PRE-TREATMENT ASSEMBLAGES OF WOOD-BORING BEETLES (COLEOPTERA: BUPRESTIDAE, CERAMBYCIDAE) OF THE HARDWOOD ECOSYSTEM EXPERIMENT

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Abstract.—Longhorned beetles are a diverse and important group of insects in forest ecosystems; several species attack weakened or stressed trees, relatively few attack healthy trees, and most species use only dead and decomposing wood. We surveyed longhorned beetles and metallic wood-boring beetles using four different types of traps at 36 Hardwood Ecosystem Experiment (Indiana) locations that spanned all silvicultural treatments from 2006 through 2008. During two of these pre-treatment years we conducted surveys on sites destined to be within treatment areas, and in one year we sampled within the landscape outside the treated areas. We found no differences in the species richness or diversity between sites destined for future treatments. We identified a difference between future treatment and non-treatment sites that appeared to be caused by sampling them in different years. We discuss the importance of taking generation times of the species into account in future surveys.

INTRODUCTION

The hardwood forests of Indiana are one of the state's greatest natural resources. Indiana's forests support nearly 130,000 workers and provide an estimated $17 billion annually in state revenue (Indiana Department of Natural Resources-Division of Forestry 2010). Additionally, the hardwood industry in Indiana consistently rates as one of the most important elements of the state's economy (e.g., Piva and Gallion 2007). Understanding how to best manage the wood resource is an important issue facing Indiana foresters, especially when the introduction of invasive species already threatens the balance and stability of the state's forests. The Asian longhorned beetle (*Anoplophora glabripennis* Motschulsky) alone has cost close to $400 million to control in its first decade in North America (Haack et al. 2010), and the emerald ash borer (*Agrilus planipennis* Fairmaire) has killed millions of ash (*Fraxinus*) trees in both natural and urban environments throughout northeastern North America (Poland and McCullough 2006). The need to improve management strategies concerning invasive species is clear, but the basic knowledge of how biogeography, biodiversity, landscape structure, and land management impact the establishment and spread of exotic species—and endemic species—is incomplete (Turner 2005). Knowledge of how both pest and non-pest xylophagous beetles respond to different forest management systems will be crucial for safeguarding the hardwood industry in Indiana.

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Longhorned beetles (Coleoptera: Cerambycidae) can have a large impact on this industry by killing valuable hardwood trees and degrading lumber (Linsley 1959). For example, larvae of the red oak borer (*Enaphalodes rufulus* Haldeman) thrive in stressed oak (*Quercus*) trees, and recent evidence shows that it may also successfully complete development in healthy oaks (Fierke et al. 2005). This beetle was a major factor in the widespread mortality of oaks in the Ozark National Forest of Arkansas (Haavik et al. 2010, Heitzman 2003). Painted hickory borer larvae (*Megacyllene caryae* Gahan) infest recently cut or killed hickory (*Carya*) (Craighead 1950) and can reach high densities within the wood (Holland 2009a), greatly degrading the value of lumber because of the extensive galleries they excavate throughout both sapwood and heartwood (Blatchley 1910, Craighead 1950). Similar damage from galleries of *E. rufulus* greatly reduces lumber value in oak (Donley 1974). Approximately one-quarter of the species of longhorned beetles in Indiana are considered pest species that cause ecological and economic losses.

Metallic wood-boring beetles (Coleoptera: Buprestidae) have a life history similar to longhorned beetles, but a larger proportion of species that are pests on living trees. Most species of Buprestidae attack weakened, dying, or recently dead trees. Females generally lay eggs singly or in small clusters in crevices on the bark of a host tree. Eggs hatch and larvae bore through the bark to the interface of the sapwood and cambial tissue, where a majority of larvae remain and feed (Drooz 1985). Some genera, such as *Dicerca* and *Texania*, usually mine through both the sapwood and heartwood of their respective hosts. Once ready to pupate, larvae of some species construct a pupal chamber just under the bark and overwinter there, while others create a chamber in the sapwood near the bark. The next spring, after pupation occurs, adults emerge by chewing through the bark, usually leaving a D-shaped exit hole (Solomon 1995). Not all genera or species in a genus are restricted to tree trunks, and they do not necessarily need a stressed host. *Brachys* and *Taphrocerus* larvae, for example, are leaf miners and feed between the upper and lower dermal layers of leaves (Bright 1987).

The ecological and economic impacts of some wood-boring beetles that attack living and recently cut trees and lumber are important, but most species are not pests (Evans et al. 2004). Rather, larvae of many species develop within decaying wood, often logs on forest floors or dead limbs and twigs on standing trees. These insects using dead wood make up an important and diverse component of forest biodiversity. By decomposing dead wood in forests, these species may contribute to nutrient cycling and to reducing the severity of forest fires by hastening decomposition of coarse woody debris (Gutowski 1987). It has even been suggested that wood-feeding insects can aid in forest productivity by cycling nutrients from weakened trees to the soil and thence to vigorous trees (Berryman 1986). Larvae of many species provide food for both invertebrate and vertebrate animals and create habitat for many species within dead wood (e.g., Holland 2009a). When adult beetles disperse and mate, many species act as pollinators while seeking floral resources (Linsley 1961) and are commonly collected on flowers (e.g., Bond and Philips 1999, Gosling 1984, Ødegaard and Frame 2007).

Different forestry management regimes influence the composition and abundance of wood-boring beetles in forests. Wood-boring beetles respond readily to disturbances such as fire and windthrow (Allison et al. 2004, Hopkin et al. 2001). Beneficial wood-boring beetles that provide ecosystem services are more abundant in managed forest areas where harvesting has left slash and dead wood. A study on the saproxylic beetles (those dependent on dead wood) in Australia showed that many species found within the old-growth assemblage did not persist in regrowth forests that had been logged (Grove 2002a). Some species of wood-boring beetles may increase in abundance

following management operations that either leave abundant freshly killed wood or alter environmental conditions and place stress on surrounding uncut trees. Other studies have shown that many non-pest species, whose major role is decomposition of dead wood and pollination, may be negatively influenced by forest management. Nonetheless, many species appear to prefer habitat with some canopy openings (Barbalat 1998).

