Examining Shifts in Carabidae Assemblages Across a Forest–Agriculture Ecotone

T. W. LESLIE,[1,2] D. J. BIDDINGER,[3] J. R. ROHR,[4] A. G. HULTING,[5] D. A. MORTENSEN,[6] AND S. J. FLEISCHER[7]

Environ. Entomol. 43(1): 18–28 (2014); DOI: http://dx.doi.org/10.1603/EN13099

ABSTRACT Northeastern U.S. farms are often situated adjacent to forestland due to the heterogeneous nature of the landscape. We investigated how forested areas influence Carabidae diversity within nearby crop fields by establishing transects of pitfall traps. Trapping extended across a forest–agriculture ecotone consisting of maize, an intermediate mowed grass margin, and a forest edge. Carabidae diversity was compared among the three habitats, and community and population dynamics were assessed along the transect. We used a principal response curve to examine and visualize community change across a spatial gradient. The highest levels of richness and evenness were observed in the forest community, and carabid assemblages shifted significantly across the ecotone, especially at the forest–grass interface. Despite strong ecotone effects, population distributions showed that some species were found in all three habitats and seemed to thrive at the ecotone. Based on similarity indices, carabid assemblages collected in maize adjacent to forest differed from carabid assemblages in maize not adjacent to forest. We conclude that forest carabid assemblages exhibit high degrees of dissimilarity with those found in agricultural fields and forested areas should thus be retained in agricultural landscapes to increase biodiversity at the landscape scale. However, ecotone species found at forest edges can still noticeably influence carabid community composition within neighboring agricultural fields. Further studies should determine how these shifts in carabid assemblages influence agroecosystem services in relation to ecosystem services observed in fields embedded in an agricultural matrix.

KEY WORDS Carabidae, biodiversity, edge effect, landscape, maize

Beneficial insects that provide important agroecosystem services, such as pest control and pollination, are often monitored within crop fields to assess nontarget impacts from agricultural practices such as tillage and pesticide use. Although many of these agricultural practices can have direct or indirect effects on nontarget insect communities at the field scale, these communities can also be influenced by habitat adjacent to the crop (Ponti et al. 2005, Marshall et al. 2006) and the surrounding landscape at broader scales (Marino and Landis 1996, Steffan-Dewenter et al. 2002, Tscharntke et al. 2005, Chaplin-Kramer et al. 2011, Watson et al. 2011). In some instances, the surrounding landscape context may override the effects of within-field agricultural inputs (Purtauf et al. 2005), indicating that maintenance of agroecosystem biodiversity and associated ecosystem services may hinge on land management at multiple scales (Landis et al. 2000, Kremen et al. 2004).

By their nature, agroecosystems in the northeastern United States have numerous habitat interfaces with unmanaged noncrop or natural areas comprising between 25 and 80% of the landscape (Egan and Mortensen 2012). Agricultural landscapes in the northeast are characterized by many farms, often small in size relative to other regions of the United States, embedded in a mosaic of forestland, grassland, riparian habitat and development around urban areas. Part of this landscape mosaic consists of large acreages of forestland, often adjacent to agricultural fields. In general, diversified agricultural landscapes with substantial areas of noncrop habitat seem to promote diversity of beneficial arthropods (Pluess et al. 2010, Watson et al. 2011) and their associated ecosystem services (Tscharntke and Kruess 1999, Bianchi et al. 2006). However, the effects of landscape complexity on biodiversity can be mixed (Kleijn et al. 2001, Winqvist et al. 2011), scale-dependent (Steffan-Dewenter et al. 2002), or inconsistent (Menalled et al. 1999).

[1] Department of Biology, Long Island University, 801 Metcalfe Bldg., 1 University Plaza, Brooklyn, NY 11201.
[2] Corresponding author, e-mail: timothy.leslie@liu.edu.
[3] Department of Entomology, Penn State University, Fruit Research and Extension Center, 290 University Dr., Biglerville, PA 17307.
[4] Department of Biology (SCA 137), University of South Florida, 4202 East Fowler Ave., Tampa, FL 33620.
[5] Department of Crop and Soil Science, Oregon State University, 109 Crop Science Bldg., Corvallis, OR 97331.
[6] Department of Crop and Soil Sciences, Penn State University, 422 ASI Bldg., University Park, PA 16802.
[7] Department of Entomology, Penn State University, 501 ASI Bldg., University Park, PA 16802.

0046-225X/14/0018–0028$04.00/0 © 2014 Entomological Society of America

Downloaded from http://ee.oxfordjournals.org/ by guest on December 31, 2016

Habitat directly adjacent to agricultural fields can act as reserves for natural enemies. For example, predatory beetles may use noncrop refugia for overwintering purposes before recolonizing arable land (Petersen 1999), and many parasitoids and pollinators seek out nectar and pollen sources at field margins (Landis et al. 2000, Carvell et al. 2007). Assessing the permeability of field edges can be important for interpreting how adjacent habitat may contribute to insect diversity within agricultural fields. The propensity for species to move from noncrop habitat into an adjacent agricultural field has been described by several distribution patterns, which can range from the extremes of stenotopic (habitat specialist) to ubiquitous (Duelli and Obrist 2003).

In this study, we sought to better understand how within-crop carabid communities are influenced by adjacent forestland habitat—a situation not uncommon in the heterogeneous landscape of the northeastern United States. We used the stark contrast in disturbance, land management practices, and plant diversity and structure between large forested areas and adjacent fields of maize to examine Carabidae community composition across the interface of these habitats. We feature several different analytical methods that may be used to describe shifts in carabid composition across the ecotone. To further understand how forested areas may influence the structure of carabid communities in neighboring maize fields, we also compared the carabid assemblages in our forest-edge maize locations with carabid assemblages collected from other recent studies in maize in the region but not adjacent to forest. Carabids were selected because they are agriculturally important predators of pest insects, slugs, and weed seeds (Sunderland 2002, Tooley and Brust 2002); as epigeal arthropods, their scale of movement may be constrained to relatively short distances; and they include taxa that have achieved relatively recent and rapid diversification (Ober 2011).

