ABSTRACT

BOUNDARY DYNAMICS AND MATRIX EFFECTS ON BEETLE COMMUNITY COMPOSITION AND MOVEMENT BETWEEN FORESTS AND AGRICULTURE

by Sarah K. Dudziak

Insect movement across habitat edges between forest and agriculture has the potential to affect ecosystem processes. In this study, I quantified aerial beetle communities in Ohio along transect lines crossing forest edges and stretching into corn and forest habitats. The goal of this study was to determine the effect of forest patch size, distance to the forest edge and agricultural matrix effects on beetle community dynamics. Beetle abundance and species richness were significantly higher at the edge throughout season. Net difference in abundance showed that in large fragments, individuals moved toward forest interior whereas beetles in small fragments flux towards corn. This suggests that large forest fragment edge were “hard” compared to small forest fragments. Non-metric Multidimensional Scaling showed log patch area and tree importance value were the two most importance variables in determining species composition. Spillover of insects across boundaries has various implications for biodiversity research in land management.
BOUNDARY DYNAMICS AND MATRIX EFFECTS ON BEETLE COMMUNITY COMPOSITION AND MOVEMENT BETWEEN FORESTS AND AGRICULTURE

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Sarah Kathleen Dudziak
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Advisor_______________________
Thomas O. Crist

Reader________________________
David L. Gorchov
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CHAPTER 1 - Introduction

Fragmentation of the natural landscape is a major concern for biodiversity because it leads to increasingly small, isolated patches of natural habitat interspersed within a matrix of agricultural and urban land uses (Heilman et al. 2002) which may lead to loss of native species and alterations in ecosystem functioning (Didham 1998; Sala et al. 2000). The two major components of fragmentation include a decrease in the size of a habitat fragment and an increase in the separation between two similar habitat patches (Murcia 1995; Saunders et al. 1991). Decreasing the total size of a habitat patch affects the number of species within the patch. The species-area relationship predicts a nonlinear decrease in species richness with habitat loss, but relationships are highly variable among taxa and environments (Connor and McCoy 1979).

There are a number of theories and hypotheses to explain the species-area relationship. As patches decrease in size they may lose unique habitat and, therefore, unique organisms. Another hypothesis is that extinction rates are inversely proportional to habitat size (Connor and McCoy 1979). If distance from a population source patch remains constant for large and small patches, abundance and richness is expected to be lower in small patches due to a higher extinction rate (MacArthur and Wilson 1967; Ricketts et al. 2001). Immigration of organisms into a patch decreases the chances of local extinction of that population. With increased isolation of habitat patches, immigration and emigration decreases (MacArthur and Wilson 1967).

The theory of island biogeography has been widely applied to fragmented landscapes in which these isolated habitat “islands” exist in a “sea” of unsuitable matrix habitat (Burke and Nol 1998; Matthysen 2002). Animals may perceive it to be increasingly risky to leave a habitat patch to enter into non-habitat that may not contain the resources necessary for survival. Nearby patches of habitat can supplement populations in other habitats. When patches are further apart there is less likelihood of immigration and emigration as stated by metapopulation dynamics (Hanski 1999). As distance to nearest habitat patch increases it becomes more difficult for individuals to move between patches (MacArthur and Wilson 1969; Ricketts et al. 2001). When organisms die off from a patch that has no source populations nearby, there is no chance
for population recovery and that organism would go extinct within that habitat. In addition to supplementation from other habitat patches it is important to consider matrix effects on a habitat since organisms in many ecological systems can move between a habitat patch and the surrounding non-habitat matrix (Bennett 1999).

With decreasing patch size there is an increase in the ratio of edge habitat to interior habitat (Murcia 1995). Collectively, the biotic and abiotic factors that exist at the interface between two habitats are known as edge effects and they comprise a larger portion of small habitats and expose patch-interior species to edge conditions. Some biotic conditions include changes in vegetation/animal density or composition. These biotic conditions are often directly related to abiotic conditions such as solar radiation, relative humidity, air temperature and wind velocity (Saunders et al. 1991; Murcia 1995).

Numerous studies have considered fragmentation and its effects on biodiversity but there is little consensus in the results (Foggo et al. 2001), partly because we lack information on the movement of individuals in the community. There is an increasing need to study the movement of organisms and spillover effects between habitat and the surrounding non-habitat matrix. This is especially true in the case of flying or highly vagile organisms (Driscoll and Weir 2005), or habitat generalists that may move between habitat patch and the adjacent matrix (Rand et al. 2006).

Movement allows organisms to relocate throughout the landscape and, potentially alter ecosystem processes (Sala et al. 2000). Gascon et al. (1999) measured significant spillover effects of organisms between habitat and matrix communities across a variety of different taxa. They found evidence of habitat invasion by non-native species as well as movement of native species to the matrix. At a finer scale, McIntyre and Wiens (1999) found that beetles moved differentially in habitat fragments of varying sizes. Areas with larger habitat patches showed beetles moving in a linear fashion with more frequent pauses while beetles in smaller patches had less directional movement and moved more slowly on average.

Studies of the movement of individuals between habitat patches are needed at the community level to understand how species richness and composition varies among habitat patches. In this study, I examined the boundary dynamics of aerial beetle communities of SW Ohio during 2003 to determine the effects of forest patch area,
distance from the forest edge, and the surrounding agricultural matrix on beetle diversity and abundance. I quantified the fluxes of beetles across forest edges bordered by corn to determine how flux rates were influenced by distance from the forest-corn boundary and forest-patch size. Finally, I assessed how different functional groups of beetles differed in their abundance and flux rates across forest edges.

In chapter 1, I focus on patterns of beetle diversity, abundance, and flux rates between forests and the surrounding agricultural fields. Here, I assess how boundary dynamics and edge effects occur within transects spanning forest-corn habitats. In chapter 2, I examine how broad-scale differences in beetle diversity and composition vary among transects to assess the effects of forest patch size and tree-species composition on boundary dynamics and patterns of beetle diversity among forest patches.
CHAPTER 2 – “Boundary Dynamics and Beetle Distribution Between Forests and Agriculture”

Humans alter the natural landscape in a way that continuous tracts of land are subdivided into smaller patches of natural land interspersed within a variety of different land uses. Although the consequences of these land-use changes are complex and have different effects on the biodiversity (Debinski and Holt 2000; Foggo et al. 2001), the general consensus is that habitat fragmentation is a major concern to the loss of native species and natural ecosystem functioning (Bennett 1999; Summerville and Crist 2002; Bascompte and Sole 1996; Ingegnoli 2002; Didham 1998b; Tscharntke et al. 2002a).

The boundaries between natural habitat and agricultural or urban areas form distinct edges that correspond to sharp changes in the abiotic and biotic conditions known, collectively, as “edge effects.” Abiotic edge effects include changes in wind disturbance, precipitation, temperature, relative humidity and solar radiation while some biotic edge effects include increased predation, competition for food sources, and mating opportunities (Saunders et al. 1991; Murcia 1995). These edge effects exist at the interface between two land-use types and then extend within the boundary of each type of habitat.

The degree to which these edge effects penetrate into a habitat is relatively consistent among habitat types. Candenasso et al. (1997) showed that a number of different abiotic edge effects were consistently detectable within 15m of the forest edge bordered by an old-field habitat. Forest and old field habitat exhibit a sharp difference in abiotic conditions that are found within each, whereas other types of habitats may not be as extreme. For example, clover patches surrounded by any variety of grasses. Vegetation characteristics also change in response to the steep abiotic gradients that occur in close proximity to edge (Burke and Nol 1998).

As natural habitat patches are fragmented into smaller patches the amount of edge area to interior area increases. Since smaller habitat patches have a higher proportion of edge area to interior area it is believed that individuals within smaller patches are more often exposed to these edge conditions than individuals within larger patches, which may rarely come into contact with the habitat edge (Murcia 1995).
There are numerous patterns of change in species richness and abundance as distance increases from the forest edge. One possible pattern is an increase in species richness or abundance from matrix to edge and then a decrease into habitat patch (Harris and Burns 2000). This pattern can be graphed as a unimodal relationship with highest species richness at the edge and a continual decrease away from the edge so that lowest levels of species richness or abundance are found in the forest and matrix interior. Rand et al. (2006) suggest that this is a common pattern for boundaries between natural and agricultural habitats because edges often contain species that occur in both habitats. Another pattern that occurs is an increase from the matrix to the habitat interior so that highest species richness and abundance is in the habitat interior rather than at the edge (Harris and Burns 2000; Barbosa and Marquet 2002). A third pattern suggests a “mid-distance peak”, where high species richness or abundance occurs along the edge followed by a drop where edge species disappear, then a subsequent increase as habitat-interior species pick up (Didham 1997).

The theory of island biogeography (MacArthur and Wilson 1967) has been widely applied to fragmented landscapes in which habitat “islands” exist in a “sea” of unsuitable matrix habitat (Burke and Nol 1998; Mattysen 2002). Island theory may have limited applicability to a terrestrial system where organisms may move between a forest and the surrounding agricultural matrix (Bennett 1999; Tscharntke et al. 2002b). Moreover, the boundary between two terrestrial habitat patches exerts varying degrees of permeability, allowing some organisms to move freely across the habitat edge while preventing dispersal by others (Fagan et al. 1999; Bommarco and Fagan 2002; Rand et al. 2006).

The surrounding non-habitat “matrix” patches play an important role as a site for reproduction and possible source of food for some individuals (Varchola and Dunn 2001). Depending on the matrix type and the degree of habitat variation between matrix and habitat fragment, the edge will affect individual movement in varying ways (Ricketts 2001). Some organisms use the matrix as preferred habitat while others will be restricted to movement within the habitat interior. Previous research has shown that some organisms can utilize matrix resources in favorable conditions but will retreat to alternate habitat fragments (hedgerows, forest edges, grassy fields, etc) during unfavorable times (Varchola and Dunn 2001; French et al. 2001; Magura et al. 2001). Alternatively,
Gascon et al. (1999) found that a number of primary forest species are not solely limited to movement within forest fragments but can utilize the agricultural matrix.