It would be beneficial to understand how different forest management strategies affect both pests and non-pest species that play roles in ecosystem services (Gutowski 1987). There is much recent interest in northern Europe in conserving remaining saproxylic insects. Much of the region has a long history of intensive management that has greatly reduced coarse woody debris and thereby threatened many species (McGeoch et al. 2007). Ten longhorned beetle species are listed on the International Union for Conservation of Nature (IUCN) Red List of endangered species (IUCN 2010).

Adults of some wood-boring beetles, such as longhorned beetles in the genus *Saperda*, prefer forest edges (Hammond 1997). Within forests, species richness and abundance of both longhorned beetles and metallic wood-boring beetles are higher near clearings (Barbalat 1996). Forestry operations that create edge habitat and openings may lead to an increase in the abundance of several species. Forest harvest operations can also influence the abundance of longhorned beetles by altering the amount of dead wood available for larval development. Harvesting creates a large sudden input of dead wood in the harvest area that slowly decreases over time as it decays. Ulyshen et al. (2004) found that the abundance and diversity of several saproxylic beetle families including cerambycids initially increased in small openings of 0.13-0.5 ha, above the levels seen in surrounding forests. However, 6-year-old clearings had a fauna that was reduced below that of the surrounding forest.

Openings from forest operations can also increase the habitat quality for many species of saproxylic beetles (Barbalat 1996) by increasing light penetration (Barbalat 1998). Finally, harvest openings have the effect of lowering the forest mantle within the harvest area. Wermelinger et al. (2007) define the forest mantle as the outer surface layer of the three-dimensional forest volume, and found that most cerambycids tended to be caught in the lower mantle and open areas. The variety of responses within the wood-boring beetles to different habitat types, and climatic conditions caused by gaps and edges, may be partially responsible for the variation in the response to forest disturbance seen within this group (e.g., Saint-Germain and Drapeau 2011).

The main factor influencing the occurrence of species of xylophagous beetles is host plant presence (Barbalat 1998). Different tree species vary in the richness of their associated wood-boring fauna (Barbalat 1998). Forest management operations that selectively promote or remove some tree species over others may influence the species richness and compositions of the native saproxylic communities. Selective operations will have a larger influence on the wood-boring species that attack and develop within living trees than on those species that develop within decayed wood, as the former are more host-tree specific (Hanks 1999, Linsley 1959).

The presence of suitable larval substrate is one necessary condition for a wood-boring species to be present; another is that adults must have the ability to reach the area containing the substrate (Grove 2002b). Forest fragmentation has extirpated at least one species of longhorned beetle from a large part of the host plant range, which includes much of Indiana (Holland 2009b,c). At smaller scales, saproxylic beetles respond to the connectedness of the network of dead wood on the forest floor within 150 m of surveyed points (Schiegg 2000). The movement abilities of longhorned beetles vary greatly, from flightless species that may move 100 m in 10 days (Baur et al. 2002) to some that

can track host plant volatiles over a distance of >0.8 km in less than an hour (Beeson 1930).

Several terrestrial insect groups including wood-boring beetles are considered to be important bioindicators of forest health and the effects of ecosystem management. Indications of forest ecosystem health and the effects of management can be assessed by studying changes in the density and species composition of these insect populations (Werner 1996). Longhorned beetles and metallic wood-boring beetles are considered to be among the most important indicators of biodiversity in forest ecosystems because of their diversity, specific habitats, and tree host species (Speight 1989). Because of this indicator value, along with the diversity of roles wood-boring beetles play both as pests and as beneficial insects, these beetles are an ideal group for studying the impact of timber harvesting practices on forest biota.

Our objective in this study was to determine the species of longhorned beetles and metallic wood-boring beetles present at the study sites of the Hardwood Ecosystem Experiment (HEE) before harvests were initiated. We tested the hypothesis that there was no difference in these beetle assemblages between the different (future) harvest types before treatment began, and the hypothesis that there was no difference between the beetle assemblages of future harvest and non-harvest areas. Differences in the guilds of wood-borers (e.g., species that develop in live trees versus rotting wood) will be the focus of future publications. A second objective was to determine how species with generation times greater than 1 year could explain any differences found.

STUDY AREA

All nine research cores making up the HEE were surveyed in the wood-boring beetle study. These replicated landscapes are each 78-110 ha of forest within Yellowwood State Forest or Morgan-Monroe State Forest in Indiana (Kalb and Mycroft, this publication). Three of these research cores were designated for treatment with one of the three types of silvicultural regeneration systems, no-harvest controls, uneven-aged management, and even-aged management, so that each system was replicated three times. To eliminate neighborhood effects each research core, regardless of the treatment, was surrounded with an approximately 300-ha buffer wherein single-tree and small-group selection harvests occurred. Within the even-aged research cores there were four intensive sampling units (ISUs) of approximately 4 ha each that would later be subjected to either clearcutting or shelterwood harvest (Fig. 1). These ISUs are so named because efforts to study the effects of harvest treatments are focused within them, although not exclusively.