Changes in community composition were assessed by pitfall trapping at three scales. At a 1) *small discrete scale*, carabid communities were compared among three habitat types: maize, grassy field-margin, and neighboring forestland. Using a novel adaptation of the principal response curve (PRC), we then assessed changes at a 2) *small continuous scale* by examining population- and community-level shifts across the ecotonal gradient, as defined by transects of traps extending from forest to maize. Finally, to assess the spillover effects of forested field edges at larger scales we considered 3) *landscape context;* similarity indices were used to compare carabid communities from forest-adjacent maize (i.e., current study) with carabid communities collected from previous studies in maize over multiple years (Leslie et al. 2007, 2009, 2010), which were embedded in an agricultural matrix and not adjacent to forest (at 250 m radius). We hypothesized carabid communities would vary greatly among the three discrete habitat types; however, species spillover from forest to maize would be sufficient enough to detect differences between carabid communities in forest-adjacent maize compared with communities found in maize surrounded by agricultural fields.

Materials and Methods

Study Sites. This experiment was carried out in the Ridge and Valley physiographic province of Pennsylvania. This region is characterized by long, relatively narrow, agriculturally dominated valleys with soils derived from limestone or shale. The valleys are bordered on each side with steep, rocky, sandstone or quartzite forested slopes. Farms located in the center of the valley are embedded in an agricultural landscape, whereas farms at the edge of the valley share a border with the forested slopes. For this ecotone study, three replicate sites (each separated by >[1/2] km) of no-till maize adjacent to forest were established in 2005 at the Russell E. Larson Agricultural Research Center in Pennsylvania Furnace, PA. Two sites consisted of Andover channery loam soil (AnB and AnC), and the third was a Hagerstown silt loam (HaA). The agricultural field portions of each site were planted to maize in 2004 to represent continuous no-till maize management and to establish a baseline community of arthropods. The grass strip was mowed several times annually and the forest edge remained unmanaged.

In the 4 yr before this study, we also monitored carabids in maize and sweet corn production at two other sites at the Russell E. Larson Agricultural Research Center to assess effects of farming systems on epigeal coleopterans (Leslie et al. 2007, 2009, 2010). The sites were embedded in an agricultural matrix and situated a substantial distance from the forest edge (400–950 m). We compared these historical data—representing 11,517 specimens from 4,032 traps over 38 sampling dates—with the carabid data from forest-adjacent maize in our current study to consider how landscape context may influence carabid communities within maize in the Ridge and Valley region of Pennsylvania, and how these large-scale patterns relate to the small-scale patterns we observed in the current study.

Insect Collection and Identification. Four transects of 10 pitfall traps were established at each of the three research sites (i.e., no-till maize field adjacent to forest), for 120 pitfall traps in total. Individual transects extended from the maize field (four traps), through a narrow grass field margin (two traps), and into the neighboring forestland (four traps). Traps were spaced 5 m apart, except for one distal trap located in the interior of the maize field and one distal trap in the interior of the forestland, which were placed 15 m from the penultimate trap in either direction. Pitfall sampling occurred on eight dates at approximately 3-wk intervals spanning late May to late October, resulting in 960 samples. Traps were open for 72 h during each sampling period. All captured carabids were sorted, pinned, and identified to species. Voucher specimens are stored in the laboratory of S.J.F. at the Department of Entomology, Pennsylvania State University. Species were identified using several

Downloaded from http://ee.oxfordjournals.org/ by guest on December 31, 2016

taxonomic keys (Downie and Arnett Jr. 1996, Ciegler 2000, Marshall 2006), voucher specimens from previous studies (Leslie et al. 2007, 2009, 2010), and assistance from Robert Davidson (Carnegie Museum of Natural History, Pittsburgh, PA).

Data Analyses. Carabid data were pooled across dates, for each trap location at each site. Beetle data were recorded as activity-density (number of beetles/trap/72 h) for each species. These data were used for analyses at the aforementioned three levels of spatial scale:

Habitat Type (Small-Scale Discrete). Carabidae species richness and evenness were compared among the three habitat types covered by the transect: maize, grass, and forestland. Species richness was examined by rarefaction curves developed in EstimateS 8.2 (Colwell 2005) using 50 permutations of the data. Individual-based rarefaction curves were used for all comparisons of carabid species richness due to the different capture rate of carabids among the habitats of varying structural complexity (Gotelli and Colwell 2001). Interpolated species richness was then compared among habitats at an equal number of individuals collected. Significance was determined by nonoverlapping confidence intervals. Evenness of the carabid community was evaluated by ranking species by proportional abundance for each habitat and calculating Pielou's index of evenness (Pielou 1966, Beisel et al. 2003). We also calculated classic Sørensen and Jaccard similarity indices in EstimateS 8.2 (Colwell 2005) to compare species complementarity among the three habitat types at the forest-adjacent location.

In addition to examining carabid diversity among the three general habitat types (i.e., maize, grass, and forestland), several continuous environmental variables were measured for analyses. Herbaceous plant diversity was assessed in a 0.25-m^2 quadrat by identifying and estimating percentage cover of each plant species at the site of each pitfall trap. From these data, plant species richness and Simpson's Index of Diversity were calculated for each trap location on the transect. Vegetative structural complexity was also measured at each trap by visual estimation of percentage ground, litter, and canopy cover within each quadrat. Plant data were recorded in all habitats in late summer with conditions representative of canopy closure in the forestland and grass and those characteristics of late-emerging summer annual weeds in the maize.