Habitat edges can be defined as either “hard” or “soft” edges to individual movement (Wiens et al. 1985; Strayer et al. 2003). Hard edges become a barrier to individual movement because as an organism approaches the edge they are unable to cross it. This may be due to the conditions at the edge such as dense vegetation or those surrounding the habitat patch such as increased solar radiations or lack of food source. Cadenasso and Pickett (2001) found that seeds penetrate further into a forest fragment when the edge vegetation was thinned. On the other hand, soft edges are barely perceived and individuals easily pass across them (Bennett 1999; Morales 2002; Haynes and Cronin 2006). While the distinction between hard and soft edges is based on individual organisms that have different preferences and survival capabilities, it is reasonable to assume that functionally similar groups of organisms may be influenced by a particular edge in the same way.

Fagan et al. (1999) expand on this idea by using reaction-diffusion models to categorize edges as reflecting, absorbing or mixed. Instead of viewing the edge as only a barrier to movement, they consider the surrounding non-habitat matrix as influencing individual movement and survival. A reflecting edge is similar to a hard edge in that as an individual approaches the edge there is no emigration because the individual will essentially “bounce off” of it. An absorbing edge occurs when emigrants from a patch are unable to return due to the harsh conditions of the non-habitat matrix or emigration to another suitable habitat patch. Mixed boundaries are thought to be the most common edge designation because they are a combination of both the reflecting and absorbing boundaries, depending on the species (Fagan et al. 1999).

Most human land uses impose a sharp boundary between natural habitat and surrounding land use. Boundaries such as those that occur between an agricultural field and a forest fragment are often referred to as hard edges (Bennett 1999), but are probably more of a mixed boundary for most individuals. In this case, the abiotic conditions in the agricultural field are more extreme than those of the forest fragment. Agricultural fields have increased solar radiation reaching the ground, increased daytime temperature, and decreased soil moisture and humidity levels (Murcia 1995; Cadenasso et al. 1997).
response of an organism to a habitat boundary depends on whether the organism prefers the habitat patch or the surrounding matrix. For example, Matthysen (2002) found that organisms within habitat patches surrounded by open space (pasture or agriculture) had high levels of mobility within the patch but experienced little movement across patch boundary.

The degree to which an edge is hard or soft depends on the degree of variability that exists between the habitat and the matrix. In forest-agriculture systems and forest-pasture systems, there is an extreme difference in abiotic conditions that exist in the forest as opposed to those that exist in the farming system (Cadenasso et al 1997). The forest offers more shade and protection from wind and solar radiation, whereas the agriculture and pasture are more open to abiotic condition and are more homogenous with respect to vegetation. Contrasting the agriculture and pasture, on might expect the forest-pasture edge to be softer than forest-agriculture because agricultural fields are disturbed each year by tillage, planting, pesticide/herbicide application as opposed to pasture, which is not disturbed in this way. In addition, agriculture-grassland systems exhibit a while different set of dynamics since there are more similar abiotic variables that exist between these two habitats.

Land use type may affect movement across the edge. In a forest-pasture system, Didham et al. (1998b) found an increase of beetles at the forest edge and then a variety of other patterns as distance increased from the edge. In an afrotomontane forest with a maintained grassland matrix, beetles increased from grassland to the forest interior with no peak in abundance at forest edge (Kotze and Samways 2001). In corn-tallgrass prairie system, highest abundance and species richness found at the edge and then decreased in corn with distance from edge. The *Diabrotica sp.* beetles involved in this study decimated the sunflower plants in the adjacent tallgrass prairie (McKone et al. 2001). Haynes and Cronin (2006) found that insects moved more across grass-grass boundaries than they moved across grass-mudflat boundaries. In a barley-ley system, Bommarco and Fagan (2002) found insects moved into ley patches early in the season and into barley late in the season. They found barley to have a repulsive edge and ley to have an attractive edge for beetle movement.
Movement across a habitat edge affects both habitat and non-habitat matrix communities. French et al. (2001) found that beetles move into crop fields in spring but out of crop fields during autumn. Both crop pests and natural enemies may use forest habitat as shelter during times of inclement weather or seasonal change (Varchola and Dunn 2001; Bommarco and Fagan 2002). Native species are often found in higher concentrations within forest fragments while exotic species are found in high numbers within crop fields (Harris and Burns 2000). McKone et al. (2001) found insect pests to be significantly more common near the crop field edge as well as significantly more abundant than their natural enemies.

There are a variety of other documented patterns of species distributions across habitat edges. The patterns that exist at the edge are often numerous and contradictory (Bender et al. 1998; Harris and Burns 2000; Barbosa and Marquet 2002), or may vary with different feeding strategies (Didham et al. 1998b; Golden and Crist 1999; Summerville and Crist 2002). For instance, woody herbivores are edge-avoiders (Didham et al. 1998b), while predators prefer edge habitat (Didham et al. 1998b; Ries and Fagan 2003). Woody herbivores are therefore predicted to increase in abundance and richness towards the forest interior where there are greater numbers of tree species or a greater availability of coarse woody debris. By separating specimens into feeding guilds, patterns of their distribution or abundance may be more apparent than if the organisms were considered, solely, on a community basis (Golden and Crist 1999; Summerville and Crist 2002).

Most studies of boundary dynamics, edge effects and species distributions consider only a single species or a few closely related species. Fewer studies have considered changes in overall species diversity or composition across habitat boundaries. In this study, I determined the effects of forest patch area and distance from the forest edge on the abundance, diversity, and species composition of aerial beetle communities in an agricultural landscape of SW Ohio. To assess the role of the surrounding matrix on forest beetle communities, I also quantified beetle communities in corn fields near the forest edge. Based on the hypothesis that forest edges contain insect species from both the forest interior and the surrounding matrix, I predicted that there would be an increase in species richness and abundance from matrix to forest edge and decrease into forest
fragment. I also predicted that the relative magnitude of edge effects on species richness and abundance would diminish as forest patch size decreases and small forest fragments become more similar to the surrounding corn matrix. My second hypothesis was that the distribution and movement of beetles across forest edges would vary among feeding guilds. In particular, I predicted that there would be: (1) a higher richness and abundance of herbivores at forest edge and in matrix due to the increased productivity in corn during the summer months, (2) an increased richness and abundance of fungivores (and woody herbivores) toward forest interior, (3) a higher abundance but lower richness of predators in corn and (4) decrease in predator abundance toward forest interior.

METHODS

STUDY SITES

Beetles were sampled on three separate occasions during the summer of 2003 (late June, August and September) using passive flight-intercept traps. Because insects are influenced by several patch characteristics (Golden and Crist 1999; Collinge and Palmer 2002), eight woodlots in southwestern Ohio were chosen based on their size, shape, orientation, and surrounding agricultural crop. Forest patches were scattered 2-20 km apart within a 50-km² area of an agricultural landscape. To minimize sources of variability, woodlots were limited to those with straight, well-defined boundaries between forest and the adjacent fields and corn planted within 10 m of the forest edge. Sites with elevation changes and those with streams were eliminated. Eight forest patches were classified as either small (3-7 ha), intermediate (15-20 ha) or large (>80 ha). Large sites are Hueston Woods (HW) and Bachelor Reserve (BR). Intermediate sites are Methodist (ME), Finch (FI) and Rosenberger (RO). Small sites are Herrmann (HE), Seals (SE), and Wendel (WE). Landowners and farmers were surveyed for each site regarding information on agricultural practices and till regimes used during the farming season. Information on site location, vegetation characteristics and agricultural practices found in Table 1.
INSECT SAMPLING

A series of 11 directional flight-intercept traps (FITs) were arranged every 10 m along a 100 m transect line running perpendicular to each forest edge (Figure 2). These traps have been shown to capture most of the beetles that occur within habitats (Hill and Cermak 1997; Kitching et al. 2001). The location of the transect line was randomly chosen along the forest edge with the constraint that it was >100 m from other edges. Transects were positioned across the forest edge by designating the edge boundary as the first tree ≥ 10 cm diameter breast height (dbh). One trapping station was located at the forest edge. Trap stations were spaced 10 m apart, with six traps extending 60 m into the forest interior, and four traps extending 40 m into the corn. More traps were positioned in the forest because of the expectation that the woodlot would be more heterogeneous than corn. Each transect line was permanently marked with flags to resample the same transects during the summer.

The flight-intercept traps consisted of a 60 x 60-cm Lexan panel within a PVC frame mounted on a pair of 1.5-m metal poles (Figure 3). Insects were collected in 60-cm PVC rain-gutter troughs capped at each end. Troughs were connected to the bottom edge of the trap face on both sides and filled with propylene glycol to capture insects traveling in either direction. To avoid wind and rain disturbances and to minimize the number of insects entering the traps from the side, a 5-cm wide connected set of plastic roof and walls were connected to the top and sides of the trap face. Poles were driven into the ground so the bottom of the trap face rested about 1.2 m above ground (Figure 3).

All transects were sampled during each of three 2-wk sampling periods in the summer of 2003: 17 June–3 July, 30 July–15 August, and 13–26 September (hereafter referred to as Jun., Aug., and Sep. samples). Four transects were sampled in the first week, and the remaining four were sampled in the second week. Sites were chosen randomly so as to include at least one small, intermediate and large site during each week of sampling. At the end of the 7-d sampling period, troughs were carefully removed and partially processed by straining the propylene glycol off of the insect sample with a sieve. All insects were then placed in labeled jars and filled with 70% ethanol. Traps were removed from the site and reassembled at the remaining four sites the same day to begin the next 7 days of sampling. Although eight sites were sampled, data are shown here for
seven sites due to trap malfunctions at one intermediate-sized site during June sampling (ME) and one large site during both August and September (HW).