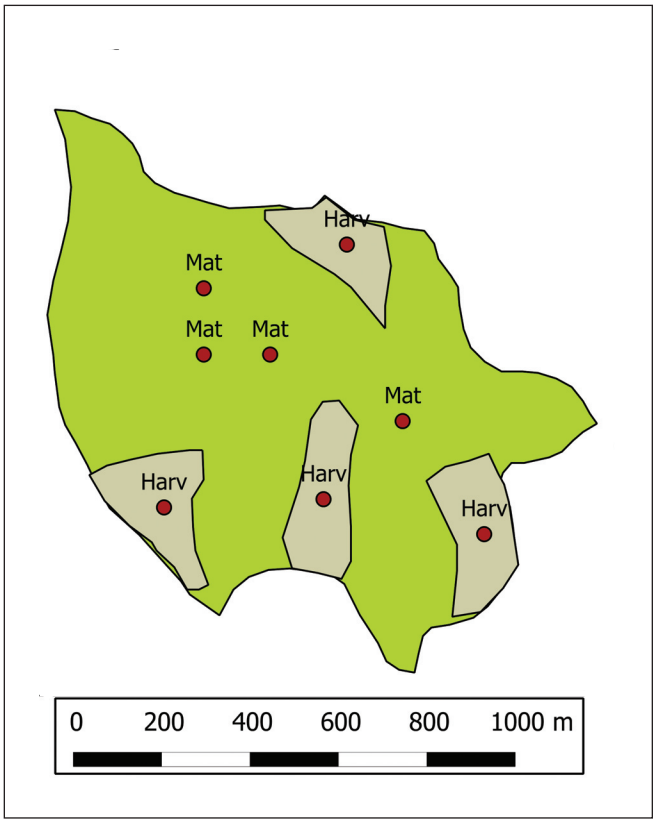

Figure 1.—Example research core showing location of intensive sampling units (ISUs) and beetle trap array locations. This even-aged research core (green) contains four 4-ha clearcuts (gray). Arrays within harvested ISUs (sampled in 2006 and 2007) are indicated by a circle labeled Harv. Arrays within the matrix (sampled in 2008) outside ISUs are indicated by a circle labeled Mat. Surrounding buffer area is not shown.

One ISU of each treatment was located on north- to east-facing slopes and one of each treatment was located on south- to west-facing slopes. The uneven-aged research cores contained eight ISUs of 0.5-2.0 ha that were later subjected to harvest. These smaller openings would rarely span ridge top to ridge bottom, and were therefore stratified across physiographic locations. The uneven-aged research cores also were subjected to single-tree harvest throughout the unit. The control units had four ISUs where no timber harvesting was to be carried out, and these also were stratified evenly among north- to east- and south- to west-facing slopes. We placed one array of traps within each of the four ISUs within all even-aged and control research cores (Fig. 1), and within four of the eight ISUs within each uneven-aged research core. Additional details on the HEE study design can be found in Kalb and Mycroft (this publication).

MATERIALS AND METHODS

Trap arrays in 2006 and 2007 within each ISU were approximately centered on the bird survey tree closest to the center of the unit (Kalb and Mycroft, this publication). Traps were randomly designated to a cardinal direction and placed approximately 20 m from the tree in this direction. They were hung so that the bottom of the trap was 1.5-2 m above the ground. The four traps making up each array were: one Lindgren multiple-funnel trap (12 funnel model; Pherotech, Delta, BC), one Panel Trap for Bark Beetles (Alpha Scents, Portland, OR), one intersecting pane window trap of our own design, and one linear purple sticky trap modeled after Oliver et al. (2005). For details on traps see Holland (2010).

We used 0.61m x 0.61m rain covers on the first three trap types, as we have found that covers greatly reduce dilution of trap fluid by rain. On each trap except the purple trap, we hung a 125-ml Nalgene bottle containing 60 ml of 99 percent ethanol that evaporated out of four 2-mm holes in the top. The beetles are assumed to be responding to the ethanol lure (Montgomery and Wargo 1983) and the dark vertical silhouette of the trap (Lindgren 1983), but it is possible that some species are not able to use primary attraction to assess individual trees for suitability (Saint-Germain et al. 2006, 2007a). The collection jar used for all but the purple traps had many centimeters of ethylene glycol to kill and preserve the beetles. A few drops of liquid soap were added to the killing fluid in each trap to limit its surface tension. Purple traps were covered with clear plastic sheeting before being coated with Tangle Trap (Tanglefoot Co., Grand Rapids, MI).

In 2008, we followed the same sampling methods but located trapping arrays outside the ISUs where the initial harvest treatments were to take place. These traps are considered to be located within the matrix of each research core. These arrays were used to examine the changes in beetle assemblages in the larger landscape outside of harvests. They were located at bird survey points that were at least 200 m from any treatment area, 50 m from any road or trail, and 100 m from any previously surveyed beetle point. Within each research core, we randomly selected four bird survey points from those that met these criteria.

Every 3 weeks we removed all insects from the traps. The plastic sheet on the purple sticky traps was removed and replaced with a new sheet. All longhorned beetles and metallic wood-boring beetles were removed from the catch in the laboratory, pinned, and identified using guides or keys by Lingafelter (2007), Linsley (1962a,b; 1963; 1964), Linsley and Chemsak (1972, 1976), and Yanega (1996). Buprestidae were identified using keys by Downie and Arnett (1996), Fisher (1928, 1942), and Wellso and Manley (2007). All specimens currently reside in the insect collection of the Biodiversity and Landscape Ecology Laboratory in the Department of Entomology at Purdue University.

We used adonis in the vegan package (Oksanen et al. 2011) for R (R Development Core Team 2010) to compare the beetle assemblages between research

cores with different planned harvest techniques. Adonis is a multivariate analysis of variance (ANOVA) that uses distance matrices and tests for differences using permutation (Oksanen et al. 2011). We used 1,000 permutations of the data to generate the null distribution and constrained the permutation according to year. In addition, we included in the adonis model a term to compare the beetle assemblages of sites within the sites destined for future harvests (all ISU regardless of planned harvest technique) and sites outside the future harvests. We label these latter sites matrix sites. The model included a year term as well.