We used a constrained ordination approach to identify species groupings within the carabid community based on their association with the three habitat types and the environmental variables related to plant diversity and vegetation structure at each trap location. The significance of carabid community gradients was assessed by redundancy analysis (RDA) performed in CANOCO 4.5 (ter Braak and Šmilauer 2002). Species–environment associations were visualized in biplots developed in CanoDraw 4.5 (ter Braak and Šmilauer 2002). A forward selection procedure using Monte Carlo permutations identified the environmental variables that most influenced carabid community composition. Only species that represented >1% of total abundance were used in ordination analyses.

Position on Transect (Small-Scale Continuous). We used a novel adaptation of PRC to measure carabid community dynamics across the trap locations on the transect. PRC is a form of constrained ordination in which communities subjected to a treatment are measured in relation to a control community over time. For our study, we used PRC to examine community dynamics over a spatial, rather than a temporal, gradient. We identified the "control" community as the carabid community collected at the distal trap location in the interior forest because this position was the furthest from the maize and theoretically was the site of lowest disturbance. Carabid communities collected at each trap location along the transect were then compared with this interior forest community. The dissimilarity between the control community and the community at each trap location was enumerated with canonical coefficients that were plotted on a distance-based gradient. On the diagram, the control community (i.e., forest-interior) is represented as a horizontal line set to 0.0, and the plotted canonical coefficients represent the extent of community differentiation across the spatial gradient. Given the association of each trap location with one of the three habitats, we then superimposed habitat delineations on the PRC diagram to visualize how communities responded within habitats and at ecotones (i.e., forest:grass and grass:maize).

In addition to the PRC trajectory, this procedure provides taxon weights for each species in the community. Taxon weights represent how closely each species follows the principal response. A positive taxon weight indicates the species follows the PRC, whereas a negative taxon weight indicates the species responds in the opposite fashion. The absolute value of the taxon weight indicates the strength of the relationship to the principal response, with greater absolute values indicating a strong relationship. Because taxon weights between −0.5 and 0.5 are generally considered insignificant, species falling between these values are not shown in the diagram.

Species-level taxonomic resolution also allowed us to investigate habitat specificity and species distributions. We conducted an indicator species analysis (Dufrene and Legendre 1997) in PC-ORD (v. 5.01; McCune and Mefford 1999) to further define species associations with each habitat type. The indicator value for a species is a product of its relative abundance (within a habitat) and its relative frequency (experiment-wide) multiplied by 100. Monte Carlo permutations randomly assigned samples among the three habitat types 9999 times, and the empirical data were compared with the permuted results to determine the significance of the indicator value for each species. To better understand species that may thrive at the forest edge and influence carabid diversity within neighboring agricultural fields, we plotted population distributions of the species with high activity-densities (>1% of total) that were not associated with

Downloaded from http://ee.oxfordjournals.org/ by guest on December 31, 2016

any single habitat as determined by indicator species analysis.

Landscape Context (Large-Scale Discrete). Carabid communities collected from maize over 5 yr at different locations throughout the Russell Larsen Agricultural Research Center were compared to examine the influence of landscape context on within-maize carabid communities. Site locations from the current ecotone study were labeled as "forest-adjacent" maize, and the study sites described by Leslie et al. (2007, 2009) were labeled as "ag-matrix" maize, as they contained no adjacent forested habitat. We measured similarity for all pairwise combinations of site locations (both forest-adjacent and ag-matrix) using classic Sørensen and Jaccard indices in EstimateS 8.2 (Colwell 2005). We note that sampling was conducted in different years, which may confound our ability to fully attribute dissimilarity among locations to landscape context alone. However, our pairwise comparisons between ag-matrix locations across multiple years provide evidence of typical variability in communities across years. Therefore, if forest-adjacent maize communities are noticeably dissimilar to ag-matrix communities, it is likely due to landscape context and not simply year-to-year variation.

To verify differences in landscape context among locations, we used clip and buffer techniques in ArcGIS to quantify percent cover at 250 m radius for each of the following five land use types: 1) developed open space, 2) cultivated crops, 3) pasture/hay, 4) open water, and 5) deciduous forest. Satellite imagery of Centre County, PA, was obtained from the PAMAP program (Cycle 1, 2006) and originated from the PA DCNR Bureau of Topographic and Geologic Survey and the U.S. Geological Survey. The 2006 United States National Land Cover Database (Fry et al. 2011) was used for the 250-m-radius map and accompanying land use statistics. A 250 m radius was chosen to accurately represent the immediate landscape context surrounding each maize field and was appropriate for potential scale of movement for epigeal arthropods based on radio-tracing (Charrier et al. 1996) and mark-and-recapture (Coombes and Sothertons 1986, Kagawa and Maeto 2009) studies.

Results

Habitat Type (Small-Scale Discrete). We identified 85 species from 960 pitfall samples. The forestland carabid community exhibited significantly higher species richness than the carabid community in maize (Fig. 1) based on nonoverlapping 95% confidence intervals, a highly conservative means of testing significance (Payton et al. 2003). Carabid species richness in the grass fell between forest and maize levels but was not significantly different from either. At a rarefied level of 300 individuals, the forestland community had accumulated an average of 50 species, compared with 40 species in grass and 29 species in maize. Based on the length of the rarefaction curves, carabid activity-density was two to three times greater in maize than in the grass and forestland (Fig. 1).

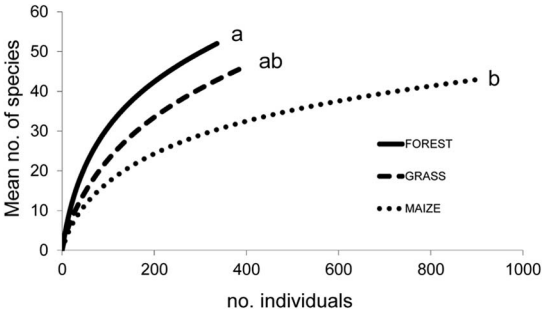

Fig. 1. *Species richness.* Individual-based rarefaction curves depicting Carabidae species accumulation in forestland, grass, and maize.

