (Rabinowitz 1981; Gaston 1994). The rarity categories, presented in percent of total catch are as follows: singleton (one individual collected, 0-0.05%), doubleton (two individuals, 0.06-0.10%), extremely rare (0.11-0.20%), rare (0.21-0.99%), common (1-9.99%), and dominant (10-19.99%). Chi-square goodness of fit test was calculated among the total catch for each of the 5 age classes to identify deviations from expected distributions.

Another way to analyze rarity is through the relationship between relative abundance and the occurrence of species in each of the 33 study sites. Species which are present in higher numbers are expected to inhabit more sites along the forest age gradient (Brown 1984).

Ordination. Ordination is a data reduction method which arranges species along a gradient in order to present it in a more organized and comprehensive manner (McCune et al. 2002). A data matrix, with rows containing the species and columns with corrected abundance, was created in order to compare the similarity of carabid beetle communities among forest age classes. The Sørensen's similarity, also known as the "Bray-Curtis coefficient", was determined via the program EstimateS to measures dissimilarity between forest age classes (Colwell 2009). Sorensen's Index calculates the shared

abundance between sites by the total abundance ($2w/(A+B)$), with w representing the shared species and A and B being the two different sites (McCune et al. 2002).

Presenting the formula as a distance measure between two items (i,h) it is calculated as:

$$S_{i,h} = \frac{\sum_{j=1}^p |a_{i,j} - a_{h,j}|}{\sum_{j=1}^p a_{i,j} + \sum_{j=1}^p a_{h,j}}$$

To study the community structure of carabids across the five forest age classes, Non-metric Multidimensional Scaling (NMDS), a commonly used ordination method, was utilized. This analysis was completed through the program PC-Ord Version 5 (McCune et al. 2002). NMDS uses the species composition of each study site to display its ranked distance, in the least stressful position in n -dimensional ordination space. It is a useful method when the underlying species response to a gradient of interest is unknown at the initiation of the project (Clarke and Ainsworth 1993; McCune et al. 2002). In contrast with other ordination methods (e.g. DCA), NMDS utilizes a ‘species composition representation’ method which has been recognized as one of the most effective techniques and one that is defensible for ecological community data (Clarke and Ainsworth 1993; De’ath 1999; McCune et al. 2002; Palmer 2009). Axes are not ranked in order of importance and the coefficients of determination (r^2) for the correlation between the locations of study sites in ordination space in relation to the dominant ordination axes are calculated. The r^2 represents the variance in species composition which is explained by the ordination axes (McCune et al. 2002).

Species classified as common or dominant according to the rarity scale of this study were included in the NMDS ordination analysis. Rarer species were not included

since two most common species categories contribute the greatest number of individuals to the carabid beetle community structure (Anderson T.M. pers. comm.; Palmer 2009). Additionally, rare species may negatively affect the results of NMDS (Anderson T.M. pers. comm.). The NMDS analysis was based on the corrected abundances of the 17 most commonly occurring species. Including abundance data in ordination analyses helps to distinguish more subtle differences in relatively homogeneous areas (i.e. different forest classes) (McCune et al. 2002).

Detrended Correspondence Analysis (DCA) was conducted for comparison to the NMDS analysis; the two types of analyses have different strengths and weakness, DCA and NMDS are both highly utilized techniques in community ecology (Palmer 2009). DCA is known as a ‘gradient analysis’ ordination technique while NMDS is referred to as ‘species composition’ analysis (De’ath 1999; Palmer 2009). DCA is an eigenvector technique which is rooted in correspondence analysis (CA). Unlike NMDS, the eigenvalues of DCA are ranked in order of importance. It is built for community data along ecological gradients (McCune et al. 2002; Palmer 2009).

In this study, a total of 43 species were included in the analysis. Species were excluded if they only occurred at a single study site. Incidence (presence-absence) data was utilized in this procedure to decrease the affect numerical dominance some species may have on the ordination results (Silman M.R. pers.comm.) When the heterogeneity of species units is high presence-absence data is a useful measure (McCune et al. 2002).

Wing State

Although there is a range of conditions for carabid beetle wing state, for the purpose of this study all beetle species were classified into one of two dichotomous

states: macropterous (potential for flight) with fully developed wings or brachypterous (no potential for flight) which includes beetles with short wing states (brachyptery) or lacking wings (aptery). The length of the hind wing in carabid beetles has been associated with dispersal ability (Erwin 1979; Gutiérrez and Menéndez 1997).

The wing state of each species was determined from the literature (Larochelle and Larivière 2003) as well as physically examining the condition of the wing for at least five individuals (for species with $n \geq 5$) from each species. Wing condition was verified by examining the degree of hindwing development beneath the hardened elytra and classifying the species as long-winged, short winged, or non-winged. Long-winged species were considered macropterous (with the potential of flight) while short-winged and non-winged species were brachypterous (no potential of flight). Wing state was analyzed on a species level and in terms of abundance (all species combined) within each forest age class. Values are reported as relative abundance since number of individuals varied among the five age classes.

Chi-square analyses were used to test whether abundance values of the wing states differed among forest age classes. Correlation and regression analyses were used to determine if there was a significant relationship between forest age and wing state.

Ecological Indicators

To identify species as potential candidates for indicators of forest age, each species was first classified according to the total number of individuals collected from each of the five forest age classes. Only species with $n > 5$ individuals collected throughout the study were included. Species were classified as follows: extreme habitat generalist (occurred in all 5 forest age classes), habitat generalist (occurred in 4 forest age

classes), habitat intermediate (occurred in 3 forest age classes), habitat specialist (occurred in 2 forest age classes), and extreme habitat specialist (occurred in 1 forest age classes). Species numbers within each of the above categories were compared through Chi-square goodness of fit test against the null hypothesis of random distribution of the number of species among forest age classes.

Species classified as a habitat specialist or extreme habitat specialist or with high abundance at a particular forest age class were analyzed as potential candidates as ecological indicators of forest age. The first requirement for a candidate to act as a forest age ecological indicator was the species presence in at least 50% of the replicates within that forest age class. This decreased the likelihood the elevated abundance within a particular age group was due to the establishment of an aggregated population of one carabid species in close proximity to one of the replicate sites. To determine if a species was a good candidate for an ecological forest age indicator a Chi-square goodness of fit test was used to determine whether the distribution of species abundances among forest age classes was random. To satisfy the assumptions of a χ^2 test, only species where $n \geq 25$ were tested therefore there was a minimum expected value of $n = 5$ for the five forest age classes. If species distributions along the classes were statistically significant, a follow-up Chi-square goodness of fit test was performed by combining adjacent forest age classes to determine if significantly more individuals occurred in a combined forest age class compared to others (e.g. values from 0 and 10 year old forest age classes were combined and compared to the values from the combined older aged forest classes). Species not meeting the minimum abundance requirement for a standard Chi-square test

but with at least 10 individuals collected over the annual study period were analyzed via a Chi-square test by combining adjacent forest age classes.

RESULTS

Abundance

A total of 2,568 individual ground beetles representing 29 genera and 66 species were collected from 33 study sites. Due to the differences in replicate number among forest age classes only average abundances will be compared. There were statistically significant differences (ANOVA, $p < 0.01$, $\alpha = 0.05$) in abundance for the 10 and 50 year forest classes (where beetle abundance was high), compared to the 150 year old forest (the lowest abundance (Table 2; Figure 2). The corrected carabid beetle abundances relative to the five forest age groups are listed in Table 3.

Diversity

The 0 age forest class had the highest values for all six measures of carabid diversity and the 150 year forest class had the lowest in all six categories. Only these two forest age classes were statistically different for most indices (Table 4). Species richness was the highest in the 0 age forest ($S_{avg} = 17$) and lowest in the 150 year forest class ($S_{avg} = 8$). Species richness initially dropped between the 0 and 10 year old forest classes, but remained relatively constant until a further decrease occurred in the transition from 85 to 150 year forest classes (Table 4; Figure 3). Species richness varied significantly between the 0 and 150 year old forest classes (ANOVA, with subsequent Tukey tests, $p < 0.0007$) and there is a negative correlation between species richness and forest age ($r = -0.939$, $p = 0.0178$) (Figure 3). ACE estimations of species richness also projected a negative relationship between species richness and forest age. However, the 85 year old forest is

projected by the ACE estimator to have a greater increase in carabid species richness compared to the 10 and 50 year old sites, which was not evident from the observed richness data (Table 5).

Shannon Diversity Index. The Shannon diversity index was highest in the 0 aged forests (2.20) and lowest in the 150 forest (1.35) (Table 4; Figure 4). Significant differences occurred between 0 and 150 year old forests ($p < 0.003$), with a significant negative correlation between Shannon diversity and forest age ($r = - 0.903$, $p = 0.035$) (Figure 4).

Simpson's Diversity Index (1-D). Simpson's diversity was highest in the clear-cut forest (0.82) and lowest in the 150 year old forest (0.64) (Table 4; Figure 5). The Games-Howell test revealed there was a significant difference between the two extreme age classes ($p = 0.05$). Correlation was significant ($p = 0.023$) with the increase in forest age and the regression analysis showed a significant negative correlation ($r = - 0.928$, $p = 0.023$). Simpson's values followed a similar trend as Shannon values with the exception of a small increase from 50 to the 85 year old forests before decreasing for 150 year old sites (Figure 5).

Shannon's Evenness Index. Differences in Shannon's evenness index among the five age classes were not significant via ANOVA.

Fisher's Alpha. Fisher's alpha decreased as forest age increased (Table 4; Figure 6). ANOVA ($p < .0001$) with a Tukey test indicating that 0 aged sites were statistically different in comparison with other age classes ($\alpha = 0.05$) (Figure 6). There was no significant correlation or regression between Fisher's alpha and the forest stage.

Dominance. The highest dominance value was for the 150 year old forest (0.645) with the lowest values for the 10 year old forest (0.348). There was a significant positive correlation with forest age ($r = 0.888$, $p = 0.04$).

Species Accumulation Curves. Species accumulation curves for each forest age class, including the curve with the highest sampling effort (e.g. 726 individuals for 85 year old forests), did not reach a complete asymptote (Figure 8), indicating that additional sampling effort would likely uncover uncollected species for each forest age. For a species accumulation curve, the sampling 'saturation' point is distinguishable by the slope of the line nearing zero and the leveling of the curve, signifying the sampling effort where most of the species in an area have been collected (Smith and Smith 2006). The steep slope of the recently logged site (0 forest age) implies there are many more species yet to be collected for this class (Figure 8). In contrast to the steep slope of the 0 year old forest the 150 year old site has the flattest slope. This finding is in concordance with the previously cited result of high species richness for the youngest sites and the low species richness at the oldest sites.

As determined by Chi-square goodness-of-fit test, there was no significant difference in number of species among the five forest age classes at the point in the curves where $n = 236$ (i.e., the number of individuals had been sampled for the forest age class with the lowest abundance (the 150 year old sites). However, when the species accumulation curve for the 150 year old age class was projected to 440 individuals through the logarithmic curve feature of Microsoft Excel (Figure 9) species numbers varied significantly. The follow up Chi-square test revealed there were differences

between the two extreme age classes (the 0 and 150 aged forest curves) in comparison to the curves of the four other age classes (Chi-square test, $\chi^2 = 0.05$).

Five specimens of a species not previously reported in North Carolina were collected during this study. *Rhadine caudata* is a medium sized (8-10mm), brachypterous (incapable of flight) species of ground beetle easily identified by its spined elytra. It is listed as troglophilic, preying on the eggs of common cave crickets (Barr 1985). However, recent information (pers. comm.) provided by Dr. Richard Hoffman, Curator (Emeritus) of recent invertebrates at Virginia Museum of Natural History (VMNH), questions the degree of necessity of caves for the life cycle of this species.

R. caudata is species of concern at the global level (G3) and state level in Virginia (S3) and Alabama (S2) (NatureServe 2006). Almost all the species for the *Rhadine* genus are located in the western United States with *R. caudata* as the only Eastern species occurring as far north as North Carolina. A more southern species (*R. larvalis*) has minimal overlap with *R. caudata* (Erwin TL pers. comm., NatureServe 2006) but does not occur in North Carolina. Pitfall trapping in Virginia has yielded approximately 60 *R. caudata* specimens from epigaeic sites, most from higher altitudinal locations. The nearest reported location of *R. caudata* to Pilot Mt. is in Carroll County, VA, (Hoffman, R.H. pers. comm.) located approximately 45 km from Pilot Mountain NC.

Community Structure

Rarity. The numbers of species classified in the each of the rarity categories are as follows: singletons = 18, doubletons = 7, extremely rare = 4, rare = 20, common = 14 and dominant = 3. Not surprisingly, species with low abundance were more likely to be collected at fewer sites than species occurring in high numbers (Figure 10). Three

species, *Cyclotrachelus sigillatus*, *Pterostichus sculptus*, and *Sphaeroderus stenostomus*, occurred in all forest classes and constituted 51% of the total number of individuals collected in the study. Regression analysis demonstrates there was a significant positive relationship between forest age and dominance of these three species (Figure 11). In contrast, the highest number of singletons ($S = 8$) and rare species ($S = 15$) occurred in the recently logged forest (Figure 12). However, the uneven number of age replicates should be taken into consideration when interpreting differences in rarity among age classes (e.g. the 150 year forest class, which was composed of the lowest number of replicated also had the lowest value for total species richness where $S = 18$).

When ACE projections were made (via EstimateS program) of singletons and doubletons for each age category (Table 5), the highest number of singletons is for the 0 aged sites ($S=13$), followed by the 85 year old sites ($S=11$) which is in agreement with the values the high observed values for these two sites.

Ordination. Non-metric multidimensional scaling (NMDS) shows a distinct grouping of the age replicates and separation of sites by age for all but one of the forest classes (Figure 13), indicating similarity in carabid species assemblages at equivalent forest classes along the age gradient.