In the laboratory, samples were processed to separate beetles from other orders of insects. Beetles were individually pinned, pointed and labeled and placed into “morphospecies” based on morphological traits. All morphospecies were later identified to the family level, and the most common morphotypes were identified to species (Appendix A and B).

Beetles were placed into one of three guild categories depending on the general feeding preferences of each family: predator, herbivore or fungivore (Arnett et al. 2002). All beetles that did not fall into one of these three guilds were classified as “other” and were not included in guild analysis. Predators kill and consume other living organisms. Herbivores feed directly on leaves, flowers or fruits. Fungivores include beetles that consume fungi, sap, or dead wood. The latter two were included as fungivores because sap or wood feeders often consume the fungi associated with these plant products.

DATA ANALYSIS

Several community measures are used to quantify patterns of species abundance, diversity, and composition along transects. In this study, I used the Sørensen quantitative index of dissimilarity to measure differences in species composition between samples because it is sensitive to both differences in species presence-absence and relative abundance (Magurran 2003). The value is equal to 0 if two sites are identical and 1.0 if the two sites are completely dissimilar and have no species in common.

Because of spatial dependence within transects, the three response variables (species richness, total abundance and Sørensen dissimilarity) were analyzed using a program created by T.O. Crist in 2004 which compares observed trap samples to null values obtained from a user-specified number of randomizations of the data. Randomization tests were conducted on species richness, total abundance, and Sørensen index. Values were randomly shuffled among traps within habitats so that trap locations “-40 m” through “-10 m” (Corn) were randomized separately from locations “0 m” through “60 m” (Forest). This constrained sample-based randomization retains the within-habitat mean and variance (Fagan et al. 2003), but randomizes the spatial position of samples within habitats.
Randomization of trap data was conducted to test two types of hypotheses. First, to test the null hypothesis that patterns of abundance, richness, and composition did not differ across forest-corn boundaries, I conducted randomization tests on the pooled-trap samples. Pooled-sample analysis combined species abundances from the two troughs of each trap and pooled samples were randomized within habitat as described above. For pooled-trap analysis, shifts in species composition along transects were quantified by the Sørensen index of dissimilarity between adjacent pooled-trap values. Second, to test the null hypothesis that beetle fluxes (corn to forest or forest to corn) did not differ along transects, I conducted paired-trap randomization tests. Here, the pairs of values from each trap were randomized among trap locations within habitats and, within each location, pairs were randomly assigned to forest or corn side of the trap. This hierarchical or two-step randomization procedure is the standard approach for conducting hypothesis tests on nested designs (Manly 1996). In the case of beetle abundance, the null hypothesis test for paired-trap randomization is whether the net movement in the number of beetles from corn to forest is equal to that from forest to corn. In the case of species richness, the test is whether the number of species moving between habitats does not differ. Paired-trap Sørensen index of dissimilarity compares dissimilarity between opposite sides of the same trap once the traps are randomized within habitat. For Sørensen index of dissimilarity, the null hypothesis is that the species composition does not differ between the two sides of the trap.

Paired-trap analysis used 22 samples per site while the pooled sampling simply combines the two troughs at each trap making 11 samples per site. In all randomization tests, 1000 random permutations of the data were conducted and the diversity metrics were calculated for each trap location (either pooled or paired). The observed values at each location were compared to the ranked null distribution of values. The P-value was then calculated as the number of null values that are greater (or less) than the observed value. I conducted two-tail tests so that the rejection region is $P \leq 0.025$ at each tail of the null distribution.
RESULTS

A total of 18,136 individual beetles were sampled during 2003: 63% during June (11,398 individuals); 18% during August (3,241 individuals); and 19% during September (3,497 individuals). Fifty-nine beetle families were represented with Nitidulidae (30% of total individuals), Latridiidae (15%), Mordellidae (8%), Staphylinidae (6%) and Brachypteridae (6%) being the 5 most abundant families. Each of these families contributed greater than 1000 individuals to the total abundance. Brachypteridae was sampled only during September (Appendix A).

Beetles were sorted into 708 morphospecies. Staphylinidae and Curculionidae each contributed >75 species throughout the season and represent 23% of the total beetle richness. A number of other families including Carabidae, Chrysomelidae, Elateridae, Nitidulidae and Mordellidae each had >30 species. Based on total abundance, 60% of the beetles (10747 individuals) were classified as fungivores, 28% (5014 individuals) as herbivores, and 11% (1994 individuals) as predators (Appendix A). The remaining 0.02% beetles were classified as scavengers or generalist feeders.

My sampling protocol captured a mixture of beetles, primarily ground and understory species and possibly a few that move between canopy and understory. Understory beetles are expected to move more while canopy beetles are expected to be more residents to trees. The beetles caught in this study were a completely different set of beetles than one might catch when using canopy fogging or other methods of insect collection, as might be expected.

SPECIES RICHNESS, ABUNDANCE, AND COMPOSITION

Species richness consistently changed with distance from the edge in June and August samples. Beetle richness values spike at the forest edge which had twice the species richness of the values found in either of the two habitats (Figure 4). Of the seven sites considered, 6 sites in both June and August had significantly higher richness at the edge than expected by chance based on pooled-sample randomization tests. In September, the pattern was more muted although 3 of 7 sites still had higher than expected richness. During all sampling periods, nearly all sites showed higher than expected richness at the first trap in corn field adjacent to edge (“-10 m” trap). Similar patterns of richness occurred from corn to edge to forest in woodlots of all sizes.
Total beetle abundance also peaked at the corn-forest boundary, but the patterns were more variable than with richness. In June and August, values for total abundance increased at the forest edge in most sites (Figure 5a and 5b). Although values were similar between sites in corn, the forest showed that intermediate sites had highest abundance, followed by small sites and large sites had the lowest total abundance (Figure 5a). During August, total abundance values in the forest decreased with distance from the edge (Figure 5b). Abundance decreased as the season progressed (Figure 5). During September, a similar pattern existed as in June with intermediate sites showing highest abundance, followed by small and large (Figure 5c).

Sørensen dissimilarity was highest at the edge for all sites during June, suggesting that changes in beetle community composition were highest along the forest-corn boundary (Figure 6). In August, however, dissimilarity generally increased from corn to the edge and then continued at high levels into the forest interior. During September, the opposite pattern exists, with a generally higher dissimilarity in the corn and lower values in the forest. Patterns of dissimilarity showed no obvious differences according to forest habitat area, except perhaps that dissimilarity between locations within forest were typically higher for larger forest patches.

In June and August, there was higher than expected abundance at the forest edge in most sites as well as in the trap adjacent to forest edge in corn (Figure 5 and 7). In both the edge trap (0 m) and -10 m trap during June, small sites had significantly higher than expected beetle abundance. During September, 6 of the 7 sites had higher than expected abundance at the -10 m trap (Figure 7). As with richness and abundance, Sørensen dissimilarity values at the -10 m trap in corn adjacent were significantly greater than expected by chance alone (Figure 7).

The confidence intervals for the randomized data illustrate how the randomization tests preserve the mean and variance within habitats (Figure 8). Observed and randomized data are shown for a transect from a small forest patch, which had a species richness, abundance and dissimilarity that were significantly higher at the edge than expected by chance: observed values occurred at the upper end of the 95% confidence intervals.
**FLUX RATES OF ABUNDANCE AND RICHNESS**

Paired-trap comparisons take the difference between corn and forest trough on each trap, illustrating any net movement per trap. In this case the paired-trap comparisons showed that the net difference in species richness was highest at the forest edge, suggesting flux rates of different beetle species were highest at the edge. In June, there was little difference between opposing sides of flight-intercept traps in the corn and in the forest interior. At the edge and the first two forest traps (10 m and 20 m), there was more variability between trap sides. Small sites had negative paired difference in species richness - indicating a net flux of species from forest to corn - at the edge (0 m), 10 m, and 20 m. The opposite pattern was exhibited in large and intermediate sites. These sites had positive paired difference at 0 m, 10 m and 20 m (Figure 9a), suggesting a net flux from corn to forest. The pattern of negative paired difference in small sites and positive paired difference in large/intermediate sites was consistent in August but is limited to 0 m, or edge traps (Figure 9b). Patterns during September were less clear and did not show net movement by habitat size (Figure 9c).

Paired-trap differences in total abundance showed small paired differences for corn traps during all sampling periods (Figure 10), suggesting little net movement in corn. During June, differences in abundance showed that small sites had negative paired-difference values while large and intermediate sites had positive values (Figure 10a), consistent with the flux patterns of species richness. Since small sites had negative paired difference values, beetles at small sites had net movements from the forest towards the corn. Beetles in large and intermediate sites showed a generalized movement from the edge into the forest consistently to 20 m trap (Figure 10a). In August, there was not much directed movement since paired difference values were consistently low among all sites (Figure 10b). September sampling showed very little directed movement in corn. The direction of movement was variable among sites and was not consistently related to size class (Figure 10c).

Paired-trap Sørensen dissimilarity in June shows that the dissimilarity was highest near the forest edge, suggesting that different species were moving between corn and forest and vice-versa (Figure 11a). Larger forest patches tended to have greater levels of dissimilarity between trap sides than smaller ones, especially in the forest interior data.
In August, dissimilarity generally increased from corn to forest interior, although there was variation among forest patches of different size (Figure 11b). Dissimilarity was even more variable in September, but there was a tendency for small and intermediate-sized woodlots to have higher dissimilarity in corn and lower dissimilarity in forest, while the large woodlot showed the opposite pattern. (Figure 11c).

**GUILD ANALYSIS**

Analysis of the total abundance of three guilds was similar to the overall community in that beetle abundance was consistently lower in corn traps, increased sharply at edge and then became more variable in the forest interior. Abundance of fungivorous beetles continued to increase slowly in forest, herbivores leveled off and predators decreased (Figure 12). Although there was a slight increase in beetle abundance at the forest edge during August sampling, patterns were less clear (Figure 12b).