Based on Pielou's evenness index, carabid community evenness was highest in forest ($J' = 0.821$), followed by grass ($J' = 0.596$) and maize ($J' = 0.493$). The carabid community in maize and grass exhibited a highly skewed dominance structure. A single species, *Harpalus pensylvanicus* (DeGeer), represented 59 and 48% of the total abundance in each habitat, respectively (Fig. 2). The remaining species in maize

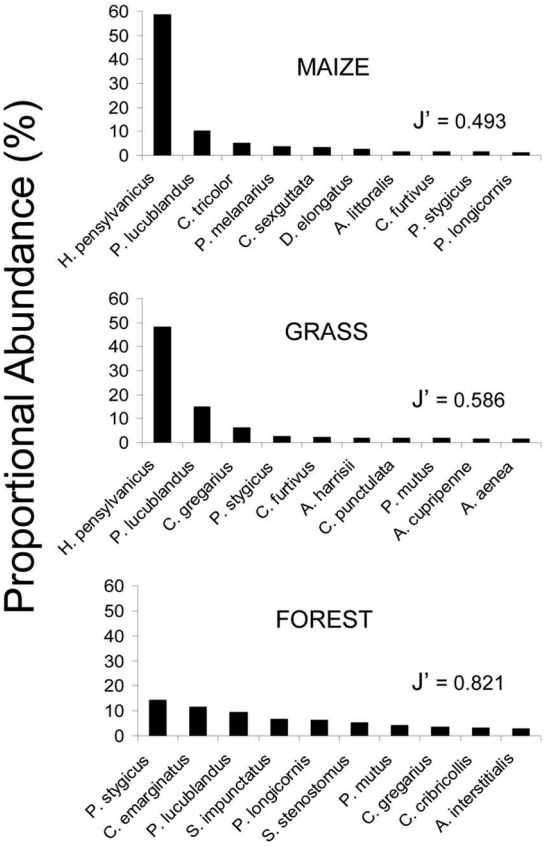

Fig. 2. *Community evenness.* Proportional abundance of carabids with the 10 highest activity-densities in maize, grass, and forest, respectively. Pielou's index of evenness (J') for entire carabid community in each habitat is also noted.

Downloaded from http://ee.oxfordjournals.org/ by guest on December 31, 2016

all represented <10% of the total abundance. Only one other species, *Poecilus lucublandus lucublandus* Say, occurred at >10% of the total abundance in grass. The forestland community was noticeably different in community composition and evenness (Fig. 2), and no species represented >15% of the total activity-density.

Indicator species analysis identified several species as reliable indicators of the different habitat types (Table 1). Abundant species that did not significantly associate with an individual habitat type, and were thus identified as potential ecotone species, included *Patrobus longicornis* (Say), *Pterostichus stygicus* (Say), *Cyclotrachelus furtivus* (LeConte), *P. lucublandus lucublandus* (Say), *Pterostichus mutus* (Say), and *Dicaelus elongatus* Bonelli. RDA also identified significant axes, or gradients, of variation in the carabid community. Species groupings were visualized in a biplot (Fig. 3) and supported the findings of the indicator analysis. The primary, horizontal, axis ($F = 6.02$, $P = 0.018$), which explained 89.9% of the constrained carabid species variation, was strongly defined by forest communities separating from maize and grass communities. The secondary, vertical, axis ($F = 8.76$; $P = 0.0010$) was associated with plant diversity and explained an additional 4.1% of the constrained species variation.

Position on Transect (Small-Scale Continuous). The spatial trajectory of the carabid community across the transect significantly deviated from the baseline (or control) interior forest carabid community ($F = 45.6$, $P = 0.002$), as shown by the PRC diagram (Fig. 4). The community trajectory exhibited the greatest shift at the interface of grass and forestland. At the interface of grass and maize, there was no abrupt change in community structure. Based on PRC scores, the carabid community found at this grass–maize interface was the most dissimilar to the interior forestland community.

Species weights were used to identify the degree at which different species followed the principal response. Carabids with positive species weights (*Synuchus impunctatus*, *Sphaeroderus stenostomus*, *Pt. mutus*, and *Chlaenius emarginatus*) were those highly associated with the forestland. Conversely, the carabids with negative species weights (*P. lucublandus* and *H. pensylvanicus*) were highly associated with grass and maize, thus acting in an opposite manner of the community trajectory in the PRC diagram (Fig. 4).

The population distributions of six potentially influential ecotone species were plotted to determine extent of movement into maize (Fig. 5). Of the six species, all except *Pt. mutus* seemed to have a strong presence in maize. Four species were even found at the most interior trap position in maize.

Landscape Context (Large-Scale Discrete). Pairwise comparisons of carabid communities in ag-matrix maize locations revealed high degrees of similarity based on Jaccard and Sorensen similarity indices (Table 2; Scale = Local [Ag-Matrix]). When these same communities were compared against forest-adjacent maize (Table 2; Scale = Landscape [Forest-Adjacent versus Ag-Matrix]), similarity values were reduced by 17.8% to 53.3%. The landscape surrounding forest-adjacent and ag-matrix field locations varied greatly (Table 3). The ag-matrix sites had no deciduous forest habitat within a 250 m radius compared with 60% in the forest-adjacent location. Ag-matrix sites also exhibited lower overall habitat heterogeneity (only two or three landcover types compared with five landcover types at the forest-adjacent location).

A comparison of the three different habitats near the forest-adjacent sites (Table 2; Scale = Local [Forest-Adjacent]) revealed that carabid communities in maize and grass had the highest similarity, grass and forestland communities were the second most similar, and maize and forestland communities were the least similar. Despite the notable differences in plant diversity and vegetative structure between maize and grass, the carabid communities in forest-adjacent maize and the neighboring grass habitat were more similar (Jaccard index = 0.508) than those in forest-adjacent maize and ag-matrix maize (Jaccard index ranged from 0.305 to 0.393).