The two axes in NMDS ordination accounted for 73% of the variance in species composition for the 17 most commonly occurring species among the 33 study sites. Polygons determined by forest age class appear in the same order as forest age cycles (with limited overlap), with the exception of the 10 year old replicates (Figure 13). The 0 aged study sites have the highest scores on axis 1. The 50, 85, and 150 polygons descend

in decreasing scores along axis 1. Age polygons become more compact with as forest age increases, indicating less variation in composition for older sites.

Adding species points representing the common species to the array of sample site points to create a biplot (species and sites ordinated together) allows for both to be analyzed simultaneously (Palmer 2009). Species may be present at multiple study sites so the species points represent an average or typical position in ordination space for species while discounting the span of distributions for ubiquitous species (Figure 14). A species point located in close proximity to an age polygon demonstrates the potential affinity of that species for the conditions of that class along the gradient. These species are candidates as ecological indicators of forest age. For example, four species (*Amara familiaris*, *Harpalus herbivagus*, *Harpalus faunus*, and *Harpalus pensylvanica*) are located in close proximity to the 0 forest age polygon, suggesting that these species prefer the conditions of clear-cut sites. *Amara familiaris*, *Harpalus herbivagus*, and *Harpalus pensylvanica* were identified as possible indicators for recently cleared forests (discussed further in ecological indicator section of this paper). The three species with the highest dominance values (*Cyclotrachelus sigillatus*, *Pterostichus sculptus*, and *Sphaeroderus stenostomus*) appear relatively close to all age polygons. These three widespread species occurred in all five forest classes including at least 25 of the 33 study site replicates. Individuals of *C. vinctus* were captured more frequently in the 10 year old forest which is supported by the location of the species point on the ordination figure.

DCA presence/absence analysis (Figure 15) shows the species present at the clear-cut sites are clearly different from the other four study sites. Only one 50 year old study site overlaps with the polygon formed by 0 year old sites. The polygon formed by

50 year old sites is positioned in between the 0 and remaining three age groups. This suggests it may be time of transition for carabid species along the forest age gradient. There is overlap between the polygons representing 10, 85, and 150 year old sites, suggesting that the species present at these three groups are more similar than the other two forest age classes.

The eigenvalues from the DCA analysis were 0.538 for axis 1 and 0.322 for axis 2. Unlike the axes reported from NMDS analysis, the eigenvalues reported from DCA analysis do not represent a proportion of the variance for species data among study sites. This is due to detrending and rescaling in order to equalize the variation of species scores (McCune et al. 2002).

Wing State

Most of the species (39 of 66 species) collected were fully winged (macropterous) with the potential for flight (Table 6). The remaining species (27) were brachypterous and are considered incapable of flight (Figure 16). Individuals collected in this study and found to contain full wings but classified as flightless in the literature were considered brachypterous species (i.e. *P. decentis*). The numbers of macropterous individuals decreases as forest age increases (Figure 17) although the correlation between macroptery and forest age was not significant. However, the difference in macropterous compared to brachypterous individuals was significant for each forest age group except for the recently logged forest in ($\chi^2 < 0.05$).

Ecological Indicators

For the 37 species where $n > 5$, most ($S = 14$) were considered habitat extreme generalists (i.e. occurred in all forest age classes) (Figure 18). Table 7 lists the habitat

specialization categories for each of the species. A Chi-square analysis of frequencies show the distribution of species among the five specialty categories is not random with more species falling in the generalist categories ($\chi^2 < 0.05$).

Eighteen species of the 27 species where $n \geq 10$ were identified with strong affinities for a forest succession classes (Table 8, $\chi^2 = 0.05$). Eight species with significant forest class affinity were classified as extreme habitat generalists (occurring in all five forest age classes) (Table 8). Fifteen species showed preference for a single forest age class and three species preferred two forest age classes (Figure 19). Of the 18 indicator species, seven species were identified as indicators of 0 year forest class, two species for 10 year old forest class, four species for 50 year forest class, two species for 85 year forest class, one species for younger forests (i.e. 0 and 10 years forest classes), one species for middle aged forests (i.e. 50 and 85 year forest classes), and lastly one species for older forests (i.e. 85 and 150 year forest classes). Four additional species had abundance distributions that were not random as determined by goodness of fit tests ($\chi^2 < 0.05$) but did not show affinity for any age sites (Table 8).

Of the potential candidate species for recently cut forests (0 age class) two were in the genus *Amara* and two in the genus *Harplaus*. The four candidate species for older forest classes (85 and 150 year old forests) are *Galerita bicolor*, *Pterostichus coracinus*, *Platynus decentis*, and *Dicaelus politus*. More than half (59%) of the *G. bicolor* individuals collected within the 85 year old forest age class were from one replicate site which is located in the Yadkin River Corridor Trail.

DISCUSSION

This study examined the diversity, community composition, and wing state of Carabidae as a function of forest age and identified eighteen species as potential ecological indicators for forest age. It is one of few, if not the only study, focusing on the community structure and diversity of carabid beetles through a forest age gradient in the United States temperate zone. Systematic trapping throughout the year with relatively high site replication separates this study from other similar carabid beetle studies. Replication within forest age classes reduces the effects of outside factors among study sites which may influence the results (Rainio and Niemelä 2003).

Although pitfall trapping has been criticized for its dependence on abundance, weather, activity of beetles, and selection for larger individuals (>5 mm) (Greenslade 1964; Thiele 1977; Lövei and Sutherland 1996; Liebherr and Mahar 1979; Werner and Raffa 2000; Larsen et al. 2003) it has been a useful collection method for comparing carabid beetles above a certain size and in the same general geographical locations. Pitfall trapping of carabid beetles can be influenced by surrounding vegetation and the susceptibility of capture differs among species (Butterfield 1997). Therefore, the carabid beetles collected in this study may not represent the entire community of the given area. The positive slopes of the species accumulation curves and the predicted ACE values for each age group supports the need for more sampling to obtain a comprehensive understanding of this Piedmont forest carabid community. However, sampling bias, if it does occur, would be expected to be consistent across all forest age classes. Pitfall traps have been shown to assess the activity abundance of larger species across habitats with

different features such as a forest age gradient (Butterfield 1997; Werner and Raffa 2000). In addition, pitfall traps yield high numbers of individuals providing power for statistical tests. The passive sampling approach of pitfall trapping also minimizes the investigator associated biases inherent in active search method. Within the goals of this study, pitfall traps are an efficient, valuable means of collection (Thiele 1977; Butterfield 1997; Larsen et al. 2000). Alternative sampling methods, such as hand collecting, canopy fogging, and soil sample collection, in conjunction with pitfall traps would likely yield different results. The additional methods would provide a more accurate insight to the entire carabid beetle diversity but would have pronounced limitations for cross comparison at the population and community levels (Greenslade 1964; Werner and Raffa 2000). In future studies, alternative sampling methods (e.g. hand sampling) could be employed to generate a more comprehensive data set to evaluate carabid diversity and species composition.

Abundance and Diversity

Total abundance (i.e. the sum of all individuals of all species) of carabid beetles varied significantly with forest age. The intermediate forest age classes (10, 50, and 85 year old) yielded the largest number of individuals while the two extreme age classes reported lower levels of abundance. However, a high number of carabid beetles did not necessarily equate to high levels of diversity (as will be discussed subsequently).

Similar studies have also found larger numbers in intermediate aged forest classes (Spence et al. 1996; Koivula et al. 2002). In a boreal forest, which had a more compact age gradient than this Piedmont study (five age classes ranging from 0 to 60 years old) the highest number of individuals occurred in the 5 and 60 year old forests (Koivula et al. 2002). Although the abundance peak was at an extreme end of the boreal forest gradient,

it is similar in terms of forest age to the middle (50 year old) aged forest of this study. The age gradient of the boreal forest study was also on a finer scale than in this study making direct comparisons difficult.

In western Canada, the highest number of carabid beetles occurred in 60 year old mixed hardwood forest, followed by a decrease (although not statistically significant) in abundance for the study's next and most mature forest age group (120 years old) (Spence et al. 1996). In an additional study (Niemelä et al. 1993) in the boreal forests of western Canada, the highest number of carabids were collected in regenerating stands (2 and 9 years old); however carabid catch from mature forests (age \geq 100 years) were almost as equally as abundant as the 2-9 year old stands. Similar to this study, several carabid investigators have reported lower carabid activity-abundance in clear-cut sites compared to more mature forest classes including younger regeneration classes (5-15 years) (Jennings et al. 1986; Niemelä et al. 1993; Koivula et al. 2002).

Overall the results of forest age studies (i.e. Niemelä et al. 1993; Spence et al. 1996; Koivula et al. 2002) which examine carabid diversity and species assemblages indicate that results vary by locations and by forest types. For the present study, only a broad response for carabids to an anthropogenic disturbance and the forest regeneration cycle can be predicted.

There are more carabid forest ecology studies conducted in northern Europe than in the Piedmont of the U.S. The majority of European carabid species have been classified as to their degree of habitat specificity. Ecological work on North American forest Carabidae has been much more limited, with knowledge of habitat and food

preferences remaining lacking or questionable for many species. One of the goals of this study was to provide data which would at least be a partial comparison to European data.

In general, the carabid response in the Piedmont NC forest sites in the study follow a similar pattern post clear cutting to that of northern European boreal forests. All diversity indices exhibited an overall decrease in species diversity as forests age increased. This has also been reported in previous studies of high latitude forests in Europe and North America (Lenski 1982; Niemelä et al. 1993; Butterfield et al. 1995; Spence et al. 1996; Niemelä 1997; Butterfield 1997; Koivula 2001; Koivula et al. 2002; de Warnaffe and Lebrun 2004). In high latitude forests, open habitat species occur at high densities for the first 20-30 years following clear-cutting, until the forest canopy closes (Niemelä et al. 1993, 1996; Butterfield 1997; Koivula et al. 2002). There are several possible reasons for this increase in species richness in young forests. A high proportion of grassland and meadow carabid species prefer warmer, open habitats such as those found in recently disturbed forests (Erwin 1979; Niemelä 1993; Niemelä et al. 2007). Since many open habitat carabid species are seed eaters, the type of food and its abundance may strongly influence whether they are present in clear-cut areas (Erwin 1979). In Iowa, the highest carabid beetle diversity and abundance were reported from tallgrass prairie habitats with the second highest values found in wooded forests. High diversity in tallgrass prairie demonstrates the high number of carabid species adapted for the warmer conditions offered by this ecosystem (Larsen et al. 2003).

In this study two widespread genera (*Pterostichus* and *Cyclotrachelus*) constituted 30% of the 0 age forest carabid population. *Pterostichus* is one of the largest genera of Carabidae with a world-wide distribution and presence in a wide array of habitats. Some

species are found in xerophilous, open habitats while others are strict forest species (Lindroth 1966). Although not as much information is available in the literature for the genus *Cyclotrachelus*, most species occur in open fields and dry woodlands (Harris and Whitcomb 1971). The most common species collected in this study (*Cyclotrachelus sigillatus*) is typically found in leaf litter of deciduous forests as well in under cover in open habitats (Harris and Whitcomb 1971; Erwin 1981).

The next most abundant genera at 0 age forest classes were *Harpalus* (22%) and *Amara* (13%), both of which are known to contain seed-eating and phytophagous species which prefer dry, open, and grassy habitats (Thiele 1977; Erwin 1979, 1981; Niemelä et al. 1993, 2007; Butterfield 1997).

Following a severe disturbance of mature forests (e. g. clear-cutting) there is an influx of rapidly colonizing, open habitat species with the combination of the temporary presence of carabid generalists typical of more mature forests. Our results indicate that the temporary increased diversity of carabid species in clear-cuts is due to the influx of open habitat carabid species. In contrast, there is little evidence for the increase of carabid species diversity due to the persistence of mature forest species in the clear-cut sites. Carabid individuals of mature forest species are able to live up to 2-3 years following a clear-cut event and most forest species can still be found in areas that have been just recently cut (Koivula 2001). High levels of species diversity in recently cut forests also appear to be common for other invertebrate taxa (i.e. ants, spiders, butterflies, and non-carabid beetles (Niemelä et al. 2007).

In this study there is a downward trend for carabid species richness for 0 through 150 year old forests. A similar trend for approximately the same age classes was found

for black spruce forests in western Quebec (Paquin 2008). However, in that study the oldest forest age class exceeded those found in our Piedmont NC study. The span of age classes in the Quebec forest study showed a U-shaped trend between carabid species richness and forest age. Species richness decreased from 0 to 200 year old forests but then increased from 200 year to 340 year old forests. Although two of the sites may have trees that are slightly older than 150 years, forest sites that exceed 150- 200 years are extremely rare or non-existent in Piedmont North Carolina. Consequently, we do not know and may never know that happens to carabid species diversity in Piedmont sites older than those sampled. Anthropogenic activities are the principle reason that the current vegetation has been highly altered in this region during the past 200 years (Peet and Christenson 1980). However, there are old-growth forests (i.e. “virgin” sites) in western North Carolina that might be studied to further explore this aspect.

In Michigan oak dominated forests a greater number of carabid species occurred at what were termed “mature” forest classes although, the exact chronological age of the forest was not reported (Liebherr and Mahar 1979). The higher carabid species richness of older forest classes was attributed to the increased habitat heterogeneity generated from the accumulation of dead wood which has not had as much time to build up in mature (70 – 170 years old) forest compared to more ancient forests (177 – 340 years old) (Paquin 2008). Microhabitats created by decaying wood are preferred by carabid beetle old-growth specialists (Niemelä et al. 1996; Paquin 2008).