For each site we summed the abundances of each species within each trapping array and within each year. We therefore did these analyses with 108 array-years: 3 yr x 9 units x 4 arrays/unit. Cerambycidae and Buprestidae species that were found at fewer than 5 percent ($n<6$) of the locations across the 3 pre-treatment years were omitted from the multivariate adonis tests for statistical reasons. Because we did not dissect logs to ensure the species caught were actually using the host wood material in the immediate area (Saint-Germain et al. 2007b), it is possible that these less commonly captured species were incidental. We then calculated the Bray-Curtis similarity on square root abundance for the remaining species. We did not standardize, so more abundant species have a larger influence on the similarity measure.

To visualize the differences in groups, we performed a non-metric multi-dimensional scaling (NMDS) on the square root abundances of all species caught using the package MASS (Venables and Ripley 2002) in R. To determine the species that were driving differences between the sampled assemblages, we used a custom R function to perform a similarities percentage (SIMPER) analysis (Clarke and Warwick 2001). This procedure uses the contribution of each species to the Bray-Curtis dissimilarity measure to determine species that are largely responsible for separating groups. If there were pair-wise differences between the assemblages at sites destined for different treatments, we used an iterative procedure to determine the subset of species causing the differences. We first removed the species that most contributed to the dissimilarity. This process was repeated until the treatments were not significantly different and the species thus removed were considered the major drivers of the differences. We then examined the generation time of the species in this subset.

Shannon diversity was calculated for all sites using the vegan package in R. We included all species in this diversity calculation and so may include some incidental captures. We used ANOVA to test for differences in diversity and species richness between the future treatment groups. We used the vegan package in R to plot a species accumulation curve, to determine how well our sampling captured the majority of species present.

RESULTS

We caught 2,058 individuals from 6 subfamiles and 85 species of longhorned beetles and 400 individuals from 17 species of metallic wood-boring beetles. We did not detect any species that are recent exotic invasive species. Some species are exotics that have been in North America for a considerable time (e.g., *Xylotrechus colonus*) and are likely now considered well established and a permanent component of the fauna. The shorter period of sampling in 2006 led to lower numbers in that year.

The species accumulation curve showed that the species richness of wood-boring beetles was leveling off (Fig. 2), suggesting that the sampling effort was adequate for determining most of the species present. There were no differences among trapping arrays of future harvest treatments (control, even-aged management, uneven-aged management) within the research cores ($p>0.05$, Fig. 3A). However, adonis did reveal differences between the assemblages of future harvest sites (ISU) and matrix sites ($p < 0.05$, Fig. 3B).

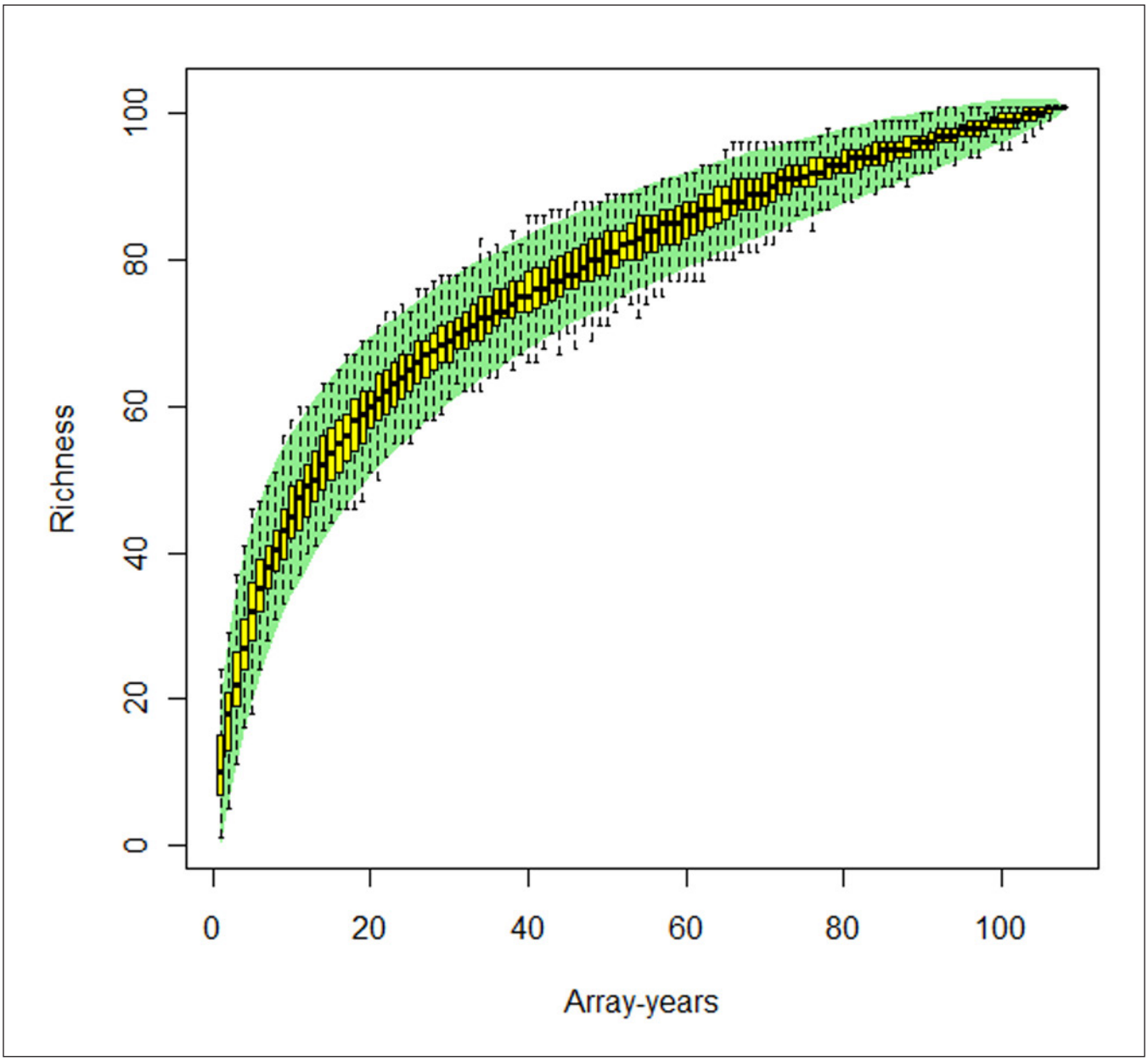

Figure 2.—Species accumulation curve for the 108 site-years sampled within the pre-treatment study. Sampling effort is given as total array-years. Boxes are first and third quartiles and whiskers are range, all derived from randomizing the order of including site-year data. A total of 102 species were identified.