Discussion

Carabidae are considered to be an important focus of conservation biological control efforts because of their abundance in agricultural settings, the temporal variation among species (Leslie et al. 2009), and the variety of feeding habits they exhibit (Toft and Bilde 2002, McGravey and Lundgren 2011). Despite strong habitat associations for some carabid species—including agricultural fields that undergo frequent disturbance—many rely on multiple habitats for reproduction, survival, or feeding (Dennis et al. 1994, French et al. 2001). Therefore, field margins and the surrounding landscape have the potential to influence carabid community composition within neighboring crop fields.

From a small-scale continuous perspective, our PRC revealed a rapid shift in community structure across the forest–agriculture ecotone and suggested a low degree of permeability for some carabids at the forest edge. Such rapid ecotonal shifts have been shown for other coleopteran communities, including scarabs (Durães et al. 2005). Our use of PRC—which is normally used to visualize community trajectories over time in relation to control—appears to be a useful approach, among others (Millar et al. 2005), to examine community dynamics across a spatial gradient. We purport that PRC can be useful for examining the spatial extent of the effects of habitat disturbance on nearby communities. Such an approach may also be particularly useful for discerning the effectiveness of field margin manipulations used to encourage the movement of beneficial arthropods into agricultural fields (e.g., beetle banks, pollinator strips). PRC analyses and diagrams provide a strong statistical and visual tool for examining community dynamics, and the inclusion of taxon weights allows users to determine the influence of individual species in the overall dynamics of the community.

Downloaded from http://ee.oxfordjournals.org/ by guest on December 31, 2016

Table 1. Carabidae collected along transects spanning forest, grass, and maize at the Russell E. Larson Agricultural Research Center in Pennsylvania Furnace, PA

Max. group[a]	Species	Total abundance	Indicator value[b]	*P* value
Forest	*Agonum ferreum* Haldeman	1	8.3	1.000
	Agonum melanarium Dejean	2	8.3	1.000
	Agonum palustre Goulet	6	16.7	0.411
	Agonum retractum (LeConte)	5	25.0	0.112
	Amara apricaria (Paykull)	9	8.0	0.896
	Amara exrata (Dejean)	1	8.3	1.000
	Amara impuncticollis (Say)	2	8.3	1.000
	Amara ovata (Fabricius)	5	8.3	1.000
	Amphasia interstitialis (Say)	13	29.7	0.119
	Apenes lucidulus (Dejean)	1	8.3	1.000
	Bembidion affine Say	1	8.3	1.000
	Bradycellus lugubris (LeConte)	1	8.3	1.000
	Chlaenius emarginatus Say	44	56.7	**0.014**
	Cymindis cribricollis Dejean	11	35.6	**0.044**
	Cymindis platicollis (Say)	1	8.3	1.000
	Notiophilus aeneus (Herbst)	7	25.0	0.137
	Olisthopus parmatus (Say)	4	33.3	0.058
	Oodes amaroides Dejean	1	8.3	1.000
	Patrobus longicornis (Say)	35	18.8	0.786
	Platynus decentis (Say)	8	41.7	**0.011**
	Pseudamara arenaria (LeConte)	4	25.0	0.107
	Pterostichus adoxus (Say)	3	25.0	0.098
	Pterostichus caudicalis (Say)	2	16.7	0.333
	Pterostichus coracinus (Newman)	3	9.0	0.779
	Pterostichus luctuosus (Dejean)	1	8.3	1.000
	Pterostichus pensylvanicus LeConte	5	25.0	0.098
	Pterostichus rostratus (Newman)	2	8.3	1.000
	Pterostichus stygicus (Say)	71	46.1	0.098
	Pterostichus tristis (Dejean)	4	16.7	0.330
	Sphaeroderus stenostomus Dejean	21	59.4	**0.003**
	Syntomus americanus (Dejean)	1	8.3	1.000
	Synuchus impunctatus (Say)	23	54.1	**0.005**
	Trichotichnus autumnalis (Say)	1	8.3	1.000
	Trichotichnus dichrous (Dejean)	2	16.7	0.333
	Trichotichnus vulpeculus (Say)	8	33.3	0.054
	Xestonotus lugubris (Dejean)	1	8.3	1.000
Grass	*Agonum cupripenne* (Say)	12	18.0	0.372
	Amara aenea (DeGeer)	6	25.6	0.083
	Amara cupreolata Putzeys	2	28.6	**0.044**
	Amara musculis (Say)	1	14.3	0.226
	Amara rubrica Haldeman	2	14.3	0.226
	Anisodactylus harrisii LeConte	13	38.1	0.054
	Anisodactylus nigerrimus (Dejean)	3	28.6	**0.043**
	Anisodactylus nigrita Dejean	1	14.3	0.218
	Anisodactylus rusticus (Say)	2	9.0	0.700
	Bradycellus tantillus (Dejean)	1	14.3	0.218
	Calathus gregarious (Say)	46	55.9	**0.007**
	Cicindela punctulata punctulata (Olivier)	7	28.6	**0.041**
	Cyclotrachelus furtivus (LeConte)	23	30.0	0.257
	Dicaelus politus Dejean	3	22.1	0.205
	Dyschirius globulosus (Say)	2	9.0	0.694
	Harpalus erythropus Dejean	3	6.6	1.000
	Harpalus longicollis LeConte	2	14.3	0.228
	Harpalus protractus Casey	8	10.4	0.982
	Harpalus rubripes (Duftschmid)	1	14.3	0.226
	Harpalus somnulentus Dejean	1	14.3	0.234
	Notiobia nitidipennis (LeConte)	2	9.0	0.689
	Poecilus lucublandus lucublandus (Say)	182	44.5	0.175
	Pterostichus mutus (Say)	22	25.4	0.311
	Stenolophus conjunctus (Say)	1	14.3	0.222
	Stenolophus rotundatus LeConte	2	9.0	0.690
	Trichotichnus fulgens (Csiki)	2	9.0	0.699