Species richness, although often a measure of concern for conservation issues, can be misleading due to the fact that disturbed sites, while high in species diversity, will be characterized by widespread, abundant generalist species (Spence et al. 1996; Niemelä et

al 2007; Paquin 2008). As Lenski (1982) has noted, a clear-cut event disrupts the competitive exclusion of more stable, mature forest habitats allowing for the increase of diversity of carabid species although most species are within the same genus and/or share similar life characteristics. Recently disturbed sites are more species diverse due to the fact the dominance of other competitive species has decreased allowing more species to thrive in a particular area (Lenski 1982). Studying the responses of individual species regarding habitat preferences or selected species assemblages rather than directly estimating species diversity may provide more insight into the underlying processes influencing the loss and persistence of carabid beetles (Spence et al. 1996; Niemelä et al 2007; Paquin 2008).

In this study, diversity indices differed statistically only between extreme forest age classes (i.e. 0 and 150 year age classes). While carabid diversity is an important ecological component, changes in species assemblages and community composition related to forest age classes may be of higher interest to those interested in conservation and forest management issues. Studies focusing different aged forests, as well as the differences between forested and non-forested habitats have shown species compositions to be more indicative of habitat change than raw estimates of species diversity (Butterfield et al. 1995; Butterfield 1997; Werner and Raffa 2000; Kiovula et al. 2002).

Community Structure

In this study, carabid beetle communities varied significantly among different aged forests. Most species collected in this study were considered rare or singletons, with only one individual of a specific species collected. Carabid beetle assemblages from mature forests are often dominated by a few abundant species, while the majority of

species are either scarce or occur at low abundance levels (Niemelä 1993; Koivula et al. 2002). The results of this study supported the expected negative relationship between the forest age and relative carabid abundance. It also supported the theory that more commonly collected species are found at a higher number of study sites than rarer species (Brown 1984).

Despite having a relatively low number of individuals sampled, the 0 age forest class contained the highest number of singletons and rare species compared to the other four forest age classes. Young forests are environmentally less stable than matured forests with a high flux of individuals, many with good dispersing abilities (Butterfield 1997; Gutiérrez and Menéndez 1997). In the present study, it's probable that high numbers of rapidly colonizing species entered the open areas following clear-cutting and persisted only for short periods therefore resulting in high species turnover for the 0 aged forest sites. Low carabid abundance may be attributed to the inability of open habitat species to establish long term communities at these sites due to unstable conditions. In addition, highly dispersing species may not be as susceptible to capture through pitfall traps and hence would not be recorded in the results of this study.

Other carabid beetle studies of various aged forests have not shown an obvious pattern for the distribution of rare species (Spence et al. 1996; Butterfield 1997). Similar results were found in this study with no significant differences detected in rarity categories among forest age classes. However, it is difficult to deduce meaningful associations between forest age and rarity for this study due to difference in numbers of species and individuals collected at each forest age class and the uneven number of age replicates.

The three most commonly collected species, *Cyclotrachelus sigillatus*, *Pterostichus sculptus* and *Sphaeroderus stenostomus*, which are classified as “dominant” by the criteria described previously (see Materials and Methods), constituted 51% of the total carabid meta-population and occurred in all forest age classes. Individuals of “common” species constituted an additional 38% the total carabid meta-population. The presence of the three dominant species across all age classes indicates that they are generalists in terms of habitat selectivity and survival requirements. The contribution made to the total abundance of each class by these ‘dominant’ species increased with forest age. In this study species occurring in the oldest forest age classes were also abundant in all age classes and made up the majority of the carabids collected from the 150 year old forest sites. This same dominance pattern is supported in the findings from Finnish, boreal forest study on carabids, spiders, and ants (Niemelä et al. 1996). In this study the data for *S. stenostomus* reinforces the results of a previous study (Larsen et al. 2003) where it was found in all forest age classes. Although many cycchrine species are both food and habitat specialists (Laroche and Larivière 2003) *S. stenostomus* can inhabit a number of different microhabitats within a given area (Erwin 1981). Although since *S. stenostomus* is a specialized predator on snails, it may be more dependent on the abundance of prey than on other habitat factors (Erwin 1981; Lövei and Sutherland 1996; Paquin 2008).

A distinction of species assemblage in relation to forest age is reinforced with NMDS ordination. The ordination figure shows the grouping of forest polygons within the same forest age classifications. The ordination analysis highlights the differences in species assemblages of carabid beetles with the change in the forest age structure.

Although some species were shared among age classes, the greatest species composition overlap occurred between the 85 and 150 year old forest classes.

For the NMDS ordination, polygons for each forest age class were arrayed by successive forest age, with the exception of 10 year old sites. Rather than appearing, as might be expected, in a cluster between the 0 and 50 year old forest class polygons, five out of the six 10 year old sites are located in close proximity to the 85 and 150 year old forest sites. This suggests that, perhaps counter intuitively, that the ten year old sites are more similar, in carabid species composition to more mature forested sites. It is worth noting that the outlying 10 year old site is geographically removed from the other 10 year old sites. In addition, the five tightly clumped 10 year old replicates are adjacent to an extensive tract of 85 year old forest. Being adjacent to or near older forests has been shown to effect carabid species composition, with species typically associated with more mature forests more likely to occur in the younger forests as well (Koivula et al. 2002). There is potential the older forests to act as a source for mature forest carabids which are able to wander into younger stands. The isolation of these 10 year old forest sites may not have been great enough to reflect the carabid community of a younger successional forest. In the NMDS analysis the point representing the 10 year old outlier site is also geographically distant from the other 10 year old sites, possibly explaining why it less representative of the carabid beetle assemblages for this age class.

Another finding from the NMDS ordination analysis is that the distance between the five polygons becomes shorter as forest age increases (with the exception of the 10 year old group). This suggests that carabid communities of younger forests change relatively rapidly and that carabid community stability increases with forest age

(Butterfield et al. 1995). Not only do distances among polygons decrease with forest age but the area of the polygons also generally decreases with forest age. The polygon representing the recently logged sites has the greatest area indicating high variability among the carabid species (i.e. high species diversity) for the 0 age forest class. In contrast, the polygon representing the 150 year old sites is the most compact, reflecting the low diversity in the most mature forest sites.

Interpretation of the presence-absence DCA figure generally supports the results of the NMDS abundance analysis. There were some minor differences, with the polygons representing 10, 85, and 150 year old classes not appearing as distinct as they were in the NMDS ordination figure. Also, species occurrence was more similar among these three classes than the 0 and 50 year old age classes. However, the clear separation of the polygon representing 0 aged forests shows the distinct species assemblage present at this age class, as was also indicated in NMDS analysis.

Carabid species assemblages change as open areas become more mature, resulting in closed canopy forests. For boreal forests canopy closure is a time of drastic change in carabid community assemblage (Niemelä et al. 1993, 1996; Butterfield et al. 1995; Butterfield 1997; Paquin 2008). One of the major associated changes is the quantity of sunlight reaching the forest floor which influences the temperature and humidity (Butterfield et al. 1995; Jacobs et al. 2008). This event typically occurs 20-30 years after a clear-cut event in boreal forests (Niemelä et al. 1996; Butterfield 1997). However, the timing and perhaps more importantly the extent of forest canopy closure probably varies considerably between boreal forests and the temperate forests. Since there is a large time gap in this study between the 10 year and 50 year old forest age classes, additional work

on a finer scale is needed to determine the effects of canopy closure on carabid communities in the temperate zone.

Data from this study demonstrates the strong effect of forest age structure on carabid beetle community assemblage. Forest structure and tree species composition associated with different forest age classes play a major role in the composition of the carabid communities (Niemelä et al. 2007). Habitat characteristics will affect carabid abundance and therefore the community composition (Larsen et al. 2003). Microclimatic conditions including moisture, temperature, and understory structure have been reported as potential factors influencing noticeable changes in carabid beetle communities (Niemelä et al. 1996; Butterfield 1997).

Wing State

The difference in the proportion of fully winged versus non-fully winged individuals among forest age classes are striking. There were significantly more flightless individuals for all forest age classes except for 0 year forest class. As forest age increases the number of carabid beetles capable of flight decreases, suggesting that the advantage of flight decreases with forest maturity. Wing state of carabid beetles has been linked to habitat stability (Darlington 1943; Thiele 1977) which, in the context of this study, is assumed to increase with forest age. In stable environments dispersal would be less important for carabid beetle survival and reproduction, allowing resources that would otherwise be used for wing development to be reallocated to developmental and/or reproductive needs (Darlington 1943; Thiele 1977; Liebherr 1988).

The highest proportions of macropterous individuals were collected at the 0 forest age class, where logging discontinued only three months prior to the start of this study.

The rapid colonization of open-habitat species to the disturbed area reflects the high dispersal ability of these species (Niemelä et al. 1996). Additionally, since ground vegetation and animal communities are less homogeneous at the recently logged sites, open-habitat carabids not only have to colonize but also be able to escape predators, hunt for prey, and eventually reproduce (Butterfield 1997; Gutiérrez and Menéndez 1997). These behaviors all require a high degree of mobility which may be less important for carabids inhabiting more mature forest classes (Butterfield 1997).

As indicated from the data in this study and from other studies (Butterfield et al. 1995; Spence et al. 1996; Gutiérrez and Menéndez 1997) carabid species found in more mature forests have lower dispersal and poor colonizing abilities than younger forest stages. Consequently low dispersing, closed-forest canopy species should be more sensitive to the effects of anthropogenic changes. Clear-cutting has a negative influence on species requiring microhabitats provided by mature forests to survive (Niemelä et al. 1993, 2007; Spence et al. 1996; Werner and Raffa 2000). Although some carabids incapable of flight may be capable of limited vagility, mobility of some species may be severely inhibited by even relatively small barriers (e.g. roads, streams,)., reinforcing the effect of fragmentation and the role of continuous mature forest tracts in maintaining species that are limited to or found primarily in mature forests (Koivula et al. 2002).

. In this study, the abundance, proportion or both of macropterous individuals becomes greater with the increase in forest age. As a forest ages, the proportion of beetles that are capable of flight generally decreases.

Ecological Indicators

Previous work with Carabidae beetles suggests that the best approach to understanding the processes and factors shaping carabid presence and abundance is through individual species responses (Niemelä et al. 2007) rather than more general indicators such as raw species counts. The results of this study indicate that selected species of carabid beetles are associated with different aged forests or alternately some species are generalists found at all forest age classes. In this study 14 species were present in all five forest succession classes and are classified as habitat generalists. Larsen et al. (2003) found that generalists dominated six different habitat types in northeastern Iowa. Most forest species occurred in several successional classes, but some species were more sensitive, requiring more mature forest (e.g. fallen wood, mesic vegetation, or other microclimatic conditions provided by closed tree canopies) (Niemelä et al. 2007). These specialist species had a clear preference for ground vegetation and litter quality, suggesting an interaction between soil type and microclimate. Even for the numerous carabid species described as generalist predators, these two factors may be key determinants for prey presence and abundance (Niemelä et al. 1993; Niemelä and Spence 1994).

Some carabid species have been shown to be associated with a number of habitat features (Thiele 1977; Niemelä and Spence 1994; Niemelä et al. 2007; Larsen et al. 2003). Specialist species whose abundances are significantly influenced by forest age are of particular interest for this study. Five species in this study were classified as specialists and three species as extreme specialists (occurring in two age classes and one age group respectively). Most species designated as possible ecological indicators in this study

were extreme generalists or generalists, due to significantly higher abundances within a particular stage or sequential classes along the forest gradient. For this study, candidates as ecological indicators do not have to be grouped into one of the two specialty categories. Instead, they may meet the candidacy requirements if they are a ‘generalist’ species exhibiting a noticeable spike in their abundance level within a forest age class or two sequential forest age classes.

Of the seven species showing an affinity for conditions of a recently logged forest (0 forest age class) two were in the genus *Amara* and two in the genus *Harplaus*; both genera are known to contain several open habitat specialist species (Niemelä et al. 1993). There was a greater number of indicator species for young, open forest habitats compared to more mature forests but this result may be influenced by the larger number of species found in younger forests. In an Iowa study, the highest species richness and specialists percentage was discovered in tall-grass prairie habitat (Larsen et al. 2003). In this study *Myas coracinus* and *Carabus goryi* were classified as indicators of open habitats. This may be questionable since in the literature fact these species are stated to prefer shaded and moist ground conditions provided by more mature forests (Laroche and Larivière 2003). It’s possible these species generally occur in more mature forests but individuals still remained in the cleared forest since the study began only two months after logging.

Four candidate species for older forest classes (85 and 150 year old forests) are *Galerita bicolor*, *Pterostichus coracinus*, *Platynus decentis*, and *Dicaelus politus*. *G. bicolor* is a gregarious, macropterous species which prefers the shaded ground cover of forests (Erwin 1979; Laroche and Larivière 2003). At one of the 85 year old forest sites more individuals were collected than the other eight replicate sites combined. Since

this is a colony forming species it's may be less useful as an indicator species. Also, this site was located along the Yadkin River Corridor Trail and hence may be subjected to the effects of fragmentation. *P. coracinus* is one of the most commonly caught carabids and its abundance is significantly affected by forest habitat features and forestry regimes. *P. coracinus* has been described as a forests species (Jennings et al. 1986; Werner and Raffa 2000). It was reported to occur at higher densities in managed Great Lakes forests (clear-cut around 1900 but left untouched since that point) in comparison to old growth sites which have never been logged (Werner and Raffa 2000). *P. decentis* is a widespread North American species, commonly collected under bark, fallen trees and stones, which has been classified as a mature forest specialist for boreal, eastern hemlock, and northern hardwood forests (Erwin 1981; Niemelä et al. 1993; Werner and Raffa 2000; Paquin 2008). In this study, most *P. decentis* individuals were found in the 50 and 85 age classes with none collected in the 150 year old category. However, the 150 year old sites in this study consist of small of fragments in otherwise urban surroundings and fragmentation has been shown to affect mature forest specialists (i.e. *P. decentis*) (Niemelä et al. 1993; Koivula et al. 2002).

No carabids in this study were found as indicator species for the most mature forest age group. The 150 year old sites are all smaller forest fragments located within the city limits of Winston-Salem, NC. The small patch size along with urban surroundings could possibly be responsible for the low overall carabid catch and diversity for this age group. A lack of specialists in the more mature forests may indicate these secondary forests are already disturbed and/or fragmented, so the characteristic stenotypic species never regained sufficient populations (Rainio and Niemelä 2003).