Compared to the total fungivore catch, their total abundance remained consistently low across corn in August and September (Figure 12b and 12c). During June, abundance jumped from ~100 individuals in corn to 300 individuals at the edge and over 400 individuals in forest interior. Values at the edge and -10 m trap were significantly higher than expected by chance ($p<0.001$) for September fungivore abundance (Figure 12c).

Herbivore abundance was much lower than fungivore abundance with 160 individuals at its highest but the patterns were similar between the two groups. Herbivores had, comparatively, low abundances throughout corn, increase at the forest edge and then, unlike fungivores, herbivore abundance remained constant into forest interior (Figure 12a). Herbivore abundance values were lowest during August but were higher than expected at the edge and -10 m trap for all sampling periods.

Predators showed similar patterns as other groups with respect to abundance although significantly fewer individuals caught with the exception of June samples. During June, predator abundance was relatively high in corn traps and then decreased into forest interior (Figure 12a). The only trap to differ from this decreasing trend was the edge trap which measured extremely high predator abundance. Values were
significant for predator abundance at the edge and -10 m traps for all sampling periods (communication with author)

Paired difference in log abundance for each guild showed some similar trends (Figure 13). No guild showed any directed movement at the edge trap. In addition, predators and fungivores showed movement into forest from 10m trap to 60m. Herbivores had very little paired difference during June across the transect (Figure 13a). With very few exceptions, all guilds moved towards the forest edge during August (Figure 13b) and no distinguishable pattern existed during September (Figure 13c).

Paired trap Sørensen dissimilarity was consistently low across the season (Figure 14), although values were higher than expected at the -40 m trap (40 m into the corn) for fungivores during June and August, herbivores during August and September and predators during June and September (communication with author). Sørensen dissimilarity values increased slightly in the forest during August (Figure 12b) and in the corn during September (Figure 12c), suggesting more variable communities.

DISCUSSION

Beetle community changes across forest-corn edge were generally consistent throughout this study: beetle abundance and richness increased from the corn field to the forest edge and then either remained high or gradually decreased into the forest interior. Results were similar whether traps were considered “pooled” entities or troughs were analyzed separately at each trapping station.

Previous research on insect diversity along forest edges also found that insect species richness and abundance are highest at the forest edge (Didham et al. 1998a; Harris and Burns 2000; Molnar et al. 2001; Magura et al. 2001; Barbosa and Marquet 2002). Although there is support for the idea that the habitat edge is a unique habitat for some individuals or species (Ries and Sisk 2004; Ries et al. 2004), the primary conclusion from these studies is that the edge is a place for two habitats to overlap. Resources from both habitats become available to the matrix- and forest-dwelling species and may be complementary for species in either habitat (Ries and Sisk 2004, Rand et al. 2006). For example, some groups such as longhorned beetles may use live or
decomposing wood for oviposition and larval development and nectar or pollen in open areas in the adult stages (Arnett et al. 2002).

There are numerous patterns of change in species richness and abundance as distance increases from the forest edge. Some of the results listed here support those seen by Harris and Burns (2000), in which beetle species richness increased from matrix to forest edge and decreased into the forest fragment. Another pattern that occurred was a significant increase from the matrix to the forest interior so that highest species richness and abundance was in the forest interior rather than at the edge. Barbosa and Marquet (2002) recorded a similar pattern of increase in beetle species richness from the matrix to forest interior.

Organisms with different feeding strategies respond to fragmentation and edge effects in different ways (Bender et al. 1998; Didham et al. 1998b; Golden and Crist 1999; Golden and Crist 2000; Summerville and Crist 2002). By analyzing data by feeding guilds, patterns of their distribution or abundance appear to be more clearly defined than if the organisms were considered, solely, on a community basis (Golden and Crist 1999; Summerville and Crist 2002). In this study, data from the pooled trap analysis did not show significant or strong patterns with respect to total beetle abundance. When the paired-trap data were analyzed by feeding guilds, however, clearer and more consistent patterns emerged. For example, abundance of beetles in all three guilds was consistently low in corn but increased sharply at the forest edge. Fungivore abundance continued to increase into the forest interior and was 4 times higher than in corn. This is consistent with my prediction and can be explained by the fungivores needing a food source that is more abundant and readily available in the forest interior. Similarly, Didham et al. (1998b) found that woody herbivores increased in abundance towards the forest interior. Woody herbivores would be predicted to increase in abundance and richness towards the forest interior where there are greater numbers of tree species or a greater availability of coarse woody debris. Although this type of dynamic is expected, no apparent differences existed in percent cover shrubs, percent cover honeysuckle or volume of coarse woody debris by site size or by habitat (Table 1).

As predicted, herbivore abundance was significantly higher at the forest edge than expected by chance. Although herbivore abundance was lower than fungivore
abundance, it was consistently higher from forest edge to interior compared to corn. In contrast, McKone et al. (2001) found herbivorous insect pests from the family Curculionidae to be significantly more common near the crop field edge as well as significantly more abundant than their natural enemies. These pest organisms preferred corn because of the feeding and mating opportunities. In my study, however, adult beetles that are corn pests as larvae, such as the corn rootworm (*Diabrotica undecimpunctata*), comprised <5% of the overall herbivore abundance.

Predators had the lowest abundance of all three feeding guilds but the patterns of their abundance were very different from those of herbivores or fungivores. As expected, predator abundance was much higher at the forest edge than expected by chance in all sampling periods. This finding is consistent with Ries and Fagan (2003) who found a threefold increase in the density of mantids at the forest edge and Jokimäki et al. (1998) who found that a specific predatory beetle family (Cantharidae) also significantly preferred the edge. It is likely that predators are influenced by complementary resources from both forest and corn habitats (Rand et al. 2006).

During June sampling, predators had higher abundance in the corn than in the forest interior. Varchola and Dunn (2001) found that beetles from the family Carabidae (predator guild) increased their activity in crop field during full corn growth but then retreated to hedgerows when this source of prey items was no longer available. This movement was believed to correspond with increased prey abundance in hedgerows. Herbivores did not show this increased activity in crop fields early in the season. This pattern of high predator abundance in corn may exist because of the rapid emergence and growth of corn plants during June sampling.

Movement across a habitat edge affects beetle communities in both forest habitat and the surrounding matrix. French et al. (2001) found that beetles move into crop fields in spring but out of crop fields during autumn. Both crop pests and their natural enemies may use forest habitat as shelter during times of inclement weather or seasonal change (Varchola and Dunn 2001; Bommarco and Fagan 2002). Native species are often more abundant within forest fragments while exotic species are found in high numbers within crop fields (Harris and Burns 2000). McKone et al. (2001) found insect pests to be
significantly more common near the crop field edge as well as significantly more abundant than their natural enemies.

Early in the season, forest patch size determined how beetles moved across the edge with beetles in large and intermediate sites moving from edge into the forest interior and small sites showing movement in the opposite direction. There is an assumption that corn fields have higher productivity early in the season than forest fragments. Beetles in large and intermediate sites follow the pattern of movement from high productivity to low productivity (Wiens et al. 1985; Polis et al. 1997). This movement was most clear during June sampling which was the time during my sampling when corn growth was at its maximum. Conversely, beetles species in small sites move into the cornfield. Other studies in agricultural systems support this movement into crop fields during this time of rapid crop growth (French et al. 2001; Varchola and Dunn 2001; Bommarco and Fagan 2002). One possible explanation for these patterns is the idea that beetles in small sites have a higher probability of encountering an edge and therefore crossing it compared to large sites where beetles would be less likely to encounter an edge (Schtickzelle and Baguette 2001).

The impact of insect movement across edges shared by natural and cultivated land is an important process (Strayer et al. 2003; Ries et al. 2004; Rand et al. 2006). In particular, I found a higher species richness and abundance of predatory beetles along forest-crop boundaries. The most important predatory beetles were in the families Staphylinidae, Coccinellidae, and Carabidae, which may be important as natural enemies in agricultural and natural ecosystems. Cross-boundary subsidies between forest and agricultural habitats may have therefore have important influences on the interactions of organisms in both native habitat and the agricultural habitats.
Table 1. Site information on woodlot vegetation characteristics and farming practices. Top five trees listed with associated tree importance value. W.Pine (White Pine), R.Pine (Red Pine), S.Hickory (Shagbark Hickory), Shl.Hickory (Shellbark Hickory). Edge habitat = 0 m, 10 m and 20 m traps. Interior habitat = 30 m, 40 m, 50 m and 60 m traps.