These differences appear to be a result of logistical constraints forcing us to sample harvest and matrix sites in different years.

A year term in the adonis model revealed that year may be a factor behind changes in the community assemblage ($p < 0.05$, Fig. 3C). The betadisper function in the vegan package revealed overdispersion in the 2006 data compared to the other years ($df = 2,105$, $F = 17.3$, Tukey post-hoc comparisons: 2006-07: $p < 0.0001$; 2006-08: $p = 0.0005$; 2007-08: $p = 0.15$). This result was not altered by using Jaccard's dissimilarity on presence-absence data. We attempted to remove the heterogeneity of dispersion by including only species caught during the 2006 season, but doing so did not alter the

results or cure the dispersion heterogeneity. We were able to compare future harvest and matrix sites by comparing only the 2007 and 2008 data. This adonis test revealed that assemblages differed according to future treatment (df = 2, F = 1.6, p = 0.016).

The arrays differed in species assemblage when grouped by year sampled, and therefore also when grouped into ISU or matrix sites. The species that contributed to these differences are listed in Table 1. At least half of these 14 species have, or may have,

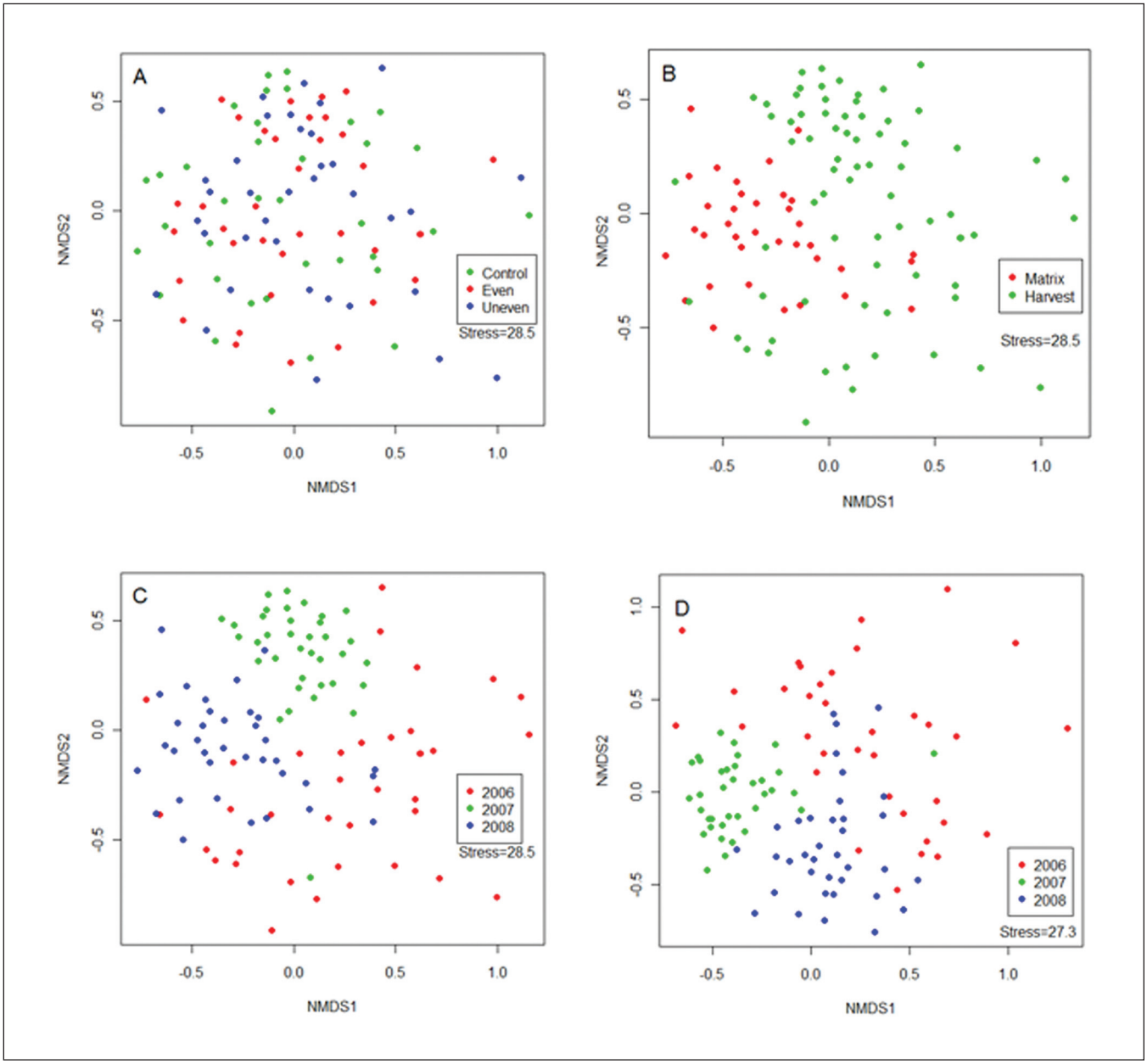

Figure 3.—Non-metric multidimensional scaling plots of 108 site-year samples where wood-boring beetles were sampled, using data from those species found at greater than 5 sites. Plots (A) through (C) represent the relative inter-sample dissimilarities of each site-year in 44-dimensional species-space. Plot (A) has samples coded according to the three future treatments: control, even-aged management, and uneven-aged management. Plot (B) has sites coded according to whether they are located in future matrix (not harvested) sites or future harvest sites. Plot (C) shows samples according to the year in which they were obtained. Plot (D) is an ordination showing the relative location of all 108 sites using only the subset of species (n=14) found by the SIMPER analysis to be driving the differences between years.