Alternatively a small number of specialists might be expected for any habitat since less than 10% of predatory arthropods and small mammals have been described as old growth specialists (Niemelä 1999). Additional work is needed to determine if these factors affect the presence and abundance of particular beetle species.

An area of on-going debate is the use of carabids as reliable indicators of biodiversity. Not all carabid species collected in this Piedmont study exhibited a response to variations in forest age classes, but 18 of the 66 species could potentially be indicators of forest age, presumably reflecting environmental changes within a forest stage. This relatively high number of eighteen indicator species supports the use of Carabidae beetles as ecological indicators of age structure in deciduous southeastern U.S. forests. Additional research is needed to determine if these species are linked to environmental or biotic features associated with a particular forest age.

Carabids have been supported as environmental and ecological indicators by several studies (Niemelä et al. 1993; Niemelä et al. 2000; Larsen et al. 2003; Rainio and Niemelä 2003). Criticisms for ground beetles as bioindicators were taken into consideration for the experimental design of this study. High spatial replication within each age class and collections over an entire year, not only during the active season, help address the issues of patchy distribution and low abundance of particular species (Rainio and Niemelä 2003). Whether responses of carabid beetles to forest age reflect the diversity and abundance other invertebrate forest fauna is not yet entirely known.

Understanding species diversity and community structure for Piedmont ground beetles is also valuable in terms of ecology and conservation biology. Although the most mature forests of this study demonstrated lower diversity than the two youngest age

classes, there was significant variation in the species compositions along the forest age gradient. Species requiring conditions offered by older growth forests will be lost if these habitats disappear from the landscape resulting in decreased regional diversity (Butterfield et al. 1995; Werner and Raffa 2000; Rainio and Niemelä 2003; Paquin 2008). On the other hand, high regional diversity does not necessarily equal high value in the context of national and global diversity (Dufrêne and Legendre 1997; Werner and Raffa 2000). Differences in species occurrence across the forest regeneration cycle in this study support the need to conserve a range of classes at the landscape level (Niemelä et al. 1996, 2007).

Only a handful of carabid beetle studies have been conducted in the temperate forests of the United States (Liebherr and Mahar 1979; Lenski 1982; Werner and Raffa 2000; Larsen et al. 2003; Jennings and Tallamy 2006). The role of the natural forest regeneration cycle on the diversity and composition of carabid beetles after a cutting event has been more intensely studied in northern boreal forests (Butterfield et al. 1995; Spence et al. 1996; Butterfield 1997; Niemelä et al. 1993, 1996, 2007; Jacobs et al. 2008). Although the ground beetles of this study followed a similar response pattern to a logging event in terms of species richness to those reported in boreal forest there were also profound changes in community composition. Our community results are unique compared to those reported in European and Canadian boreal forests. Since the habitat differences between boreal forests and temperate forests have been shown to influence carabid species (Butterfield et al. 1995; Spence et al. 1996) much additional work is needed not only in the temperate deciduous forests but also in additional forest types (e.g.

tropical lowland, montane tropical forests) before carabid responses to forest disturbance
can be categorized at both the species community levels

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Table 1. Information for the 33 study sites.

Sites	Elevation (feet)	Largest Tree Species	Circumference (in.)	Next Largest Tree Species	Circumference (in.)
0-A	1019				
0-B	985				
0-C	992				
0-D	974				
0-E	983				
0-F	1002				
10-A	1090	<i>Populus</i> (Yellow Poplar)	21.2, 23.7	<i>Populus</i> (Yellow Poplar)	23.2, 22.8, 24.2
10-B	1079	<i>Pinus</i> (VA Oldfield Pine)	12.1	<i>Pinus</i> (VA Oldfield Pine)	9.8
10-C	1101	<i>Populus</i> (Poplar)	6.5	<i>Prunus pensylvanica</i> (Cherry)	8.9
10-D	1045	<i>Quercus</i> (White Oak)	11.7	<i>Pinus</i> (VA Oldfield Pine)	11.9
10-E	1030	<i>Pinus</i> (VA Oldfield Pine)	15.6	<i>Populus</i> (Poplar)	14.6
10-F	1095	<i>Pinus</i> (VA Oldfield Pine)	13.5	<i>Pinus</i> (VA Oldfield Pine)	13.2
50-A	1095	<i>Pinus</i> (VA Oldfield Pine)	34.6	<i>Pinus</i> (VA Oldfield Pine)	25.9
50-B	1068	<i>Pinus</i> (VA Oldfield Pine)	26.5	<i>Pinus</i> (VA Oldfield Pine)	25.9
50-C	1133	<i>Quercus</i> (Oak)	31.3	<i>Quercus</i> (White Oak)	33.7
50-D	1048	<i>Pinus</i> (VA Oldfield Pine)	51.4	<i>Pinus</i> (VA Oldfield Pine)	43.9
50-E	1020	<i>Pinus</i> (VA Oldfield Pine)	41.1	<i>Pinus</i> (VA Oldfield Pine)	40.6
50-F	1136	<i>Pinus</i> (VA Oldfield Pine)	43.3	<i>Pinus</i> (VA Oldfield Pine)	39.8
50-G	924	<i>Pinus</i> (VA Oldfield Pine)	36.5	<i>Quercus</i> (White Oak)	36.6, 22.7, 31.7
85-A	1166	<i>Populus</i> (Yellow Poplar)	49.5, 56.05, 54.5	<i>Populus</i> (Yellow Poplar)	40.3, 44.3, 48.1

85-B	1046	<i>Quercus</i> (White Oak)	81.1	<i>Populus</i> (Yellow Poplar)	70.5
85-C	1040	<i>Quercus</i> <i>prinus</i> (Chesnut Oak)	82.3	<i>Quercus</i> (Oak)	87.6
85-D	1039	<i>Quercus</i> <i>prinus</i> (Chesnut Oak)	72.5	<i>Quercus</i> <i>prinus</i> (Chesnut Oak)	68
85-E	976	<i>Quercus</i> (White Oak)	64.9	<i>Quercus</i> (Oak)	49.6
85-F	1331	<i>Quercus</i> (White Oak)	55.5	<i>Quercus</i> (Black Oak)	51.8
85-G	834	<i>Quercus</i> (White Oak)	93.9	<i>Quercus</i> (White Oak)	53.1
85-H	902	<i>Quercus</i> (White Oak)	48.2	<i>Quercus</i> (White Oak)	44.3
85-J	943	<i>Quercus</i> (White Oak)	58.4	<i>Quercus</i> (White Oak)	46.5
150-A	898	<i>Acer</i> (Red Oak)	86		
150-B	894	<i>Populus</i> (Poplar)	93		
150-C	850	<i>Fraxinus</i> (Ash)	125		
150-D	850	<i>Acer</i> (Red Oak)	160		
150-E	893	<i>Acer</i> (Red Oak)	112		

Table 2. Replicate number and general results from this study for each forest age class.

Site	Number of Replicates	Abundance	Avg. Abundance	Genera	Species
0	6	443.26	73.88	22	45
10	6	538.85	89.81	21	34
50	7	626.72	89.53	19	31
85	9	725.61	80.62	22	36
150	5	233.57	46.71	11	18
Total	33	2568.01		29	66

Table 3. List of Carabidae species (S =66) with corrected abundance for forest age classes of interest.

Species	0	10	50	85	150	Grand Total
<i>Agonum punctiforme</i> (Fabricius)	4.83					4.83
<i>Agonum unknown species</i>					0.53	0.53
<i>Amara aenea</i> (De Geer)	22.98		1.05			24.02
<i>Amara crassispina</i> (LeConte)	5.58	1.52				7.10
<i>Amara cupreolata</i> (Putzeys)	2.21	0.99	1.17			4.37
<i>Amara familiaris</i> (Duftschmid)	19.57		14.25	0.95		34.77
<i>Amara impuncticollis</i> (Say)	4.29		4.81			9.10
<i>Amara musculus</i> (Say)	1.04					1.04
<i>Amphasia interstitialis</i> (Say)		1.90		1.22		3.12
<i>Anisodactylus carbonarius</i> (Say)	1.13					1.13
<i>Anisodactylus furvus</i> (LeConte)	2.33					2.33
<i>Anisodactylus haplomus</i> (Chaudior)	0.92					0.92
<i>Anisodactylus harrisii</i> (LeConte)	8.15	1.26				9.41
<i>Anisodactylus rusticus</i> (Say)	7.79					7.79
<i>Apenes lucidulus</i> (Dejean)		1.14	0.84	0.84		2.83
<i>Calathus opaculus</i> (LeConte)	4.57	31.66	84.05	14.49		134.77
<i>Carabus goryi</i> (Dejean)	17.44	0.82	5.37	14.41		38.05
<i>Carabus sylvosus</i> (Say)	4.82	0.92	1.94			7.68
<i>Chlaenius aestivus</i> (Say)	21.13	19.00	2.23	17.86	4.83	65.06
<i>Chlaenius amoenus</i> (Dejean)	1.84	0.95		1.94	12.12	16.85
<i>Chlaenius emarginatus</i> (Say)		6.81				6.81
<i>Cicindela sexguttata</i> (Fabricius)		2.80	2.43	3.		8.98
<i>Cicindela unipunctata</i> (Fabricius)				0.92		0.92
<i>Colliuris pensylvanica</i> (Linnaeus)	1.11					1.11
<i>Cyclotrachelus freitaga</i> (Bousquet)	0.98	6.40	41.58	14.02	0.77	63.75
<i>Cyclotrachelus sigillatus</i> (Say)	98.46	23.96	75.30	155.88	104.92	458.52
<i>Cyclotrachelus vinctus</i> (LeConte)	0.87	171.90	5.78	26.83	6.20	211.57
<i>Cymindis americanus</i> (Dejean)	0.92	2.89	1.01	3.77	1.01	9.61
<i>Cymindis limbatus</i> (Dejean)		1.84				1.84
<i>Cymindis neglectus</i> (Haldeman)				1.22		1.22
<i>Cymindis platicollis</i> (Say)				2.34		2.34
<i>Dicaelus ambiguus</i> (LaFerté-Sénectéré)	2.03	24.74	11.80	19.13	8.52	66.22
<i>Dicaelus dilatatus</i> (Say)	3.17	11.45	23.87	4.86		43.35
<i>Dicaelus elongatus</i> (Bonelli)	5.71	2.01	4.40			12.12
<i>Dicaelus politus</i> (Dejean)	0.92	10.93	1.72	12.87	11.59	38.02
<i>Dicaelus purpuratus</i> (Bonelli)				0.84		0.84

<i>Galerita bicolor</i> (Dry)	2.31	20.54	6.25	58.18	6.33	93.60
<i>Harpalus compar</i> (Leconte)	1.13					1.13
<i>Harpalus erythropus</i> (Dejean)			0.82			0.82
<i>Harpalus faunus</i> (Say)	12.32		13.59	4.05		29.96
<i>Harpalus fulgens</i> (Csiki)	1.35					1.35
<i>Harpalus herbivagus</i> (Say)	36.41					36.41
<i>Harpalus katiae</i> (Battoni)	1.13					1.13
<i>Harpalus pensylvanica</i> (De Geer)	46.40	2.90	8.83	0.84	1.50	60.47
<i>Harpalus spadiceus</i> (Dejean)				1.90		1.90
<i>Harpalus unknown species A</i>					0.84	0.84
<i>Harpalus unknown species B</i>					0.51	0.51
<i>Megacephala virginica</i> (Linnaeus)	1.13	0.92				2.05
<i>Myas coracinus</i> (Say)	12.77				2.84	15.61
<i>Notiobia terminata</i> (Say)	0.92					0.92
<i>Notiophilus aeneus</i> (Herbst)			1.22	0.78		2.00
<i>Oodes fluvialis</i> (LeConte)			1.22			1.22
<i>Pasimachus depressus</i> (Fabricius)	14.55	1.90	0.95	1.77		19.16
<i>Pasimachus punctulatus</i> (Haldeman)	8.70	3.80		0.92		13.42
<i>Platynus decentis</i> (Say)	2.05		9.39	7.69		19.13
<i>Poecilus lucublandus</i> (Bonelli)	3.99	0.95	6.38	2.30	0.77	14.39
<i>Pterostichus coracinus</i> (Newman)	11.34	4.97	3.67	34.14	6.94	61.06
<i>Pterostichus moestus</i> (Say)				9.60		9.60
<i>Pterostichus sculptus</i> (LeConte)	22.99	34.83	228.96	71.65	1.27	359.70
<i>Rhadine caudata</i> (LeConte)		1.97		3.66		5.63
<i>Scaphinotus andrewsii</i> (Valentine)		4.74	1.17	5.06		10.96
<i>Scaphinotus unicolor</i> (Fabricius)	1.90					1.90
<i>Scaphinotus violaceus</i> (LeConte)		0.95				0.95
<i>Scarites subterraneus</i> (Fabricius)	4.85	4.40		1.22		10.46
<i>Selenophorus ellipticus</i> (Dejean)				1.17		1.17
<i>Sphaeroderus stenostomus</i> (Weber)	12.23	130.08	60.67	222.53	62.09	487.60
Grand Total	443.26	538.85	626.72	725.61	233.57	2568.01

Table 4. Mean abundance and six diversity indices for five forest age classes.