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<th>Land** Management</th>
<th>Trees</th>
<th>Importance Value**</th>
<th>Habitat</th>
<th>Total Herbs</th>
<th>%Cover</th>
<th>%Cover Herbs</th>
<th>%Cover Shrubs</th>
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* Shows insecticide use on/near date of planting corn. All sites received similar herbicide application on date of planting.
** Land Management represents the tillage regime by listing the percent plant material remaining on ground.
*** Tree Importance Value is a measure of dominance calculated by relative frequency, relative density and basal area.
Figure 1. Observed changes in species richness or abundance with distance from edge in habitat and non-habitat. (A) Harris and Burns (2000); (B) Barbosa and Marquet (2002); (C) Didham et al. 1997.
Figure 2. Belt transect line. Eleven traps in total (only 7 shown). Inset is a detailed representation of vegetation sampling stations within each 10x10m quadrat. Sampling for insects, trees, woody stems and herbaceous vegetation in filled circles, 10m² quadrats, and 5m² and 1m² subquadrats, respectively. Of the 1x1m subquadrats, 2 of the 4 were chosen randomly within each 10m² quadrat for sampling.
Figure 3. Trap design of directional flight-intercept trap. a) Front view showing trap face, 1 trough to catch insects, roof and walls, all mounted on 2-5 ft. metal poles. b) Side view showing two troughs mounted on opposite sides of trap face with roof to cover troughs.
Figure 4. Total pooled trap Species Richness for a) June, b) August and c) September sampling. Open squares=Large sites, filled squares=Intermediate sites and filled triangles=Small sites. Negative transect distance values designate trap position in Corn, 0m=Edge, and positive distances are trap positions in Forest.
Figure 5. Pooled trap total abundance for a) June, b) August and c) September sampling. Open squares = Large sites, filled squares = Intermediate sites and filled triangles = Small sites.
Figure 6. Number of significant departures from the expected pooled-trap values during a) June, b) August and c) September sampling. Solid bars show Species Richness, open bars show total Abundance, and horizontally hatched bars show Sorensen Dissimilarity. All significant departures are greater than expected Null values (P<0.05).
Figure 7. Total pooled trap Sorensen Dissimilarity for a) June, b) August and c) September sampling. Open squares = Large sites, filled squares = Intermediate sites and filled triangles = Small sites.
Figure 8. Pooled trap values for a small woodlot during June 2003 sampling with 95% confidence intervals shown as solid lines. a) Species Richness, b) total abundance, and c) Sorensen Dissimilarity.
Figure 9. Paired difference in Species Richness between corn and forest side (C-F) of trap for a) June, b) August and c) September sampling. Open squares = Large sites, filled squares = Intermediate sites and filled triangles = Small sites. Positive values show species richness greater in corn side, negative values greater in forest side.
Figure 10. Paired difference in total abundance between corn and forest side (C-F) of trap for a) June, b) August and c) September sampling. Open squares = Large sites, filled squares = Intermediate sites and filled triangles = Small sites. Positive values show species richness greater in corn, negative values greater in forest.
Figure 11. Paired trap Sorensen Dissimilarity values for a) June, b) August and c) September sampling. Open squares = Large sites, filled squares = Intermediate sites and filled triangles = Small sites.
Figure 12. Paired-trap Log10 total abundance values for guilds during a) June, b) August and c) September sampling. Fungivores (filled squares), Herbivores (open squares) and Predators (filled triangles).
Figure 13. Paired differences in Log10 abundance values (corn side of trap – forest side of trap) for guilds during a) June, b) August and c) September 2003. Fungivores (filled squares), Herbivores (open squares) and Predators (filled triangles).
Figure 14. Paired-trap Sorensen Dissimilarity values for guilds during a) June, b) August and c) September 2003. Fungivores (filled squares), Herbivores (open squares) and Predators (filled triangles).
CHAPTER 3 – ”Matrix Effects on Beetle Species Composition Among Woodlots”

Land-use changes result in the fragmentation of natural habitats into smaller, more isolated patches that are surrounded by a variety of land-use types (Murcia 1995), such as urban development and agriculture (Heilman et al. 2002). Habitat fragmentation and land use vary and have complex effects on biodiversity (Debinski and Holt 2000; Foggo et al. 2001), including the loss of native species and alteration in ecosystem functioning (Bascompte and Sole 1996; Didham 1998; Bennett 1999; Summerville and Crist 2002; Ingegnoli 2002).

The two major components of fragmentation are decreased size of habitat patches and increased separation between two patches (Murcia 1995; Fahrig and Jonsen 1998; Bennett 1999), which have different effects on the species diversity found in habitat patches. According to the species-area relationship, a decrease in species richness and abundance results as the area of a particular habitat decreases (Connor and McCoy 1979).

In addition, smaller habitat patches have a higher proportion of edge to interior area. This increase in edge area to interior area is responsible for a change in the biotic and abiotic conditions that exist at the interface between the habitat patch and the surrounding land use. The conditions, known as edge effects, comprise a larger portion of smaller habitat patches and exposes patch-interior species to edge conditions. This may differentially influence species composition and distribution, as well as other natural processes within habitat patches (Murcia 1995; Bennett 1999; Rand et al. 2006).

The second component of fragmentation is an increase in isolation between two habitat patches. As distance to nearest habitat patch increases it becomes progressively more difficult for individuals to move between patches (MacArthur and Wilson 1969; Ricketts et al. 2001). Individuals respond differently to this level of isolation, altering metapopulation dynamics (Hanski 1999). There is a decreased probability that individuals are able to supplement declining populations, recolonize habitats following local extinctions, and colonize new habitats.

Reduction in habitat area and an increase in isolation of patches have different effects on the species diversity found within habitat patches. A decrease in the size of patches often results in a loss of native insect species as well as a decrease in habitat heterogeneity and plant diversity (Connor and McCoy 1979; Benitez-Malvido 1998;
Golden and Crist 1999). The individuals that are most sensitive to disturbance and removal of native habitats are usually habitat specialists or rare species, which are most susceptible to population decline (Straw and Ludlow 1994; Bennett 1999; Golden and Crist 1999; Ingegnoli 2002). On the other hand, in disturbed areas habitat generalists are more likely to be widespread and abundant since they are capable of utilizing a more broad range of habitats (Golden and Crist 1999).

The theory of island biogeography (MacArthur and Wilson 1967) has been widely applied to fragmented landscapes in which habitat “islands” exist in a “sea” of unsuitable matrix habitat (Mattysen 2002; Burke and Nol 1998). Island theory may have limited applicability to a terrestrial system where organisms may move between a forest and the surrounding agricultural matrix (Bennett 1999; Tscharntke et al. 2002b). Moreover, the boundary between two terrestrial habitat patches exerts varying degrees of permeability, allowing some organisms to move freely across the habitat edge while preventing dispersal by others (Fagan et al. 1999; Bommarco and Fagan 2002).

Most research has examined how habitat area and isolation influence species responses to fragmentation, but fewer studies consider the type of surrounding land use (see Gascon et al. 1999; Harris and Burns 2000; Ricketts et al. 2001). For example, Ricketts et al. (2001) found that the type of matrix habitat significantly affected the degree to which different butterfly species can move between isolated patches: most species moved freely through a matrix habitat of willow trees but were more isolated by a coniferous forest matrix.

The surrounding matrix habitat patches play an important role as a site for reproduction and possible source of food for some individuals (Varchola and Dunn 2001). Depending on the matrix type and the degree of habitat variation between matrix and habitat fragments, the edge will affect individual movement in varying ways (Ricketts 2001). Some organisms use the matrix as preferred habitat while others will be restricted to movement within the forest interior. Previous research has shown that some organisms can use matrix resources in favorable conditions but will retreat to alternate habitat fragments (hedgerows, forest edges, grassy fields, etc) during unfavorable times (Varchola and Dunn 2001; French et al. 2001; Magura et al. 2001). Alternatively, Gascon et al. (1999) found that a number of primary forest species are not solely limited
to movement within forest fragments but can utilize the matrix. Although there is support for movement in both directions across the edge, studies in agricultural landscapes suggest that is likely that there is a higher flux of insects from areas of high productivity to areas of lower productivity (Rand et al. 2006).

In this study, I examined the interactive effects of forest patch area, edge effects, and the surrounding agricultural matrix on beetle species richness and composition. Aerial beetle communities were sampled along 100-m transects that spanned the forest interior and into adjacent corn fields in eight forest patches of different size. As predicted by the species-area relationship, I expected to find high beetle species richness in larger patch areas. I hypothesized that the relationship between patch area and species richness would depend on edge effects. Because higher species richness occurred near forest edges, I predicted a greater difference in species richness and composition between edge and interior locations in large forest patches than in small ones. Finally, I predicted that the effects of area and edge on species richness would vary among beetle functional groups and variation in beetle composition would be related to differences in tree species composition among forest patches.

METHODS

STUDY SITES

Beetles were sampled from woodlots in southwestern Ohio on three separate occasions during the summer of 2003 (late June, August and September) using passive flight-intercept traps. Because insects are influenced by patch characteristics (Golden and Crist 1999; Collinge and Palmer 2002), woodlots were chosen based on their size, shape, orientation, and surrounding agricultural crop. Forest patches were scattered 2-20 km apart within a 50-km² area of an agricultural landscape. To minimize sources of variability woodlots were limited to those with straight, well-defined boundaries between forest and the adjacent fields and corn planted within 10 m of the forest edge. Sites with elevation changes and those with streams were eliminated. Eight forest patches were classified as either small (3-7ha), intermediate (15-20ha) or large (>80ha). Large sites are Hueston Woods (HW) and Bachelor Reserve (BR). Intermediate sites are Methodist (ME), Finch (FI) and Rosenberger (RO). Small sites are Herrmann (HE), Seals (SE), and
Wendel (WE). Landowners and farmers were surveyed for each site regarding information on agricultural practices and till regimes used during the farming season. Information on site location, vegetation characteristics and agricultural practices listed (see Table 1).

**INSECT SAMPLING**

A series of 11 directional flight-intercept traps (FITs) were arranged every 10 m along a 100 m transect line running perpendicular to each forest edge (Figure 2). These traps have been shown to capture most of the beetles that occur within habitats (Kitching et al. 2001; Hill and Cermak 1997). The location of the transect line was randomly chosen along the forest edge with the constraint that it was >100 m from other edges. Transects were positioned across the forest edge by designating the edge boundary as the first tree ≥ 10cm diameter breast height (dbh). One trapping station was located at the forest edge. Trap stations were spaced 10 m apart, with six traps extending 60 m into the forest interior, and four traps extending 40 m into the corn. More traps were positioned in the forest because of the expectation that the woodlot would be more heterogeneous than corn. Each transect line was permanently marked with flags to resample the same transects during the summer.

The flight-intercept traps consisted of a 60 x 60-cm Lexan panel within a PVC frame mounted on a pair of 1.5-m metal poles (Figure 3). Insects were collected in 60-cm PVC rain-gutter troughs capped at each end. Troughs were connected to the bottom edge of the trap face on both sides and filled with propylene glycol to capture insects traveling in either direction. To avoid wind and rain disturbances and to minimize the number of insects entering the traps from the side, 5-cm wide a plastic roof and walls were connected to the top and sides of the trap face (Figure 3). Poles were driven into the ground so the bottom of the trap face rested about 1.2m above ground.