Table 1.—The 14 species of wood-boring beetles that account for the differences among species assemblages between years. At least half of these species are likely to spend more than 1 year in the larval stage. For four species, we did not find voltinism data in the literature.

Family	Scientific name	Voltinism	Source
Buprestidae	*Agrilus bilineatus* Weber	1	Bright 1987
Buprestidae	*Agrilus cephalicus* LeConte		
Buprestidae	*Dicerca divaricata* Say	2-3	Bright 1987
Cerambycidae	*Analeptura lineola* Say		
Cerambycidae	*Anelaphus villosus* Fabricius	2	Solomon 1995
Cerambycidae	*Clytus ruricola* Olivier		
Cerambycidae	*Cyrtophorus verrucosus* Olivier	1	Linsley 1964
Cerambycidae	*Elaphidion mucronatum* Say	2	Linsley 1964
Cerambycidae	*Molorchus b. bimaculatus* Say	1-2	Blackman and Stage 1924
Cerambycidae	*Neoclytus a. acuminatus* Fabricius	1-2	Blackman and Stage 1924
Cerambycidae	*Orthosoma brunneum* Forster	2-3	Linsley 1962a
Cerambycidae	*Typocerus v. velutinus* Olivier	2	Linsley 1976
Cerambycidae	*Urgleptes querci* Fitch		
Cerambycidae	*Xylotrechus colonus* Fabricius	1	Blackman and Stage 1924

a generation time greater than 1 year. Much of the dissimilarity between assemblages sampled in different years is due to these 14 species (Fig. 3D). This analysis should be viewed as a post-hoc test, and the voltinism hypothesis remains to be tested in future work.

No differences were found in the Shannon-Wiener diversity estimates at sites scheduled for future treatments ($df = 1,106$, $F = 0.238$, $p = 0.627$, Fig. 4). The Simpson diversity index showed similar results ($df = 1,106$, $F = 0.075$, $p = 0.785$) and were not plotted. Species richness was also similar among arrays in different future treatments ($df = 1,106$, $F = 1.2608$, $p = 0.2640$, Fig. 4). Adjusting the degrees of freedom to account for the arrays being nested within research cores (4 arrays per unit) would not change the outcome that there are no differences in these metrics.

DISCUSSION

The number of individual wood-boring beetles captured by this sampling effort is similar to other studies carried out in Indiana using similar techniques (e.g., Holland 2006). The species richness is slightly higher than another survey carried out by Holland in Indiana, likely because several species that are sensitive to forest fragmentation at large spatial scales remain extant in the heavily forested landscapes of south-central Indiana where the present study was conducted. Several uncommon species (Appendices 1 and 2) were found that had not previously been found in a survey across Indiana (Holland 2006), and we will publish several new state and county records as a result. Most species of Buprestidae commonly collected in this study are known to use oak as a host. The only species that we captured in large numbers that does not have oak recorded as a host were *Dicerca lurida* Fabricius and *Agrilus cephalicus* LeConte. *Dicerca lurida* is known from *Alnus*, *Carpinus*, *Carya*, *Prunus*, and *Salix*, while *A. cephalicus* is known from *Cornus* (Nelson et al. 2008).

As expected, there did not appear to be differences among the trap arrays in ISU destined for different treatments in the future (Fig. 3A), but we were unable to test this hypothesis statistically because data were overdispersed in 2006. The comparison with 2007 and 2008 data did show differences among future treatments. The differences between the ISU array locations sampled in 2006 and 2007 were different