Age	Avg. Abundance	95% CI	Richness	95% CI	Shannon Diversity	95% CI	Simpson Diversity (1-D)	95% CI	Fisher's Alpha	95% CI	Dominance	95% CI
0	73.88	12.44	17.7	1.95	2.20	0.182	0.822	0.017	12.55	1.15	0.354	0.106
10	89.81	12.14	14.0	4.69	1.84	0.17	0.776	0.006	8.06	0.76	0.348	0.011
50	89.53	66.81	12.9	3.27	1.80	0.34	0.748	0.122	6.84	0.56	0.465	0.17
85	80.62	19.46	12.2	2.10	1.79	0.25	0.761	0.075	7.96	0.51	0.391	0.10
150	46.71	31.45	8.0	3.17	1.35	0.46	0.637	0.219	4.53	0.72	0.645	0.17

Table 5. Observed and estimated values for singletons and doubletons for each forest age category. Estimated values are derived from EstimateS ACE (abundance-based coverage estimator) estimates. Obs. S is the actual species observed for this study.

Forest Age	Obs. S	ACE	Singletons	Doubletons
0	45	57.31	13	7
10	34	40.89	9	6
50	31	39.6	9	4
85	36	47.59	11	5
150	18	33.74	7	1

Table 6. Wing state of 66 carabid species collected in this study. Macropterous species have the potential for flight and brachypterous species are flightless.

Species	Wing State
<i>Agonum punctiforme</i>	Macropterous
<i>Agonum unknown sp.</i>	Brachypterous
<i>Amara aenea</i>	Macropterous
<i>Amara crassispina</i>	Macropterous
<i>Amara cupreolata</i>	Macropterous
<i>Amara familiaris</i>	Macropterous
<i>Amara impuncticollis</i>	Macropterous
<i>Amara musculus</i>	Macropterous
<i>Amphasia interstitialis</i>	Macropterous
<i>Anisodactylus carbonarius</i>	Macropterous
<i>Anisodactylus furvus</i>	Macropterous
<i>Anisodactylus haplomus</i>	Macropterous
<i>Anisodactylus harrisii</i>	Macropterous
<i>Anisodactylus rusticus</i>	Macropterous
<i>Apenes lucidulus</i>	Macropterous
<i>Calathus opaculus</i>	Macropterous
<i>Carabus goryi</i>	Brachypterous
<i>Carabus sylvosus</i>	Brachypterous
<i>Chlaenius aestivus</i>	Brachypterous
<i>Chlaenius amoenus</i>	Macropterous
<i>Chlaenius emarginatus</i>	Macropterous
<i>Cicindela sexguttata</i>	Macropterous
<i>Cicindela unipunctata</i>	Macropterous
<i>Colliuris pensylvanica</i>	Macropterous
<i>Cyclotrachelus freitaga</i>	Macropterous
<i>Cyclotrachelus sigillatus</i>	Brachypterous
<i>Cyclotrachelus vinctus</i>	Brachypterous
<i>Cymindis americanus</i>	Brachypterous
<i>Cymindis limbatus</i>	Macropterous
<i>Cymindis neglectus</i>	Brachypterous
<i>Cymindis platicollis</i>	Macropterous
<i>Dicaelus ambiguus</i>	Brachypterous
<i>Dicaelus dilatatus</i>	Brachypterous
<i>Dicaelus elongatus</i>	Brachypterous
<i>Dicaelus politus</i>	Brachypterous
<i>Dicaelus purpuratus</i>	Brachypterous

<i>Galerita bicolor</i>	Macropterous
<i>Harpalus compar</i>	Macropterous
<i>Harpalus erythropus</i>	Macropterous
<i>Harpalus faunus</i>	Macropterous
<i>Harpalus fulgens</i>	Brachypterous
<i>Harpalus herbivagus</i>	Macropterous
<i>Harpalus katiae</i>	Macropterous
<i>Harpalus pensylvanica</i>	Macropterous
<i>Harpalus spadiceus</i>	Brachypterous
<i>Harpalus unknown sp. A</i>	Macropterous
<i>Harpalus unknown sp. B</i>	Macropterous
<i>Megacephala virginica</i>	Macropterous
<i>Myas coracinus</i>	Brachypterous
<i>Notiobia terminata</i>	Macropterous
<i>Notiophilus aeneus</i>	Macropterous
<i>Oodes fluvialis</i>	Macropterous
<i>Pasimachus depressus</i>	Brachypterous
<i>Pasimachus punctulatus</i>	Brachypterous
<i>Platynus decentis</i>	Brachypterous
<i>Poecilus lucublandus</i>	Macropterous
<i>Pterostichus coracinus</i>	Brachypterous
<i>Pterostichus moestus</i>	Brachypterous
<i>Pterostichus sculptus</i>	Brachypterous
<i>Rhadine caudata</i>	Brachypterous
<i>Scaphinotus andrewsii</i>	Brachypterous
<i>Scaphinotus unicolor</i>	Brachypterous
<i>Scaphinotus violaceus</i>	Brachypterous
<i>Scarites subterraneus</i>	Macropterous
<i>Selenophorus ellipticus</i>	Macropterous
<i>Sphaeroderus stenostomus</i>	Brachypterous

Table 7. Categorization for specialization by forest age for 37 carabid species where n>5.

See text for description of each category.

Species	Specialty Group
<i>Amara aenea</i>	Specialist
<i>Amara crassispina</i>	Specialist
<i>Amara familiaris</i>	Intermediate
<i>Amara impuncticollis</i>	Specialist
<i>Anisodactylus harrisii</i>	Specialist
<i>Anisodactylus rusticus</i>	Extreme Specialist
<i>Calathus opaculus</i>	Generalist
<i>Carabus goryi</i>	Generalist
<i>Carabus sylvosus</i>	Intermediate
<i>Chlaenius aestivus</i>	Extreme Generalist
<i>Chlaenius amoenus</i>	Generalist
<i>Chlaenius emarginatus</i>	Extreme Generalist
<i>Cicindela sexguttata</i>	Intermediate
<i>Cyclotrachelus freitaga</i>	Extreme Generalist
<i>Cyclotrachelus sigillatus</i>	Extreme Generalist
<i>Cyclotrachelus vinctus</i>	Extreme Generalist
<i>Cymindis americanus</i>	Extreme Generalist
<i>Dicaelus ambiguus</i>	Extreme Generalist
<i>Dicaelus dilatatus</i>	Generalist
<i>Dicaelus elongatus</i>	Intermediate
<i>Dicaelus politus</i>	Extreme Generalist
<i>Galerita bicolor</i>	Extreme Generalist
<i>Harpalus faunus</i>	Intermediate
<i>Harpalus herbivagus</i>	Extreme Specialist
<i>Harpalus pensylvanica</i>	Extreme Generalist
<i>Myas coracinus</i>	Specialist
<i>Pasimachus depressus</i>	Generalist
<i>Pasimachus punctulatus</i>	Intermediate
<i>Platynus decentis</i>	Intermediate
<i>Poecilus lucublandus</i>	Extreme Generalist
<i>Pterostichus coracinus</i>	Extreme Generalist
<i>Pterostichus moestus</i>	Extreme Specialist
<i>Pterostichus sculptus</i>	Extreme Generalist
<i>Rhadine caudata</i>	Specialist
<i>Scaphinotus andrewsii</i>	Intermediate
<i>Scarites subterraneus</i>	Intermediate
<i>Sphaeroderus stenostomus</i>	Extreme Generalist

Table 8. Carabid species that could potentially be indicator species for a stage(s) of Piedmont forest succession. Macropterous (M), Brachypterous (B).

Species	Forest Age	Total Abundance	Specialization	Wing state	Rarity
<i>Amara aenea</i>	0	24.02	Extreme Generalist	M	Rare
<i>Amara familiaris</i>	0	34.77	Intermediate	M	Common
<i>Carabus goryi</i>	0	38.05	Generalist	B	Common
<i>Harpalus herbivagus</i>	0	36.41	Extreme Specialist	M	Common
<i>Harpalus pensylvanica</i>	0	60.47	Extreme Generalist	M	Common
<i>Myas coracinus</i>	0	15.61	Specialist	B	Rare
<i>Pasimachus depressus</i>	0	19.16	Generalist	B	Rare
<i>Cyclotrachelus vinctus</i>	10	211.57	Extreme Generalist	B	Common
<i>Dicaelus ambiguus</i>	10	66.22	Extreme Generalist	B	Common
<i>Calathus opaculus</i>	50	134.77	Generalist	M	Common
<i>Cyclotrachelus freitaga</i>	50	63.75	Extreme Generalist	B	Common
<i>Dicaelus dilatatus</i>	50	43.35	Generalist	B	Common
<i>Pterostichus sculptus</i>	50	359.70	Intermediate	B	Dominant
<i>Galertia bicolor</i>	85	93.60	Extreme Generalist	M	Common
<i>Pterostichus coracinus</i>	85	61.06	Extreme Generalist	B	Common
<i>Pasimachus punctulatus</i>	0,10	13.42	Intermediate	B	Rare
<i>Platynus decentis</i>	50,85	19.13	Intermediate	B	Rare
<i>Dicaelus politus</i>	85,150	38.02	Extreme Generalist	B	Common

Figure 1a. Map of the 33 study sites.

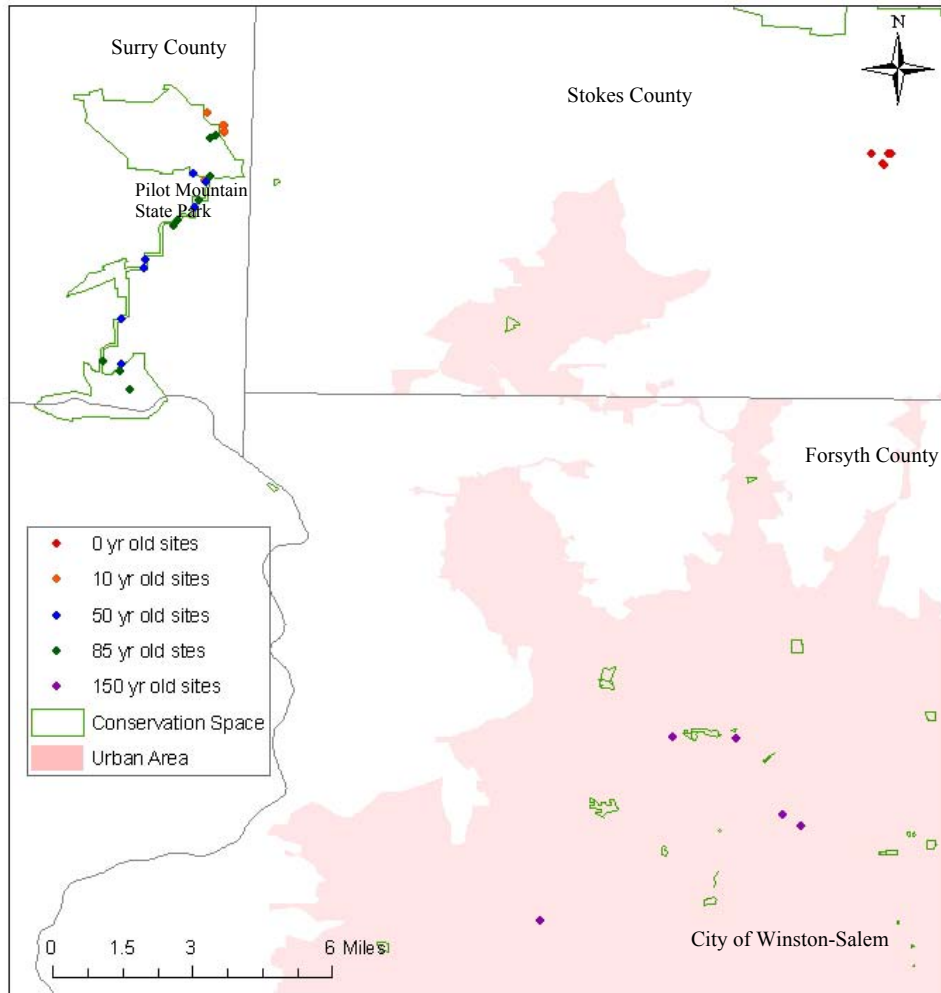


Figure 1b. Generalized diagram of pitfall trap (represented by hollow circles) array used at each study site.

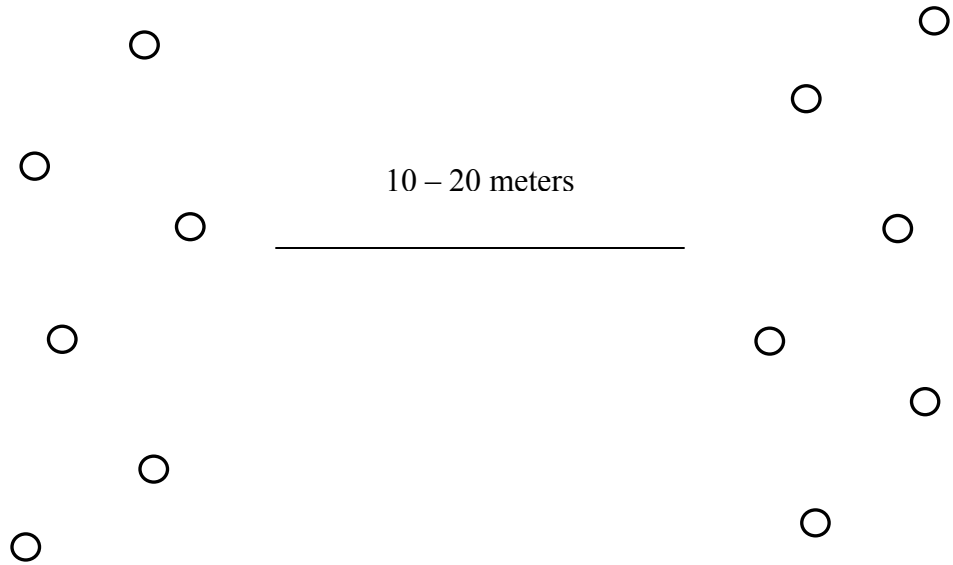


Figure 2. Mean abundance of carabid beetles for forest age classes. Statistically significant differences (ANOVA, $p < 0.01$, $\alpha = 0.05$) in abundance occurred for the 10 and 50 year forest classes compared to the 150 year old forest. Error bars represent 95% confidence intervals (CIs).