All transects were sampled during each of three 2-wk sampling periods in summer 2003: 17 June–3 July, 30 July–15 August, and 13–26 September (hereafter referred to as Jun, Jul, and Sep samples). Four transects were sampled in the first week, and the remaining four were sampled in the second week. Sites were chosen randomly so as to include at least one small, intermediate and large site during each week of sampling. At the end of the 7-d sampling period, troughs were carefully removed and partially
processed by straining the propylene glycol off of the insect sample with a sieve. All insects were then placed in labeled jars and filled with 70% ethanol. Traps were removed from site and reassembled at the remaining four sites the same day to begin the next 7 d of sampling. Although eight sites were sampled, data are shown here for seven sites due to trap malfunctions at one intermediate-sized site during June sampling (ME) and one large site during both August and September (HW).

In the laboratory, samples were processed to separate beetles from other orders of insects. Beetles were individually pinned, pointed and labeled and placed into “morphospecies” based on morphological traits. All morphospecies were later identified to the family level, and the most common morphotypes were identified to species (Appendix A and B).

Beetles were placed into one of three guild categories depending on the general feeding preferences of each family: predator, herbivore or fungivore (Arnett et al. 2002). All beetles that did not fall into one of these three guilds were classified as “other” and were not included in guild analysis. Predators kill and consume other living organisms. Herbivores feed directly on leaves, flowers or fruits. Fungivores include beetles that consume fungi, sap, or wood. The latter two were included as fungivores because sap or wood feeders often consume the fungi associated with these plant products.

VEGETATION SAMPLING

To assess how beetles responded to changes in forest vegetation within and among transects, I conducted vegetation sampling during late May and early June 2003. A 10 x 110-m belt transect was set perpendicular to forest edge, and was centered on insect trapping stations. The belt transect was divided into 10 x 10-m quadrats. Trees ≥10 cm dbh were sampled through entire belt transect (Figure 2). Tree identity, dbh and location on transect were noted for each tree (Table 1).

DATA ANALYSIS

Here I was interested in overall patterns of beetle species diversity in relation to forest patch area, tree species composition, and edge effects, so I summed the species abundances from the two troughs at each trap location and across the three sampling periods. Next I summed together the pooled species abundances from each trap into one of three habitats; corn, edge or interior. Corn habitat is defined as the four traps that
extend 40 m into the corn, edge as the trap at the forest edge and those 10 m and 20 m into the forest, and interior as the four traps from 30 to 60 m from the forest edge.

Comparisons of species among forest patches and habitat type (corn, edge, forest) were conducted using sample-based rarefaction (Gotelli and Colwell 2001). Program EstimateS 7.5 (Colwell, 2004) was used to construct species rarefaction curves, which are plots of the observed species richness with the number of individuals sampled. These 95% confidence intervals of rarefaction curves were used to distinguish observed differences in species richness among forest patches and habitat types by comparing the overlap or non-overlap in confidence intervals at a fixed number of individuals sampled. The total beetle species richness present in all sampled areas was also estimated from the Chao 2 estimator, which is based on the number of observed species and the proportion of unique individuals to the number of duplicate individuals (Colwell, 2004). Unique individuals are those that are detected in only one sample, whereas duplicate individuals are those that are detected in, at least, two samples.

Non-Metric Multidimensional Scaling (NMS) was used to compare overall beetle species composition among forest patches and habitat types, and to examine the role of vegetation characteristics in determining beetle composition. This nonparametric ordination method positions samples according to their ranked species dissimilarity along two or more axes. The NMS algorithm seeks the best solution between the sample distances in ordination space and their pairwise dissimilarity (Ludwig and Reynolds 1988, McCune and Grace 2002). Samples that are closer together in the ordination are therefore more similar in species composition. A level of “stress” is a measure of the discrepancy between the rank order of sample dissimilarities and the ordination distances, which the NMS algorithm minimizes by iteratively altering values in ordination space (McCune and Mefford 1995). I used the Sørensen index as a measure of dissimilarity in species composition, and PC-Ord software (McCune and Mefford 1995) to conduct NMS analysis.

Several environmental variables were related to differences in beetle species composition among forest patches. Based on quadrat sampling the importance value of each tree species was calculated by habitat type in each patch. Importance values are the sum of the relative basal area, relative frequency, and relative density (0-3.0) for the 3 or
4 quadrats sampled in each forest patch and habitat type. I considered the importance values for the six most common tree species (those with average importance values of >0.20: ash, sugar maple, black walnut, hackberry, shagbark hickory, bitternut hickory). In addition to vegetation data, several other environmental variables were calculated from Digital Ortho Quarter Quad (DOQQ) images using ArcGIS (ver 9.1). These included forest patch area (ha), patch isolation (distance to nearest forest patch in km), total amount of edge in each patch (km), and total amount of forest cover within 1-km radius in the center of the focal patch. To determine which environmental variables were associated with differences in beetle composition among forest patches and habitat types (forest edge vs interior), the environmental variables were correlated with the NMS ordination axis scores for each forest patch and habitat type using PC-Ord.

RESULTS

A total of 18,136 beetles comprising 708 morphospecies and 59 families were sampled during the study. Sample-based rarefaction curves for all samples combined showed that species richness was still increasing by the end of sampling, but was beginning to level off slightly (Figure 15). Chao2 values also increased with increased sampling and only begin to level off to a stable estimate of species richness of 902 species towards the end of sampling with >15,000 individuals sampled. Although duplicate individuals rose steadily with number of individuals sampled, number of unique individuals does not reach an asymptote (Figure 15). Thus, new species continued to be encountered even after a total of 1848 trap-days (8 transects x 11 traps x 7 d/sample x 3 samples) that were conducted during the study.

There were clear differences in overall species richness among corn, edge, and interior habitat types (Figure 16). Forest-edge and interior locations had higher beetle abundances compared to corn habitat. To control for differences in the number of individuals sampled, species richness was compared among habitats at 3870 individuals (the total number found in corn). Here, species richness of edge habitat was significantly higher than corn and interior habitats as determined by overlap in 95% confidence intervals. On the other hand, corn and interior habitats were not significantly different
from each other because 95% confidence intervals for these habitats overlapped at this point on the graphs (Figure 16).

When compared among sites with abundances in all 3 habitats combined, species richness and total abundance varied widely (Figure 17). Rarefaction curves compared at 1092 individuals sampled (the lowest abundance, which was recorded in BR) showed that large (BR and HW) and small sites (WE, HE and SE) had distinctly higher species richness than intermediate sized sites (FI, RO and ME). Small sites clumped together with slightly lower richness than large sites.

Rarefied species richness values were further subdivided into species richness values by habitat (Figure 18). Total species richness was rarefied at 1092 individuals as shown in Figure 17, and comparisons of species richness by forest habitat types (edge+interior) were conducted at 702 individuals. Similar to the previous graph of rarefied species richness, intermediate sites (FI, RO and ME) showed lowest species richness, followed by small sites (SE, HE and WE) and large sites (BR and HW) had the highest species richness (Figure 18a).

Clear differences in species richness by site emerged when rarefaction is conducted by forest patch and habitat type (Figure 18b). Species richness of corn habitat was similar across sites regardless of forest patch size, with all sites showing overlapping confidence intervals. Species richness in edge and interior habitats, however, varied significantly among forest patches, and was largely responsible for the separation by size classes in overall species richness. Intermediate sites had the lowest edge and interior species richness, which was clearly lower than the species richness in the corn habitat. Small sites showed a similar species richness in all 3 habitat types, while large sites had higher species richness at the edge and interior than in corn habitat (Figure 18b).

For all three feeding guilds (predator, herbivore or fungivore), the highest abundances usually occurred in forest or at edge (Figure 19). Specifically, herbivores were most often sampled in the interior and at edge. Predators were most often sampled at the edge, and fungivores were most often sampled in the interior (Figure 19). By rarefying data to the lowest number of individuals sampled, there was overlap of all of the 95% confidence intervals for herbivores and fungivores (Figure 19a and 19c), suggesting that these two groups did not differ in species richness among habitats. The
species richness of predators, however, was significantly greater at edge than in corn but not greater than forest interior as judged by the overlap in 95% confidence intervals (Figure 19b).

Since site differences were important to forest diversity, multiple regression of environmental variables were calculated to determine what factors most affected forest species richness. Among the environmental variables tested, the log of forest patch area and importance values for sugar maple were the best predictors of site-level differences in rarefied species richness in the two forest habitat types combined (edge and interior) (F=5.83; p=0.049; df=2,5). These two variables both had positive effects on species richness and explained 70% of the variation in species richness among forest patches (Figure 20).

In the initial NMS ordination, I considered how beetle species composition was influenced by forest patches and all three habitat-type comparisons (Figure 21a). For samples including corn, the preliminary NMS analysis using 100 runs of the observed data showed that the 2-dimensional solution had stress values (mean=20.77) significantly lower (p=0.001) than those from 999 simulations of the randomized data (mean=28.03). Of the 100 runs on the observed data, the best NMS solution using two axes resulted in a stress=12.78. This best-fitting NMS ordination explained a total of 84.7% of the variation (Axis 1=53.0%, Axis 2=31.7%) in the Sørensen dissimilarity among sites. The stress-iteration plot for the best-fitting ordination showed a monotonic decrease in stress across 37 iterations to the final solution (final instability=0.00354).

Species composition due to habitat occurs along NMS axis 1, which was clear from the organization of corn, edge and interior from left to right along this axis (Figure 21a). Since there is less variation among corn samples (even from different sites) the data points converged with each other along the left side of axis 1. Nonetheless, beetle species composition in corn-edge-interior samples was similar within sites as shown by the consistent alignment of scores along NMS Axis 2, suggesting a proximity effect on beetle species composition between forest and corn habitat (and vice-versa). More variability in species composition occurred among edge and interior samples from different sites because of the greater range in ordination scores along axis 2. In addition,
there is probably some level of variability that can be explained, solely, by considering the different study sites involved in analysis.