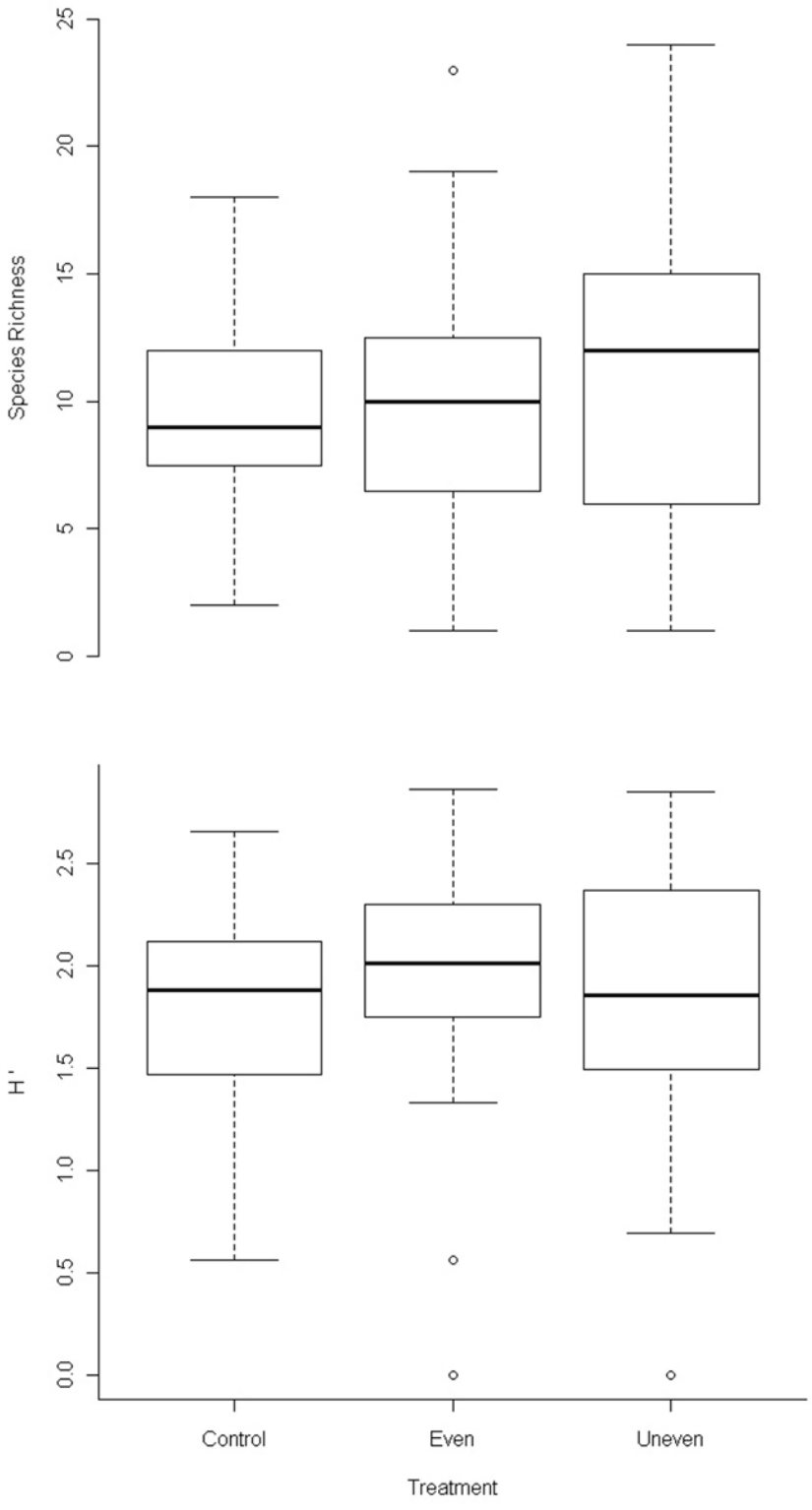

Figure 4.—No differences were found in species richness or Shannon diversity index (H') at future control, even-aged management, and uneven-aged management sites. Thirty-six sites were sampled across the future treatment groups.

from the landscape matrix locations sampled in 2008 (Fig. 3B). This finding would seem at first to suggest that later comparisons between harvested areas and the landscape around them would not be possible as differences were already evident before harvesting. However, there are several possible reasons for the differences between these years. Taking these differences into account may help with future comparisons.

In 2006, logistical constraints led to a much shorter collecting period, which influenced year-to-year comparisons. The summer of 2007 in south-central Indiana was slightly warmer and drier than average, with mean temperature for June-August (24.3 °C, 75.8 °F) 2 percent above average and rainfall (206 mm, 8.12 inches) only 66 percent of normal summer conditions. By comparison, summer 2008 mean temperature (23.4 °C, 74.2 °F) was approximately average, and summer rainfall (271 mm, 10.7 inches) was 87 percent of the long-term average (Indiana State Climate Office 2011). The warmer and drier conditions of 2007 may have altered the species assemblage or flight activity of the beetles, making annual comparisons difficult. Ideally, samples in different groups (harvest or matrix) should be taken at the same time. Unfortunately, logistical constraints prevented us from sampling matrix and harvest locations in the same years.

Another possible cause for the different assemblages in different years is that many species of wood-borers remain several years in the larval stage. Some species of wood-borers with generation times longer than 1 year are known to synchronize adult emergence, leading to year-to-year fluctuations that can influence the number and species of beetles captured (Barbalat and Borcard 1997). We tested this relationship in a post-hoc way, and found that at least half of the species that were responsible for distinguishing the year-to-year differences, and thus the future harvest site and landscape matrix site differences, have, or may have, generation times longer than 1 year (Table 1). If these species undergo variation in their annual abundance caused by synchronization of adult stages, such variation would have contributed to the differences we report.

The species listed in Table 1 represent less than 20 percent of the species captured. Consequently, one way to minimize the influence of longer-lived species on comparisons would be to exclude these species, but this step may bias results toward species that use living wood. The latter species tend to have shorter generation times, likely because of the higher-quality larval food. A better approach would be to have a priori information on the species that are unlikely to be in the adult stage for a particular year and either adjust the timing of sampling to obtain the most species possible, or remove those species previously determined to have most individuals in the larval stage. Combining data from several years of surveying may also allow us to minimize the influence of annual variation.

The oak forests in the HEE support a diverse assemblage of wood-boring beetles, with most species using decaying wood as larval habitat. The great diversity is not surprising, as oak supports more beetle species than other trees, such as beech (*Fagus*) (Barbalat 1998). Tree species diversity will also increase species richness of wood-using insects, especially among those groups with specialized diets or habitat requirements. A diversity of dead wood is also important in supporting diverse saproxylic assemblages (McGeoch et al. 2007), in terms of wood species, as is a range of decay classes and microclimates.

Saproxylic insects and the ecological roles they play are recognized as important, but populations of these insects can decrease in response to disturbance. There may also be thresholds in the response to disturbance so that once the intensity or extent of disturbance crosses some level, the populations and the ecosystem function they play, decrease rapidly. These threshold

responses are unpredictable and poorly understood (Niwa et al. 2001). With the many roles that saproxylic insects play, such as pollination and nutrient cycling, attention must focus on the coarse woody debris that serves as habitat for this group. Sustainable forest management should strive to retain this habitat (Ulyshen et al. 2004). Many forest species, including saproxylic insects, have evolved to use coarse woody debris long before humans became interested in it (Hagan and Grove 1999). However, post-harvest management techniques may reduce coarse woody debris habitat greatly, some more than even fire (Tinker and Knight 2001).

Conservation of the diversity of agents that perform ecological roles and maintain forest health and function, including wood-boring beetles, is known to be important in ensuring sustainable use and enhancing resilience (Fischer et al. 2006). Fischer et al. (2006) have published 10 general guiding principles for such conservation in forestry and agricultural landscapes. The details of how the different taxa respond and thereby further alter forested systems remain to be filled in by long-term, large-scale experiments such as the HEE.