Continued on following page

Downloaded from http://ee.oxfordjournals.org/ by guest on December 31, 2016

Table 1. Continued

Max. group[a]	Species	Total abundance	Indicator value[b]	*P* value
Maize	*Agonum muelleri* (Herbst)	10	28.8	0.107
	Agonum punctiforme (Say)	4	33.3	0.054
	Amara familiaris (Duftschmid)	8	12.8	1.000
	Amara littoralis Mannerheim	15	46.7	**0.014**
	Anisodactylus melanopus Haldeman	2	8.3	1.000
	Anisodactylus sanctaecrucis (Fabricius)	9	18.0	0.400
	Badister notatus Haldeman	1	8.3	1.000
	Bembidion mimus Hayward	1	8.3	1.000
	Bembidion quadrimaculatum oppositum Say	4	33.3	0.056
	Bembidion rapidum LeConte	1	8.3	1.000
	Chlaenius tricolor tricolor Dejean	55	66.9	**0.001**
	Cicindela sexguttata Fabricius	36	59.8	**0.004**
	Clivinia impressefrons LeConte	2	16.7	0.330
	Dicaelus elongates Bonelli	34	22.1	0.205
	Harpalus compar LeConte	3	16.7	0.312
	Harpalus herbivagus Say	4	15.9	0.519
	Harpalus pensylvanicus (DeGeer)	726	61.6	**0.019**
	Poecilus chalcites (Say)	7	33.3	0.055
	Pterostichus commutabilis (Motschulsky)	2	4.2	1.000
	Pterostichus melanarius (Illiger)	37	52.6	**0.016**
	Scarites quadriceps Chaudoir	5	23.3	0.178
	Scarites subterraneus Fabricius	6	9.2	0.832
	Stenolophus rotundicollis (Haldeman)	1	8.3	1.000

Total abundance and information related to habitat specificity included. *P* values of significant ($P < 0.05$) indicator species are in bold type.
[a] Max. group = habitat representing highest activity-densities for each species.
[b] Indicator value = product of species relative abundance (within a habitat) and relative frequency (exp-wide) multiplied by 100 (Dufrene and Legendre 1997).

Despite the strong community shifts observed across the ecotone, the indicator species analysis (Table 1) found few species to be significant indicators of a single habitat, suggesting movement across the ecotone. In fact, RDA (Fig. 3) and individual population distributions (Fig. 5) revealed that some species with high activity-densities thrived at the ecotone and moved freely among habitats. Bedford and Usher (1994) noted this "sharing" of species between agricultural and forested habitats, and other studies have documented greater abundances of carabids at ecotones between forestland and agricultural fields (Kotze and Samways 1999, Kagawa and Maeto 2009).

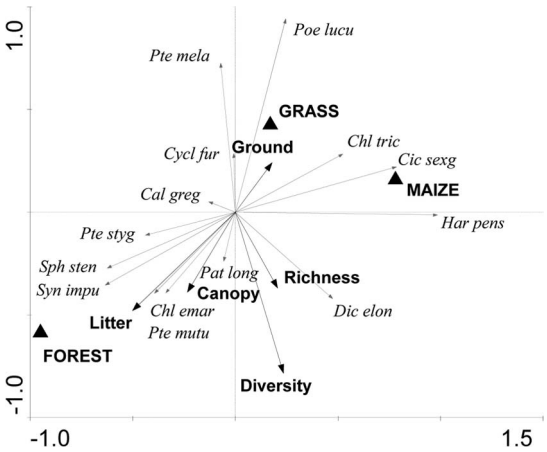

Fig. 3. *Species–environment associations.* Redundancy analysis (RDA) biplot depicting associations between carabids and environmental variables. Discrete explanatory variables, shown as triangles, are the three habitat types (i.e., forest, grass, maize). Continuous explanatory variables, shown as dark vectors, are associated with plant diversity (i.e., plant richness or "Richness," and Simpson Index of Diversity or "Diversity") and vegetation structure (i.e., % Litter, % Ground, and % Canopy cover). Carabid species, represented by gray vectors, are abbreviated with the first three letters of their genus and first four letters of the species epithet (see Table 1 for complete species names).

Our large-scale discrete analyses suggest that ecotone species can noticeably alter community composition within neighboring agricultural fields. A comparison of carabid communities from different locations in the landscape revealed that carabid communities collected in maize adjacent to forest differed from those collected in maize embedded in an agricultural matrix (Table 2). For example, two large-bodied species, *C. furtivus* and *Pt. stygicus*, were abundant at the forest-adjacent locations, but were never or rarely found in ag-matrix maize. Two other species, *Poecilus chalcites* (Say) and *P. lucublandus lucublandus*, were found at both sites but differed in relative abundance based on the location; in ag-matrix maize, *P. chalcites* exhibited high activity-densities, whereas *P. lucublandus lucublandus* was found more frequently at forest-adjacent locations. Aviron et al. (2005) noted that landscape context related to extent of hedgerows and woodland area can influence carabid assemblages. Similarly, Holland and Fahrig (2000) report that total length of woody borders is positively correlated with insect diversity within agricultural lands.