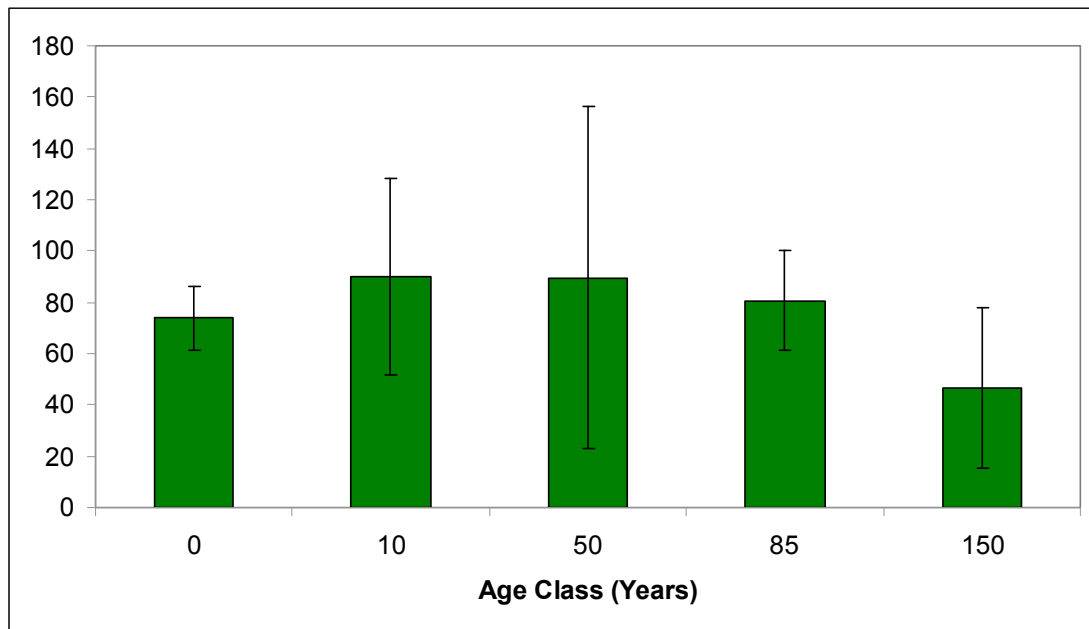


Figure 3. Average carabid species richness of five forest age classes. Error bars represent 95% confidence intervals (CIs) and stars denote significance ($p < 0.0007$). There was a negative correlation between mean species richness and forest age ($r = -0.939$, $p = 0.0178$).

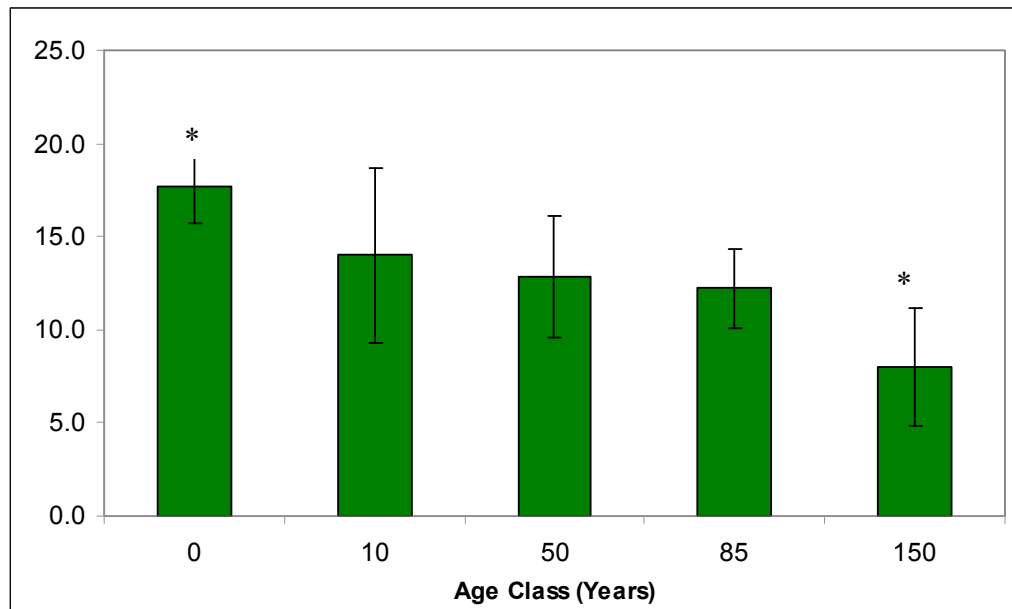


Figure 4. Average Shannon diversity index values for carabid beetles from five forest age classes. Error bars represent 95% confidence intervals (CIs) and stars denote significance from one another. Significant differences were detected between 0 and 150 year old forest classes ($p < 0.003$). There was a negative correlation between Shannon Diversity and forest age ($r = -0.903$, $p = 0.035$).



Figure 5. Simpson's diversity index of carabid beetle species for five forest age classes.

Error bars represent 95% confidence intervals (CIs) and stars denote significance.

Games-Howell (Games and Howell 1976) test revealed there was a significant difference

between the two extreme age classes ($p = 0.05$). There was a negative correlation

between Simpson's Diversity and forest age ($r = - 0.928, p = 0.023$).



Figure 6. Fisher's alpha diversity of carabid beetle species for five forest age classes.

Error bars represent 95% confidence intervals (CIs) and a star denotes significance ($p < 0.0001$) from other age classes.

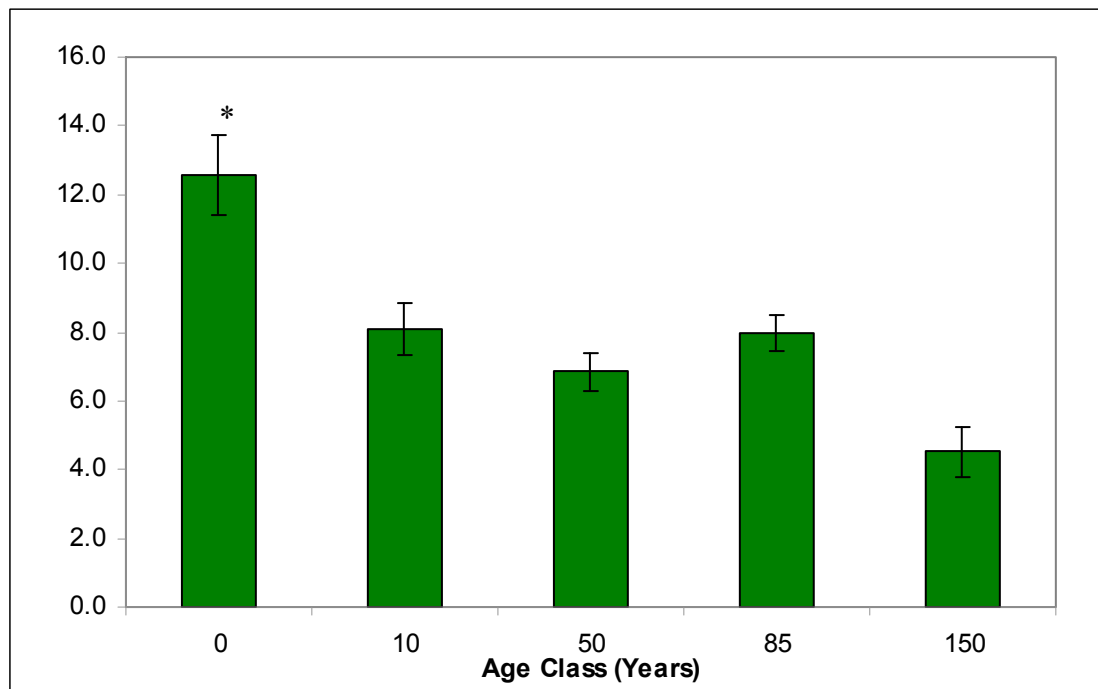


Figure 7. Dominance values of carabid beetle species for five forest age classes. Error bars represent 95% confidence intervals (CIs) and stars denote significance ($p < 0.005$).

Dominance was positively correlated with forest age ($r = 0.888$, $p = 0.04$).

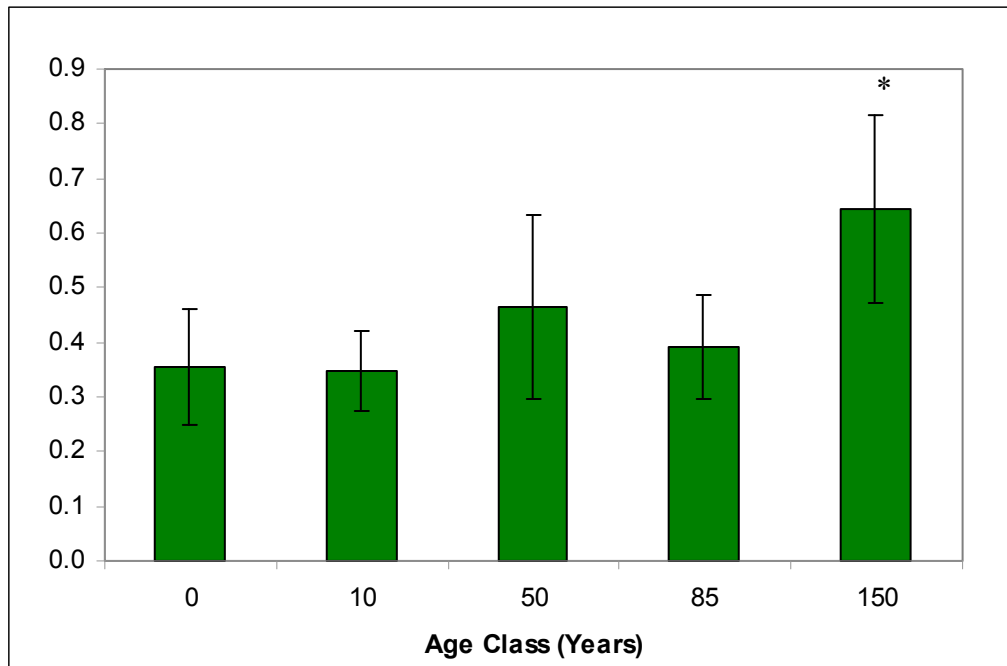


Figure 8. Carabid beetle species accumulation curves for five forest age classes. Vertical line indicates species richness of each curve at $n = 236$ individuals.

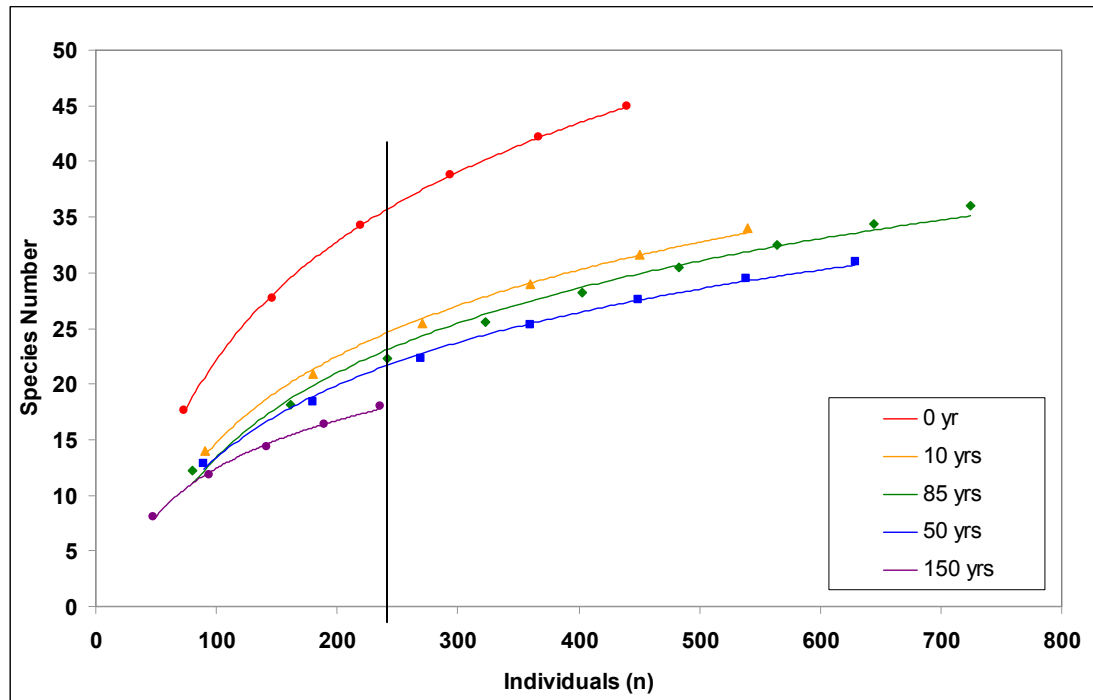


Figure 9. Species accumulation curves for the five forest classes with 150 year old age class projected to n = 440 individuals. Curves are significantly different ($\chi^2 = 0.05$).

Vertical line indicates where n = 440 individuals.