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APPENDIX 1.

Species of Cerambycidae caught 2006-08. Recent changes in taxonomy are indicated in parentheses and follow Bousquet (2007). Abundance and prevalence are the total number of individuals and the number of site-years (out of 108 possible) where the species was detected, respectively.

Species	Abundance	Prevalence
Aegomorphus modestus Gyllenhal	14	11
Analeptura lineola Say	85	29
Anelaphus parallelus Newman	2	2
Anelaphus pumilus Newman	1	1
Anelaphus villosus Fabricius	415	60
Astyleiopus variegatus Haldeman (=Sternidius)	1	1
Astylidius parvus LeConte	5	5
Astylopsis macula Say	23	17
Astylopsis sexguttata Say	1	1
Bellamira scalaris Say	7	6
Brachyleptura champlaini Casey	2	1
Brachyleptura rubrica Say	4	4
Clytus ruricola Olivier	77	41
Cyrtophorus verrucosus Olivier	69	39
Dorcaschema cinereum Olivier	3	3
Ecyrus d. dasycerus Say	4	4
Elaphidion mucronatum Say	49	30
Elytrimitatrix undata Fabricius	1	1
Enaphalodes atomarius Drury	1	1
Enaphalodes rufulus Haldeman	1	1
Encyclops caerulea Say	1	1
Euderces picipes Fabricius	8	8
Eupogonius pauper LeConte	12	11
Gaurotes cyanipennis Say	30	24
Glycobius speciosus Say	2	2
Goes pulverulentus Haldeman	1	1
Grammoptera haematites Newman	1	1
Graphisurus despectus LeConte (=Urographis)	24	18
Graphisurus fasciatus DeGeer (=Urographis)	45	25
Hesperophanes pubescens Haldeman	1	1
Heterachthes quadrimaculatus Haldeman	19	16
Hyperplatys aspersa Say	6	4
Hyperplatys maculata Haldeman	3	3
Leptostylus transversus Gyllenhal	20	17
Lepturges confluens Haldeman	13	12
Lepturges symmetricus Haldeman	1	1
Megacyllene caryae Gahan	4	4
Metacmaeops vittata Swederus	18	16
Micranoplium unicolor Haldeman	2	2
Microclytus gazellula Haldeman	1	1
Microgoes oculatus LeConte	18	15
Molorchus b. bimaculatus Say	68	20

(Appendix 1 continued on next page)

APPENDIX 1 (continued).

Species of Cerambycidae caught 2006-08. Recent changes in taxonomy are indicated in parentheses and follow Bousquet (2007). Abundance and prevalence are the total number of individuals and the number of site-years (out of 108 possible) where the species was detected, respectively.

Species	Abundance	Prevalence
Neandra brunnea Fabricius	25	22
Necydalis mellita Say	4	4
Neoclytus a. acuminatus Fabricius	91	52
Neoclytus m. mucronatus Fabricius	16	12
Neoclytus scutellaris Olivier	23	13
Oberea deficiens Casey	1	1
Oberea praelonga Casey	4	4
Oberea ruficollis Fabricius	1	1
Obrium maculatum Olivier	5	4
Obrium rufulum Gahan	1	1
Orthosoma brunneum Forster	68	46
Parelaphidion aspersum Haldeman	1	1
Parelaphidion incertum Newman	11	9
Phymatodes amoenus Say	22	14
Prionus laticollis Drury	16	14
Psenocerus supernotatus Say	14	9
Rhopalophora longipes Say	2	2
Saperda discoidea Fabricius	2	2
Saperda imitans Felt and Joutel	4	3
Saperda lateralis Fabricius	10	9
Saperda vestita Say	1	1
Sarosesthes fulminans Fabricius	4	4
Sphenostethus taslei Buquet	5	5
Stenelytrana emarginata Fabricius	5	5
Stenocorus cinnamopterus Randall	0	0
Stenocorus schaumii LeConte	1	1
Stenosphenus notatus Olivier	1	1
Sternidius alpha Say (=Liopinus)	3	3
Sternidius punctatus Haldeman (=Liopinus)	1	1
Strangalepta abbreviata Germar	30	13
Strangalia bicolor Swederus	2	2
Strangalia luteicornis Fabricius	49	31
Strophiona nitens Forster	4	4
Tessaropa tenuipes Haldeman	11	8
Trachysida mutabilis Newman	6	6
Trigonarthris proxima Say	1	1
Typocerus deceptus LeConte	12	8
Typocerus v. velutinus Olivier	238	59
Urgleptes facetus Say	1	1
Urgleptes querci Fitch	43	30
Urgleptes signatus LeConte	10	10
Xylotrechus aceris Fisher	1	1
Xylotrechus colonus Fabricius	245	83

APPENDIX 2.

Species of Buprestidae caught 2006-2008. Abundance and prevalence are the total number of individuals and the number of site-years (out of 108 possible) where the species was detected, respectively.

Species	Abundance	Prevalence
Actenodes acornis Say	1	1
Agrilus amelanchieri Knull	2	2
Agrilus bilineatus Weber	89	25
Agrilus bilineatus carpini Knull	1	1
Agrilus cephalicus LeConte	215	41
Agrilus lecontei Saunders	3	2
Agrilus masculinus Horn	2	2
Agrilus obsoletogutatus Gory	10	7
Agrilus olentangyi Champlain & Knull	1	1
Agrilus putillus Say	8	5
Anthaxia viridifrons Gory	2	2
Chrysobothris sexsignata Say	8	7
Dicerca asperata Laporte & Gory	1	1
Dicerca divaricata Say	32	23
Dicerca lepida LeConte	2	2
Dicerca lurida Fabricius	20	17
Ptosima gibbicollis Say	3	2