Downloaded from http://ee.oxfordjournals.org/ by guest on December 31, 2016

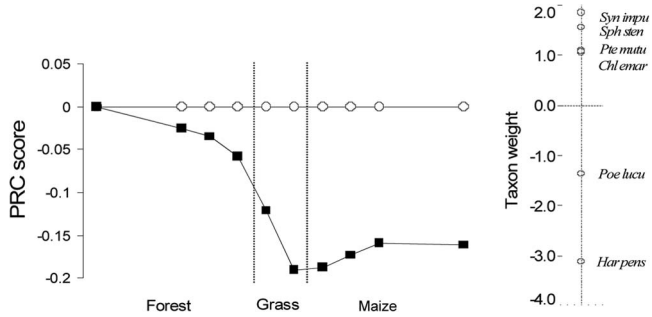

Fig. 4. *Community dynamics across a spatial gradient.* Principal response curve (PRC) and taxon weights indicating shifts in carabid community structure across a transect of 10 pitfall traps extending from forest, through a grassy margin, and into maize. Traps were 5 m apart, except for the distal traps, which were situated 15 m from the adjacent trap. The shifts in carabid community composition represent by the PRC (black squares) are shown in relation to the interior forest carabid community (shown as open circles on the horizontal 0.0 line). Species with positive taxon weights (>0.5) follow the principal response, whereas species with negative taxon weights (<0.5) respond in the opposite fashion. Carabid species are abbreviated with the first three letters of their genus and first four letters of the species epithet (see Table 1 for complete species names). Vertical lines indicate habitat interfaces.

Shifts in species assemblages related to landscape context have been linked to ecosystem services. In a review of the influence of landscape context on natural pest control, Bianchi et al. (2006) conclude that wooded habitats can contribute to increased activity of natural enemies. Conversely, Jonason et al. (2013) found rates of weed seed predation by carabids increased in simplified landscapes. Whether the ecosystem services provided by carabids differ between forest-adjacent maize and ag-matrix maize in the ridge and valley region of the northeastern United States remains to be seen. However, the relatively small field sizes of northeastern U.S. farms may enhance the benefits from any such forest edge effects on ecosystem services in neighboring agricultural fields.

In landscapes with some mix of arable fields and areas of the landscape in forest, riparian, and grassland cover, a disproportionately large contribution to plant biodiversity comes from the noncrop and natural areas (Egan and Mortensen 2012). It is clear from this work

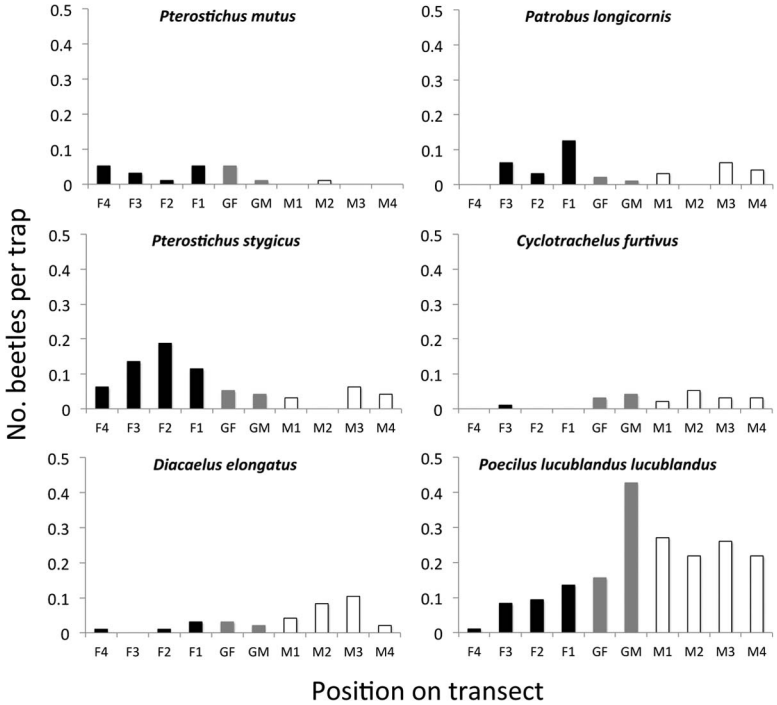

Fig. 5. *Ecotone species and/or habitat generalists.* Distribution of six species of Carabidae along a transect extending from forest (F4–F1), through a mowed grassy margin (GF and GM), and into maize (M1–M4). Traps were 5 m apart, except for the distal traps (F4 and M4), which were situated 15 m from the adjacent trap.

Downloaded from http://ee.oxfordjournals.org/ by guest on December 31, 2016

Table 2. Pairwise comparisons (similarity indices) of Carabidae communities sampled from forest, grass, maize adjacent to forest, or maize and sweet corn embedded in an agricultural matrix

Scale (location)	Comparison	Shared species	Similarity index	
			Jaccard classic	Sørensen classic
Local (forest-adjacent)	Maize (FA) vs. grass	30	0.508	0.674
	Maize (FA) vs. forest	21	0.284	0.442
	Grass vs. forest	23	0.307	0.469
Local (ag-matrix)	SwCorn (AM) vs. Maize03 (AM)	30	0.652	0.789
	SwCorn (AM) vs. Maize04 (AM)	22	0.478	0.647
	Maize03 (AM) vs. Maize04 (AM)	29	0.617	0.763
Landscape context (forest-adjacent vs. ag-matrix)	Maize (FA) vs. SwCorn (AM)	21	0.375	0.545
	Maize (FA) vs. Maize03 (AM)	24	0.393	0.565
	Maize (FA) vs. Maize04 (AM)	18	0.305	0.468

Higher values indicate greater similarity. Maize (FA) = Forest-adjacent maize; SwCorn (AM) = sweet corn from a diversified vegetable farm embedded in an agricultural matrix in 2001 and 2002; Maize03 (AM) and Maize04 (AM) = maize embedded in an agricultural matrix in 2003 and 2004, respectively.

that the contribution of noncrop areas to floristic biodiversity is matched by increasing the diversity of the carabid community. Our small-scale discrete analyses suggest that forestland supports a diverse assemblage of carabids that exhibit high degrees of dissimilarity with agricultural fields in the same region, even those in proximity (Table 2; see Local [Forest-Adjacent]). This study and our previous studies in this region found that carabid species richness within agricultural fields ranges from 43 to 49 species. By including the grass margin and forested habitat in the current study, species richness increased to 85 species. The forestland supported higher levels of species richness than maize (Figs. 1 and 2); however, differences in species richness between the grassy field margin and maize were not evident, a result supported by Saska et al. (2007).