There was a tendency for intermediate sites (ME, RO, FI) to group together as well as small sites (SE, WE, HE). Ordination distances between forest edge and interior locations were small compared to distances between forest and corn. This shows that, although edge and interior samples differed from each other, they were more similar to each other than they were to corn samples (Figure 21a).

I further considered how among-site and edge-interior forest habitat related to shifts in beetle species composition. Preliminary NMS analysis using 100 runs of the observed data showed that the 2-dimensional solution had stress values (mean=16.23) that were significantly lower (p=0.003) than the stress values from 999 simulations of the randomized data (mean=23.09). From 100 runs using the real data, the best NMS solution using two axes resulted in a stress=12.38. This best-fitting NMS ordination explained a total of 80.9% of the variation (Axis 1=70.1%, Axis 2=10.8%) in the species dissimilarity among sites. The stress-iteration plot for the best-fitting ordination showed a monotonic decrease in stress across 28 iterations to the final solution (final instability=0.00386).

Five environmental variables of forest-patch area and tree importance values were correlated ($r^2=0.15$) with NMS axis 1 or 2 (Figure 21b). With the exception of total amount of edge, however, all other landscape variables were highly correlated with patch area. The most important variables associated with insect species dissimilarity among sites were hackberry importance ($r^2=0.42$), sugar maple importance ($r^2=0.33$), and patch area ($r^2=0.17$) on axis 1, and patch area ($r^2=0.13$) on axis 2. Edge was not correlated with either NMS axis. Other variables measured, such as volume of coarse woody debris, percent cover herbs, percent cover shrubs/honeysuckle did not appear be related to size or habitat type and are, therefore, not discussed (Table 1).

Beetle species composition among the eight forest patches could therefore be characterized by a gradient from hickory to maple tree dominance, with a secondary influence of patch area (Figure 21b). Forest patches of intermediate size were dominated by hickory while small patches were primarily composed of sugar maple. Patch area most influenced beetle species composition of large vs intermediate and small patches,
but did not distinguish beetle composition between intermediate and small patches. Site identity was also important in that edge and interior locations within the same site were always more closely associated with each other than they were with the same habitat types in different sites.

**DISCUSSION**

My study supports the role of forest patch size on beetle species richness, such that larger sites have higher species richness, but goes beyond previous studies by documenting differences in species richness in forest interior and edge as well as the surrounding agricultural matrix habitat. Although there were clear effects of patch area on beetle species richness present in this study, shifts in beetle species composition among habitat types and forest patches were even more important.

Patch size played a large role in determining beetle species richness (Connor and McCoy 1979; Summerville and Crist 2001; Krauss et al. 2003). Large forest fragments supported the highest beetle species richness, followed by small sites. Intermediate sized sites had the lowest species richness. Golden and Crist (1999) showed that abundance and species richness was higher in unfragmented habitat patches compared with highly fragmented patches. In addition to this, Barbosa and Marquet (2002) found this same pattern in species richness with small patches (2m fragment) having higher richness than the species richness of the intermediate patches (14.2m fragment) in all but summer.

This pattern of highest species richness in large fragments, followed by small and intermediate is more clearly detailed when divided by habitat. Species richness values throughout corn fields at all sites are generally the same. In this study, species richness for a site was driven by the species richness of the forest (Figure 17). Intermediate sites showed much lower species richness than small and large sites. In the case of this study, the departure of intermediate sites from other size classes was, most likely, caused by the tree composition within each site. Intermediate forest stands were dominated primarily by hickory trees whereas small and large sites had stands composed of maple trees. Small sites showed similar species richness values in all 3 habitats. This is in support of my Chapter 2 hypothesis that small sites would be most similar to the matrix. Finally, large sites showed much higher richness at the edge and interior than in the corn. This is
in agreement with the species-area relationship (Connor and McCoy 1979) which suggests higher species richness in larger habitats.

Forest patch area and tree importance value of sugar maple influenced beetle species richness. There was a shift in tree dominance from hickory in intermediate sites to sugar maple in small sites. This was a likely outcome due to the fact that beetles are often found to be closely associated with vegetation in a particular area (Foord et al. 2003), or particular host trees (Gering and Crist 2002). Summerville and Crist (2004) found a similar set of tree composition and diversity, and forest log area to be most important in determining moth species richness. They found that sites with high tree species diversity and large area supported greater diversity of Lepidopterans. My study supports that large sites have higher diversity. In this case, dominant forest composition was more important than, solely, the total diversity of trees within the forest.

Beetle composition may be directly linked to specific types of trees or there may be an indirect connection with tree type and the environmental conditions that these trees grow preferentially in. For instance, soil moisture levels that support a particular assemblage of trees may also influence the plant diversity of the site. Jokimäki et al. (1998) found that arthropod abundance was significantly and positively affected by 20 different vegetation characteristics. They showed that total number of trees in an area was a better predictor of abundance than other edge effects measured. At a finer scale, Gering and Crist (2002) found significant variation in the beetle species richness found on different host-tree species.

The findings of this study emphasize the importance of the surrounding matrix on the diversity and composition within natural habitat remnants. A number of other studies have found the matrix to be important in determining species composition within patches (Duelli et al. 1990; French et al. 2001; Barbosa and Marquet 2002; Bommarco and Fagan 2002). This study further demonstrates potential for spillover effects on species composition between a natural habitat into an agricultural matrix (and vice versa). Gascon et al. (1999) found 40-80% of primary forest species of vertebrates and ants also occur in the matrix. They also found that those species that utilize the matrix increase or remain stable in forest fragments while those that do not utilize the matrix are susceptible to decline.
Analysis of feeding guilds illustrates how these different functional groups of beetles respond to different habitats. Predators were most influenced by differences in habitat type. Predator species richness was significantly higher at the edge than in corn. This is consistent with Chapter 1 analysis in which predators showed a huge spike in abundance at the forest edge compared to relatively low abundances throughout corn and forest habitat (Figure 13). Other studies report high abundance and richness of predators at a habitat edge (Didham 1998b; Jokimäki et al. 1998; Magura et al. 2001; Ries and Fagan 2003). This is suspected to be the case because of the complementary resource use by predators. By using resources in both the forest and corn predators will have access to increased food availability or ease in catching prey although this is not specifically addressed in my study.

Studies of insect biodiversity often fail to completely sample the true species richness (Didham 1998a). In this study, the sampled species richness did not reach an asymptote with increasing sampling effort. With a Chao2 value of 902 species and an observed species richness of 708, an estimated 78% of the total species richness was sampled during this study. As sampling approaches the true species richness unique species are expected to decrease while duplicate species are expected to increase. When studying beetles in agricultural regions it is common to find that even with high numbers of samples, Chao2 does not level off as expected suggesting that new species are often encountered with increased sampling effort. Duelli et al. (1990) found that the number of insects flying over the corn is larger than the number of adults in the corn field. This may not be important early in my sampling season when the corn plants were just emerging and not impeding beetle flight, but in August and September sampling trap faces were covered by the cornstalks and some beetles moving away from forest may have flown above level of corn and, therefore the level of the trap. Another possible reason we do not see Chao2 level off is because spillover effects make it hard to completely sample each habitat. Finally, more seasonally intensive sampling would likely help because some unique individuals might represent species at the tail end (or beginning) of their adult activity period. For instance, in this study, the family Brachypteridae occurred only in September sampling. Even after 2 sampling periods new species emerge as adults. Conversely, it is possible that early in June sampling some beetles completed their adult
life cycle prior to trapping but stragglers remained although there is not the opportunity to
catch duplicate individuals.

There are many important questions to consider when focusing on species
composition or biodiversity of a location. Here I illustrated that forest size, tree
dominance, habitat type and guild classification are all valuable measures to the
determination of species composition. Consideration of matrix species presents a more
complete view of the community since habitat edges vary in their permeability (Fagan et
al. 1999). It is clear that cross-boundary subsidies are a real and important process that
exists in natural-agricultural systems such as suggested by Rand et al. (2006). Some
beetles have been identified as significant pest to crops and predators for native
organisms while other native organisms are significant predators of non-natives.
Understanding the dynamics of one of the most diverse groups of organisms will help us
to predict the impact of agricultural land use on species diversity and composition.
Figure 15. Rarefaction curves showing overall species richness for all samples combined. The curve for observed species richness shows a 95% confidence interval.
Figure 16. Rarefaction curves comparing species richness among habitats. In all figures, Corn = traps 0-3, Edge = traps 4-6 and Interior = traps 7-10.
Figure 17. Rarefactions curves showing species richness as a function of the number of individuals in each site individually.
Figure 18. Species richness for each site broken down by a) total vs. forest richness and b) richness by habitat. Large sites (BR, HW), Intermediate sites (ME, RO, FI) and Small sites (WE, HE, SE)
Figure 19. Rarefaction curves showing species richness of beetles in different feeding groups divided by habitat. a) herbivores, b) predators and c) fungivores.
Figure 20. Line graph to compare predicted and observed values of species richness for 8 woodlots. Plotted with data from multiple regression analysis showing maple importance value and log area to be most important predictor variables (a). Individual line graph showing species richness by b) maple importance value and c) patch log area.
Figure 21. NMS ordination plots showing analysis results with: a) corn trap data included and b) without corn trap data but with significant environmental variables overlaid. Open squares = Corn, filled squares = Edge and filled triangles = Interior samples. Dashed lines connect habitat values from same site.
CHAPTER 4 – Synthesis and Conclusions

Forest fragmentation is hypothesized to affect community dynamics as well as ecosystem functioning (Didham 1998; Sala et al. 2000). In this study, forest patch area and tree importance values were shown to be the best predictors of site-levels differences in beetle composition. Large sites have the highest species richness and total abundance values, followed by small sites and intermediate sites have the lowest species richness and beetle abundance (general findings listed in Table 2).