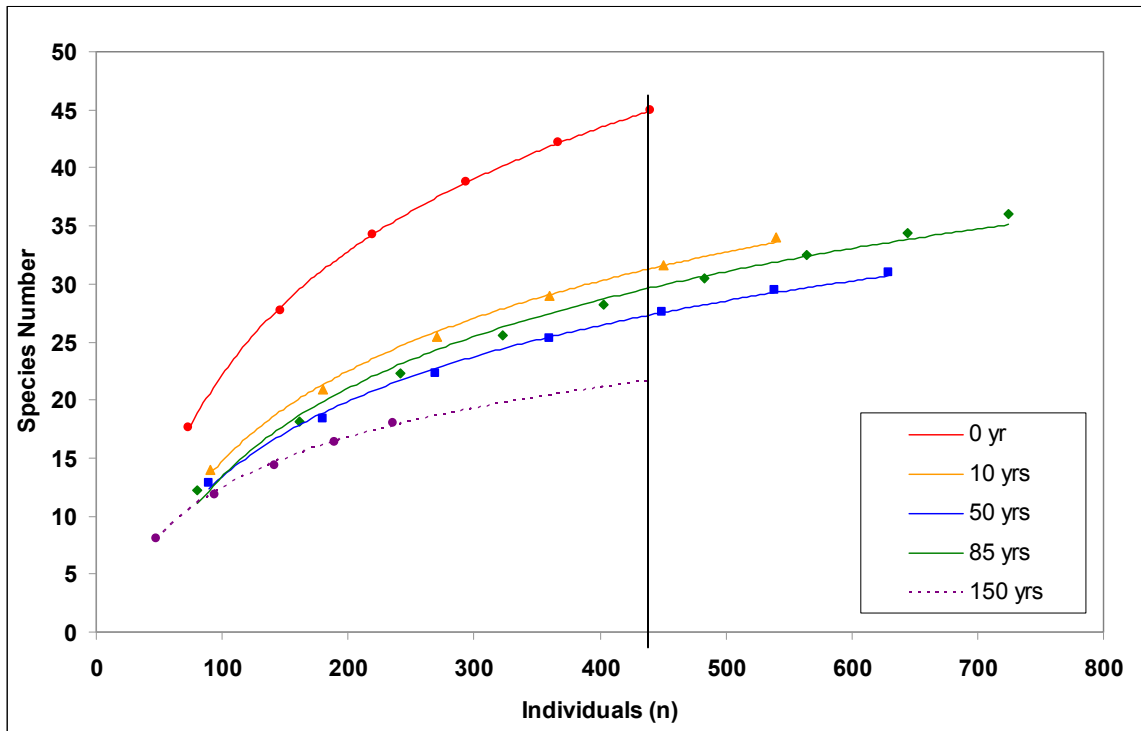


Figure 10. Relative abundance (log values) of all carabid beetle species (n = 66) in relation to the 33 study sites (representing all forest age classes).

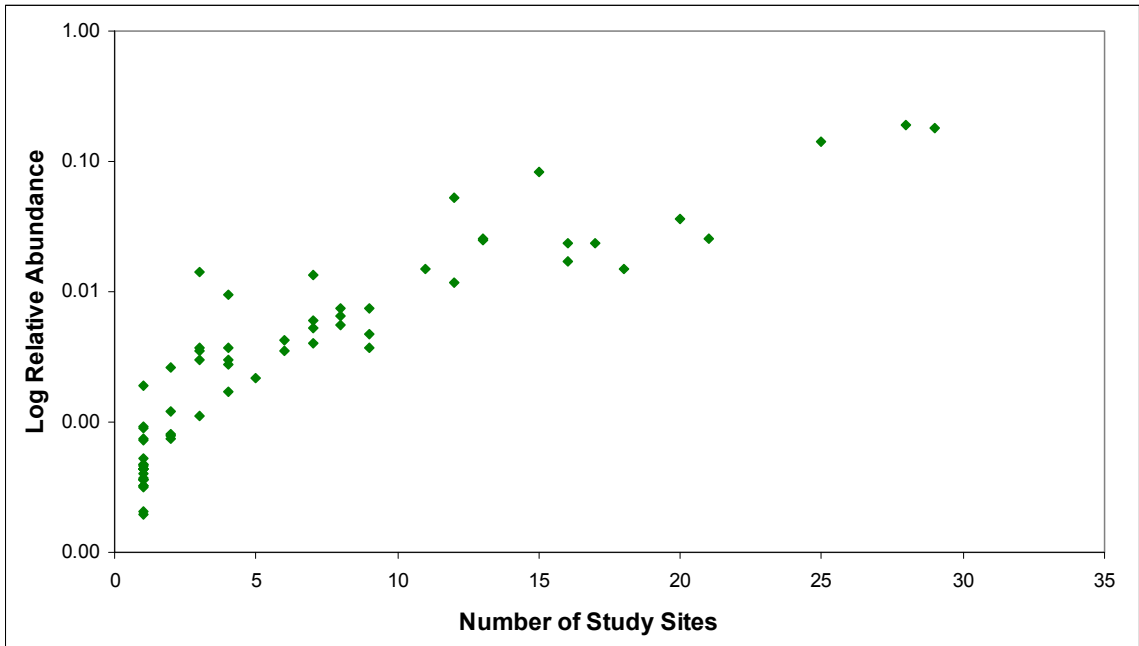
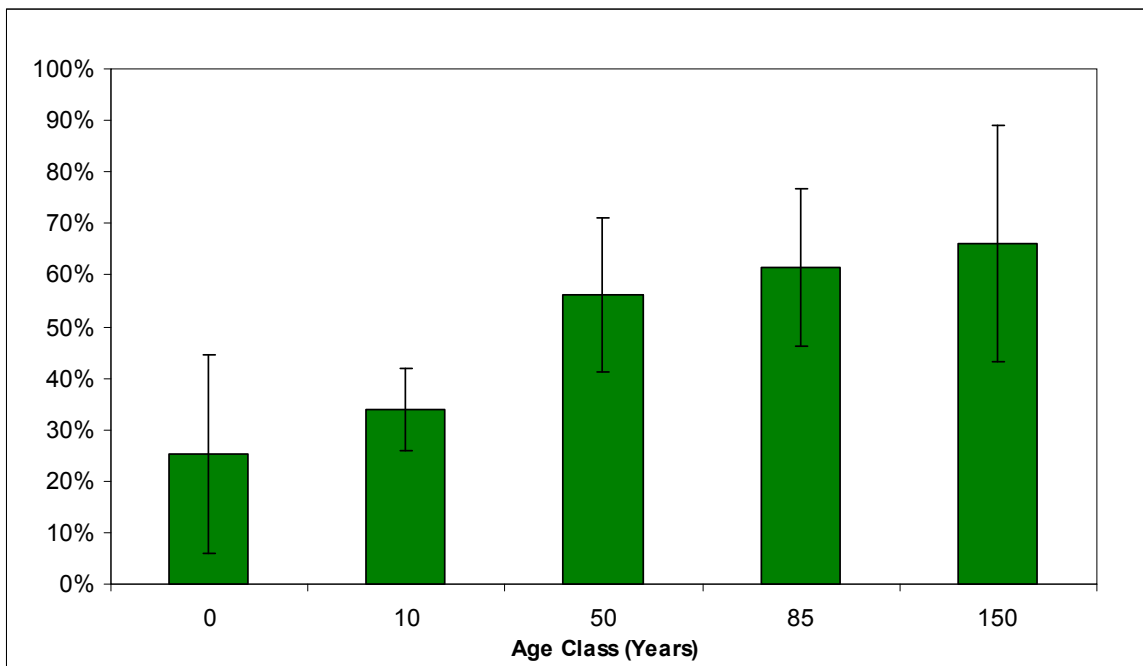


Figure 11. Contribution of three dominant species (*Cyclotrachelus sigillatus*, *Pterostichus sculptus*, and *Sphaeroderus stenostomus*) to the overall carabid catch for the five forest age classes. There is a strong positive correlation ($r = 0.902$, $p < 0.05$) between forest age and the percent catch comprised by the dominant species.



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Figure 12. Number of carabid beetle species for five forest age classes for six ecological/taxonomic classifications (see text for definitions of each classification).

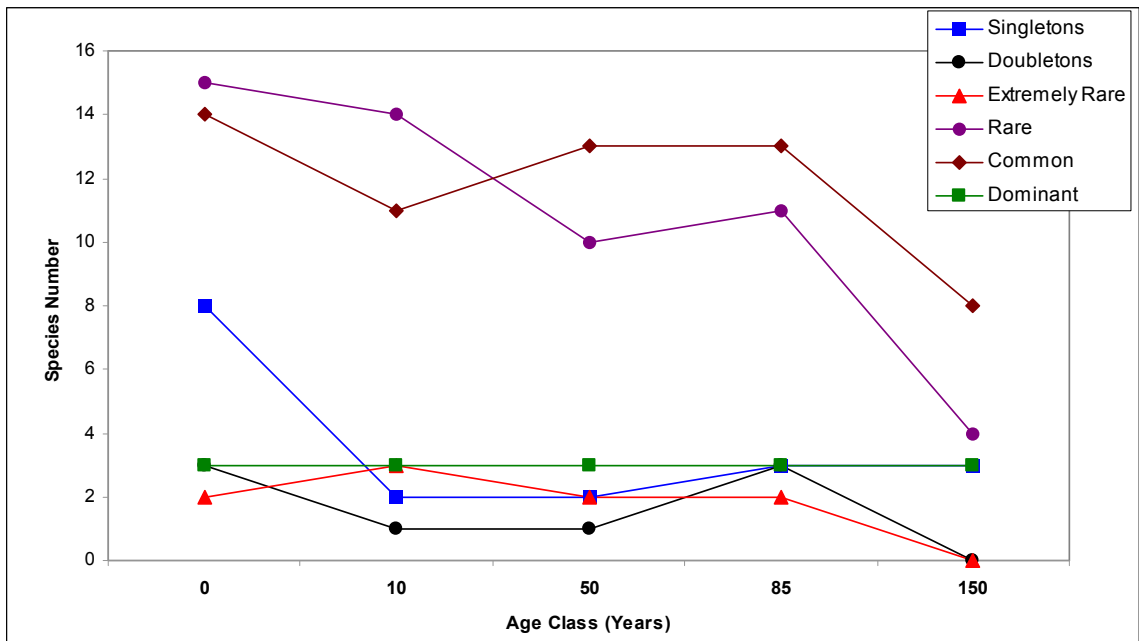


Figure 13. Results of Non-Metric Multidimensional Scaling (NMDS) analysis for 33 sample sites. The analysis was based on the 17 most common carabid beetle species from five forest age classes (0, 10, 50, 85 and 150 years). Each the five polygons represent different forest age classes, as indicated by different color shades.

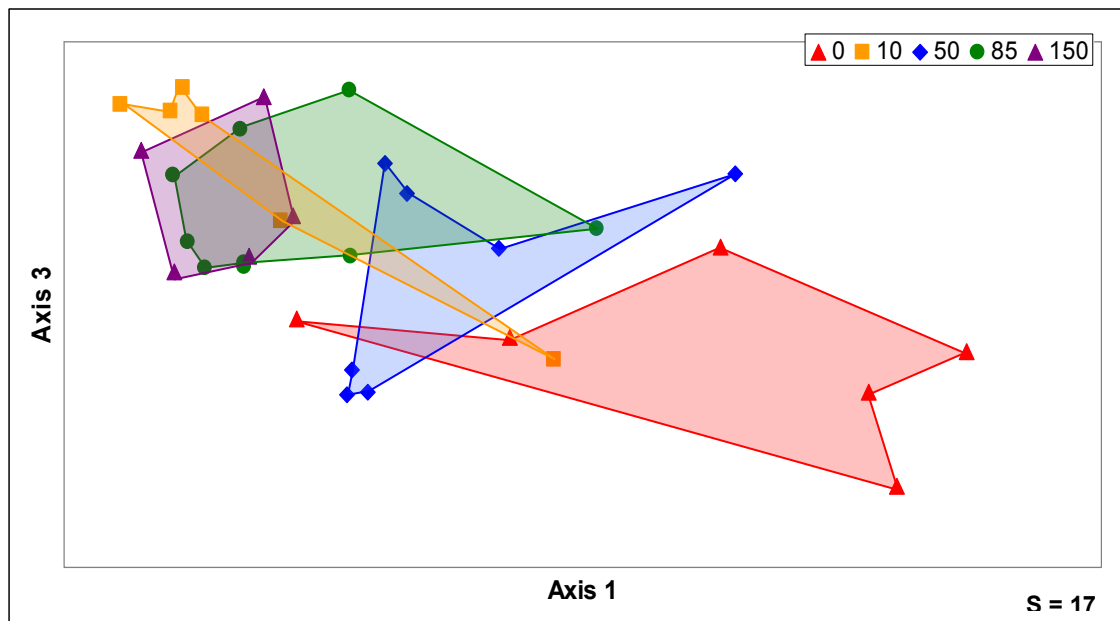


Figure 14. Results of Non-Metric Multidimensional Scaling (NMDS) analysis for 33 sample sites with selected carabid species depicted in relation to the position in ordination space for forest age replicates. The analysis was based on the 17 most common carabid beetle species from five forest age classes. Color scheme depicting forest age is the same as that in Figure 13.

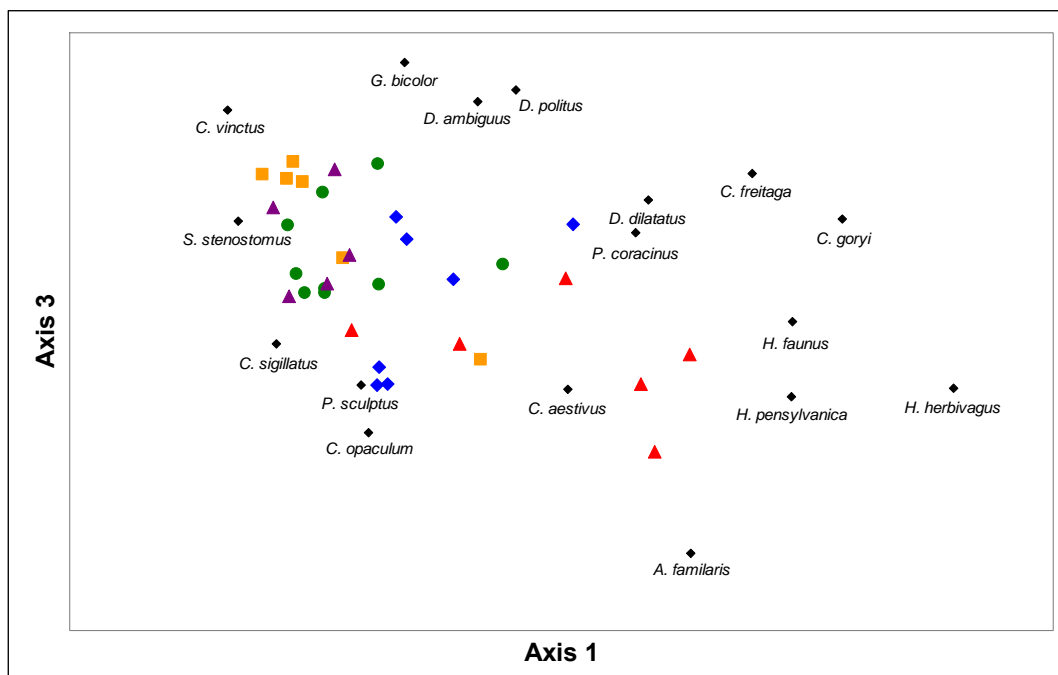


Figure 15. Results of DCA ordination based on presence/absence of carabid species for the 33 study sites plotted against the two most relevant axes. Color scheme depicting forest age is the same as in Figure 13.