There are a few possibilities to explain the variability in beetle species richness and abundance in different-sized forest sites. The first possibility is the type of tillage regime used in the adjacent agricultural field. Both large and small sites were adjacent to corn fields under a no-till (100% plant residue remaining) or conservation tillage (>30% plant residue remaining) regime. Intermediate sites were either reduced-till (15-30% plant residue) or conventional till (<15% plant residue)(see Table 1). Tscharntke et al. (2005) suggests that some organisms increase in abundance in natural habitats after disturbances in a crop field. This would explain the higher than expected abundance and beetle species richness values shown in chapter 2. The second possible explanation for the variability in beetle species richness and abundance would be the use of pesticides to control crop pests (vegetative or insect pests). In the case of this study, all intermediate sites, as well as, one large and one small site, had insecticides applied to the adjacent crop field around the time of planting (Table 1).

Although intermediate sites have both, a more intensive tillage regime and insecticide application to crop fields, this does not appear to explain the variation in beetle species richness or abundance. Figure 19 shows no outliers from the predicted pattern of values, with the exception of one. If the tillage regime or insecticide use was affecting intermediate sites separately from patch size effects the intermediate sites would be expected to diverge from the line together.

Intermediate sites showed much lower species richness than small and large sites. In the case of this study, the departure of intermediate sites from other size classes was, most likely, caused by the tree composition within each site. Intermediate forest stands were dominated primarily by hickory trees whereas small and large sites had stands composed of maple trees. For the purposes of conclusions, intermediate sites will be left
out. Future work on forest fragmentation should focus on minimizing site level
differences in tree stand composition.

Cross boundary subsidies are thought to influence both the native and non-native
species in the landscape (Rand et al. 2006). I found the largest values of paired
differences at the edge traps, suggesting movement across the edge. In addition, patch
size determined how beetles moved at the edge with beetles in large sites moving towards
the interior and those in small sites moving towards corn. One possible explanation to
explain these patterns is that beetles in small sites have a higher probability of
encountering an edge and, therefore crossing it, compared to large sites (Schtickzelle and
Baguette 2001).

Another explanation for patterns of movement in large and small fragments is the
percentage of the community that is made up of specialists versus generalist beetles. The
general consensus is that by decreasing the size of natural habitat, habitat specialists and
other organisms susceptible to population fluctuations decrease in numbers (Straw and
found that 14 out of 16 “hard edge” species were found only in large patches. Within
their agricultural systems, “hard edge” species were habitat specialists on natural land.

More details will emerge from this data (or other future datasets) if feeding guilds
are further subdivided into habitat specialists and generalists. It is more likely that large
sites have a higher proportion of habitat specialists and this could explain the movement
away from the edge into the forest. If this is the case it will support the movement of
beetles (more generalists) across the edge into the corn for small sites as shown in chapter
2.

The two data chapters in this thesis consider different approaches with regards to
determining species composition. Chapter 2 analysis focused on flux-based measures to
determine beetle composition. This type of approach assumed that there were specific
edge-associated species that exhibited some level of movement. In addition, it assumed
that there was no distinct community that existed in each habitat because of the fluidity of
organisms moving within the site. Chapter 3 used a more classical, resident-based,
approach. This type of analysis assumed that a distinct community of resident species in
each site with little movement between habitats.
Although these two chapters use the data separately with different sets of assumptions, they are, in essence, snapshots of the same thing. The question to consider is: were the movement patterns seen in Chapter 2 due to transient species or was the edge acting as a hard (impermeable) edge and beetles stayed in the habitat they prefer? There was an expectation that there were a certain percentage of the beetle community that were resident species that did not move much. These beetles would be part of a particular habitat and would not be caught in any other habitat. For instance, in this study, flat bark beetles (family Cucujidae) and members of the family Brachypteridae were found only in interior samples. These beetles are associated with woody habitats and were, rarely, caught out of interior habitat. In addition, click beetles (family Elateridae; false wireworm larvae) and long-horned beetles (family Cerambycidae) were caught most often at the edge. They are capable of using resources from both habitats at some point in their life history.

The data matrix for this project showed that a high proportion of individuals showed this pattern of high abundance and species richness at the edge. They were often found in low numbers, or not at all, throughout the rest of the habitats. These “edge” species show high levels of movement to access multiple resources and would be expected to have no net difference in individuals or species because they would cancel each other out. In the case of my study, species using both sides of the edge drove the patterns seen in net difference in total abundance and species richness. The community response showed abundance and richness higher at the edge.

Although there was higher species richness and total abundance of beetles at the edge it was impossible to separate this from the sampling effort or real effects of habitat heterogeneity. Habitat heterogeneity would be expected to influence higher number of individuals at the edge and the possibility of a higher flux of organisms. In Chapter 3, I corrected for sampling effect differences between sites by using rarefaction. Even after this rarefaction, the edge still showed highest levels of beetle species richness and total abundance, suggesting that habitat heterogeneity influences beetle community dynamics. Unfortunately, none of the vegetation variables (% cover herbs, % cover shrubs, % cover honeysuckle, volume CWD) measured appeared to show any differences by size or habitat.
In conclusion, this study shows evidence for directed movement across an edge between forest and corn. Understanding the forest patch qualities (patch area and stand composition) that influence species composition at a site and how beetles move between habitats is important to maintain current levels of biodiversity. Movement between habitats can have significant effects on, not only, native species within forest patches but on possible biological control of insect pests within agricultural fields.
Table 2. Comparisons of beetle community responses from analyses within and among transect samples in forest interior, edge, and corn habitats at eight different locations.

<table>
<thead>
<tr>
<th>Community Response or Habitat Effect</th>
<th>Chapter 2 Within Sites</th>
<th>Chapter 3 Among Sites</th>
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<tbody>
<tr>
<td>Total abundance</td>
<td>Highest in interior or edge</td>
<td>Highest in interior</td>
</tr>
<tr>
<td>Species richness</td>
<td>Highest at edge</td>
<td>Highest at edge</td>
</tr>
<tr>
<td>Species dissimilarity</td>
<td>Highest at edge</td>
<td>Forest distinct from corn, but site proximity effects between forest and corn</td>
</tr>
<tr>
<td>Fungivores</td>
<td>Highest abundance in interior; net fluxes from corn to forest</td>
<td>Highest abundance in interior, but similar richness across habitats</td>
</tr>
<tr>
<td>Herbivores</td>
<td>Highest abundance at edge and interior; net fluxes variable</td>
<td>Higher abundance at edge and interior but similar richness across habitats</td>
</tr>
<tr>
<td>Predators</td>
<td>Highest abundance at edge; net fluxes variable</td>
<td>Highest richness and abundance at edge</td>
</tr>
<tr>
<td>Forest area</td>
<td>Net flux of beetles from corn to forest in large patches; forest to corn in small patches</td>
<td>Larger forest patches had higher species richness; no effect on corn</td>
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<tr>
<td>Tree species composition</td>
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<td>Sugar maple vs hickory affected beetle composition</td>
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LITERATURE CITED


Oecologia 116: 397-406.


Appendix A. Beetle families listed in order of abundance. F = fungivore, H = herbivore, P = predator, S = scavenger.

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Appendix B. Some of the more commonly found beetles that were identified past the family level listed here by family with either Subfamily or *species information* below each.

- **Aderidae**
- **Anobiidae**
- **Anthicidae**
  - *Notoxus desertus*
  - *Notoxus murinipennis*
- **Anthrribidae**
- **Biphyllidae**
- **Bostrichidae**
- **Brachypteridae**
- **Bruchidae**
- **Buprestidae**
- **Byrrhidae**
- **Bytiridae**
  - *Byturus unicolor*
- **Cantharidae**
- **Carabidae**
  - *Lebia analis*
  - *Lebia sp.*
  - *Selenophorus hylacis*
  - *Cinindela sp.*
- **Cerambycidae**
  - *Cyrtophorus verrucosus*
  - *Strangalia luteicornis*
  - *Oberea affinis*
  - *Orthosoma brunneum*
- **Ceratocanthidae**
- **Cerylonidae**
- **Chrysomelidae**
  - *Diabrotica undecimpunctata*
  - *Ceratoma trifucata*
- **Cleridae**
  - *Charisessa pilosa*
  - *Charisessa p. marinata*
- **Coccinellidae**
- **Coccinellini**
- **Colydiidae**
  - *Eucicones marginicollis*
- **Coryphidae**
- **Cryptophagidae**
- **Curculionidae**
  - *Scolytinae*
- **Dermestidae**
  - *Attagenus unicolor*
  - *Trogoderma inclusum*
- **Elateridae**
- **Elmidae**
- **Endomychidae**
- **Erotylidae**
- **Eucnemidae**
- **Heteroceridae**
- **Histeridae**
- **Laemophloeidae**
  - *Cryptolestes sp.*
- **Laguridae**
- **Lampyridae**
- **Latridiidae**
- **Leiodidae**
- **Lucanidae**
  - *Alleculinae*
- **Lyctidae**
- **Melandryidae**
- **Mordellidae**
- **Mycetophagidae**
- **Nitidulidae**
  - *Carpophilus sp.*
  - *Glistrochilus quadrisignatus*
  - *Glistrochilus fasciatus*
- **Oedemeridae**
- **Passadridae**
- **Phalacridae**
- **Ptiliidae**
- **Ptilodactylidae**
  - *Ptilodactyla sp.*
- **Pyroceridae**
  - *Neopyrocerhioa flabellata*
  - *Anisotria sp.*
- **Scarabaeidae**
  - *Papillia japonica*
- **Silphidae**
  - *Nicrophorus sp.*
  - *Slipa sp.*
- **Silvanidae**
  - *Telephanus sp.*
  - *Uleiota sp.*
  - *Silvanopris sp.*
- **Sphindidae**
  - *Sphindus americanus*
- **Staphylinidae**
- **Tenebrionidae**
  - *Alleculinae*
  - *Statira sp.*
  - *Arthromacra sp.*
- **Tetramotidiae**
- **Throscidae**
- **Trogidae**
- **Trogossitidae**