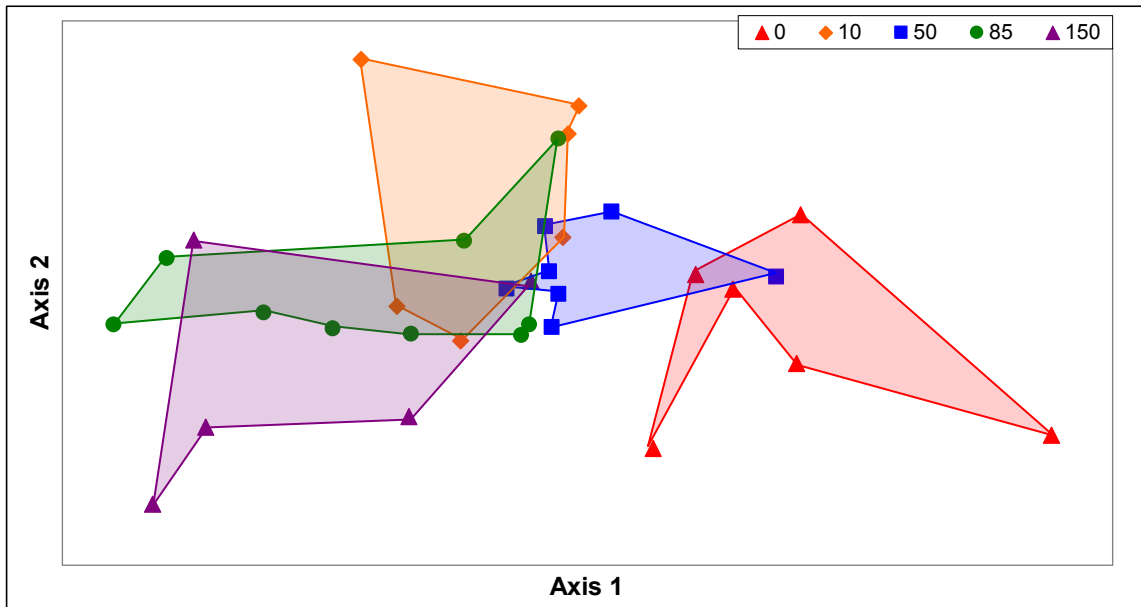


Figure 16. Wing state of 66 Carabidae species sampled from the combined forest age classes. Brachypterous species are considered to be incapable of flight while macropterous species have the potential to fly.

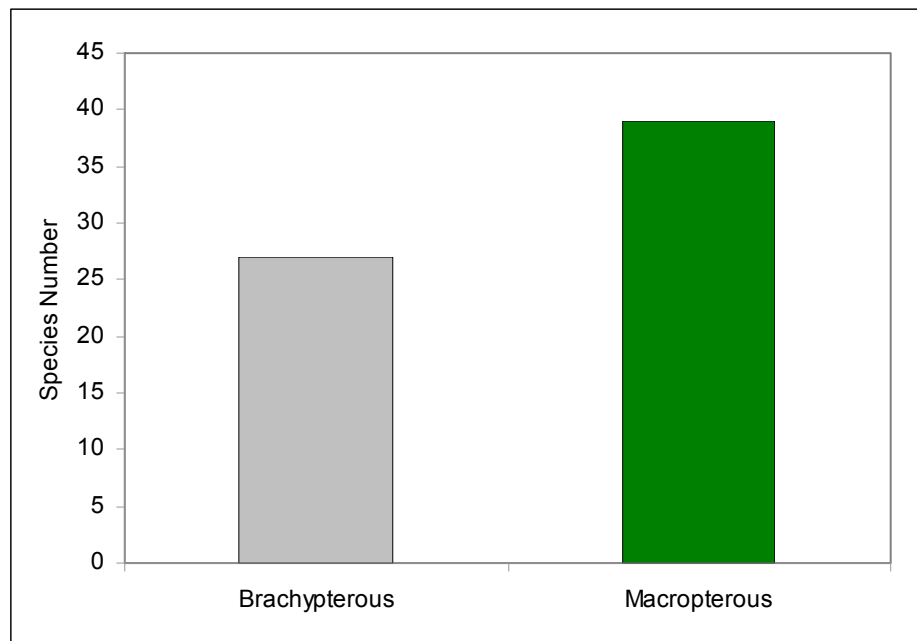


Figure 17. Proportion of carabid population that is brachypterous or macropterous in five forest age classes. Significant differences occurred for all forest age classes except the zero age class ($\chi^2 \leq 0.05$).

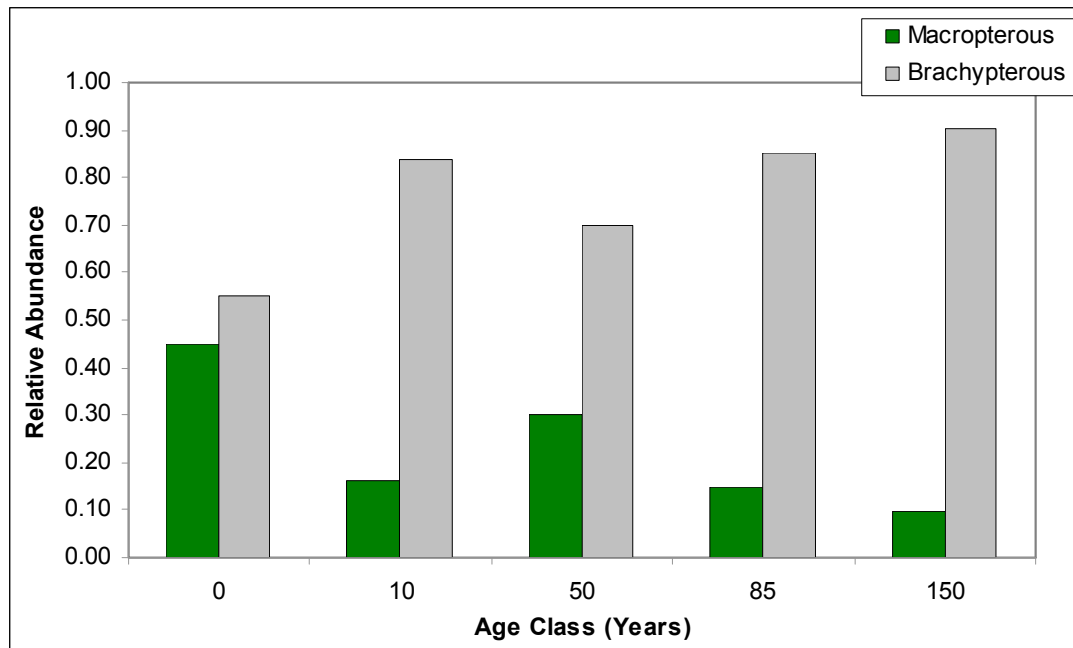


Figure 18. Ecological habitat classifications for carabid beetle species (n = 66) collected from five forest age classes. See text for classification parameters.

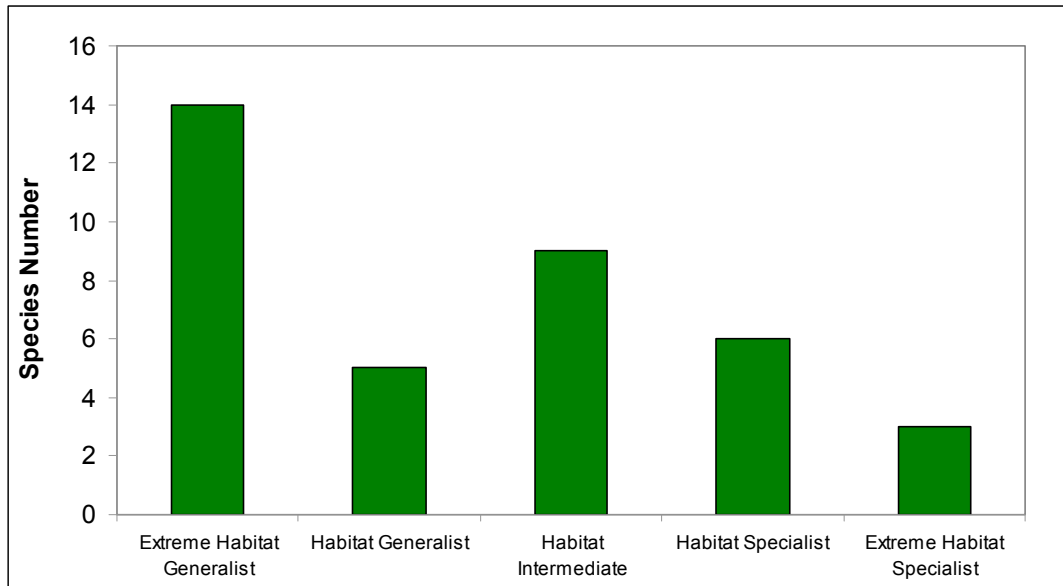
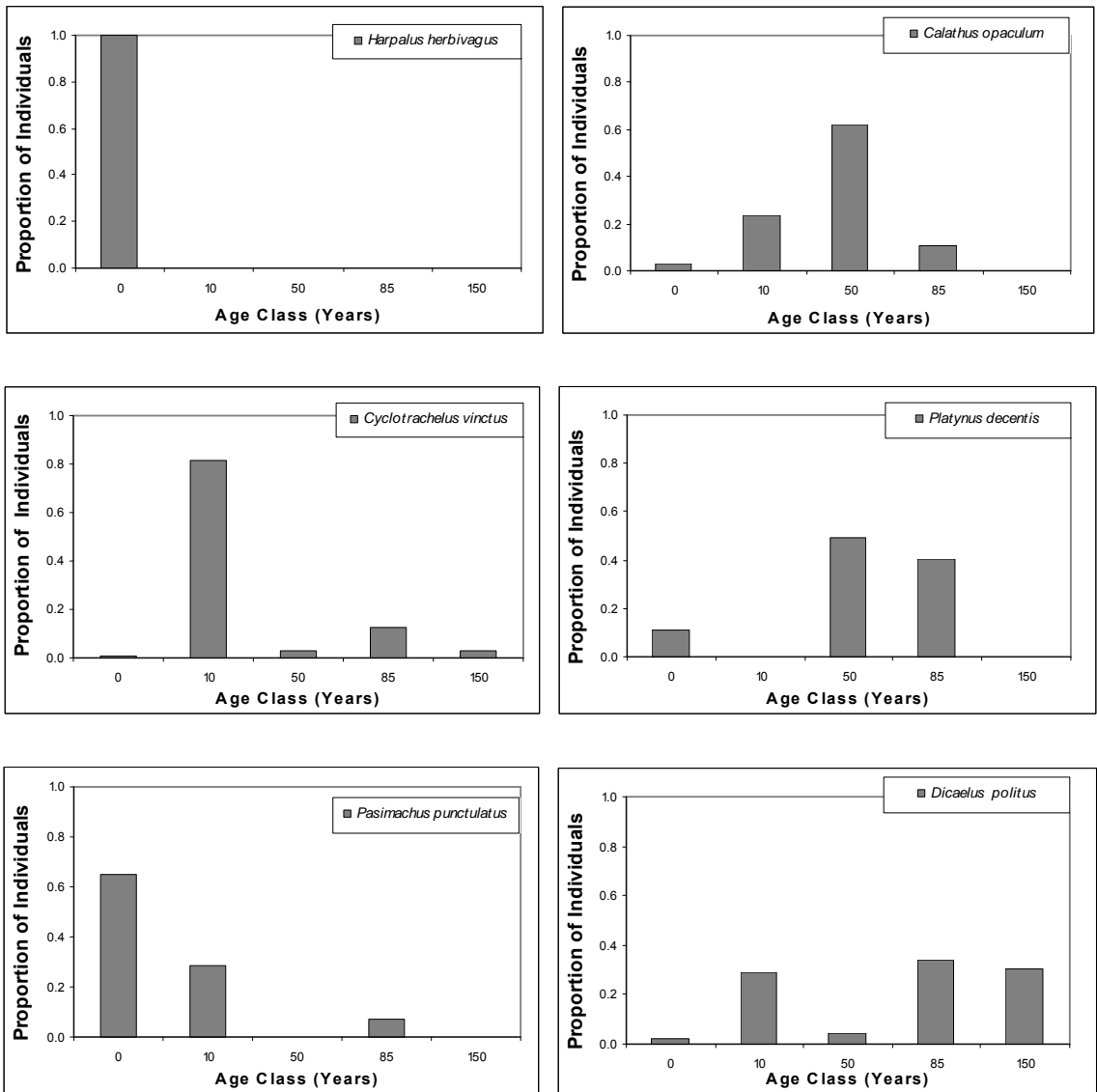


Figure 19. Relative abundance across the forest age gradient for one representative species from each of the six indicator classes (See text for definition of indicator classes).

See Table 8 for information on each of the 18 indicator candidates.



SCHOLASTIC VITA

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