The patterns of carabid diversity and species composition in our study were likely driven by the stark variation in diversity and structural complexity of the plant community (Brose 2003) between forestland and maize, in addition to the strong disturbance gradient across the ecotone. Community variation may also reflect variation in host resources and/or abiotic conditions (Matlack 1993, Kagawa and Maeto 2009). In addition, the contiguous area of forestland in our study region was quite extensive. This likely supported a higher beta-diversity of carabids between forest and agricultural fields, than if the forested areas existed as small fragments. Although relationships between forest patch size and species richness are inconsistent (Niemalä 2001), studies have shown that fragmentation of forests into small patches often results in the loss of interior forest-specific species (Halme and Niemalä 1993, Fujita et al. 2008). The diversity and complementarity patterns we found in our study highlight the importance of retaining extensive forested areas in agricultural landscapes from the standpoint of biological conservation.

In conclusion, forestland in agricultural landscapes of the northeastern United States serves as an important reservoir for numerous carabid species and contributes to regional biodiversity through high levels of species complementarity with surrounding agricultural fields. Carabid community composition changes rapidly at the interface of forestland and agricultural fields and a PRC can serve as a useful tool to assess and visualize these community shifts across a spatial gradient. Despite these strong community shifts, individuals of many species thrive at the ecotone, move readily into neighboring agricultural fields, and seem to noticeably alter community composition in these fields as compared with other field sites located at a further distance from forestland.

Table 3. Landscape context at a 250-m radius for forest-adjacent maize (Maize FA) and maize at two field locations found in an agricultural matrix (Sweet Corn 01/02 and Maize 03/04)

Landcover type	Maize FA	Agricultural matrix	
		Sweet Corn 01/02	Maize 03/04
Developed, open space	7,567 (0.04)	35,371 (0.18)	17,554 (0.09)
Cultivated crops	54,805 (0.28)	158,323 (0.82)	122,867 (0.63)
Pasture/hay	14,033 (0.07)	–	55,300 (0.28)
Deciduous forest	116,838 (0.60)	–	–
Open water	2,700 (0.01)	–	–

For each location, landcover types are presented in square meters with proportion of total area indicated in parentheses.

Acknowledgments

We thank Scott Smiles and Vaughn Hauck for farm operations, Justin Kozak and Miles Saunders for collection and curation of carabids, and Daniel Heggenstaller and Steven Kinneer for their assistance in collecting the plant-related data. We relied on the expertise of Robert Davidson at the Pittsburgh Museum of Natural History for assistance with carabid taxonomy, and Susie Anderson from the Earth and Environmental Systems Institute at Penn State University for the GIS-based analyses and landscape context measures. Partial funding was provided by the USDA NRI Biotechnology Risk Assessment Research Grants Program, Grant 2002-33522-12719.

References Cited

Aviron, S., F. Burel, J. Baudry, and N. Schermann. 2005. Carabid assemblages in agricultural landscapes: impacts

Downloaded from http://ee.oxfordjournals.org/ by guest on December 31, 2016

of habitat features, landscape context at different spatial scales and farming intensity. Agric. Ecosyst. Environ. 108: 205–217.

Bedford, S. E., and M. B. Usher. 1994. Distribution of arthropod species across the margins of farm woodlands. Agric. Ecosyst. Environ. 48: 295–305.

Beisel, J.-N., P. Usseglio-Polatera, V. Bachmann, and J.-C. Moreteau. 2003. A comparative analysis of evenness index sensitivity. Int. Rev. Hydrobiol. 88: 3–15.

Bianchi, F.J.J.A., C.J.H. Booij, and T. Tscharntke. 2006. Sustainable pest regulation in agricultural landscapes: a review on landscape composition, biodiversity and natural pest control. Proc. R. Soc. Lond. B 273: 1715–1727.

Brose, U. 2003. Bottom-up control of carabid beetle communities in early successional wetlands: mediated by vegetation structure or plant diversity? Oecologia 135: 407–413.

Carvell, C., W. R. Meek, R. F. Pywell, D. Goulson, and M. Nowakowski. 2007. Comparing the efficacy of agri-environment schemes to enhance bumble bee abundance and diversity on arable field margins. J. Appl. Ecol. 44: 29–40.

Chaplin-Kramer, R., M. E. O'Rourke, E. J. Blitzer, and C. Kremen. 2011. A meta-analysis of crop pest and natural enemy response to landscape complexity. Ecol. Lett. 14: 922–932.

Charrier, S., S. Petit, and F. Burel. 1996. Movements of *Abax parallelepipedus* (Coleoptera Carabidae) in woody habitats of a hedgerow network landscape: a radio-tracing study. Agric. Ecosyst. Environ. 61: 133–144.

Ciegler, J. C. 2000. Ground beetles and wrinkled bark beetles of South Carolina. *In* A. G. Wheeler (ed.), South Carolina Agriculture and Forestry Research System, Clemson University, SC.

Colwell, R. K. 2005. Estimate: Statistical estimation of species richness and shared species from samples. Version 7.5. (purl.oclc.org/estimates)

Coombes, D. S. and N. W. Sothertons. 1986. The dispersal and distribution of polyphagous predatory Coleoptera in cereals. Ann. Appl. Biol. 108: 461–474.

Dennis, P., M. B. Thomas, and N. W. Sotherton. 1994. Structural features of field boundaries which influence the overwintering densities of beneficial arthropod predators. J. Appl. Ecol. 31: 361–370.

Downie, N. M., and R. H. Arnett Jr. 1996. The beetles of northeastern North America, vols. I and II. The Sandhill Crane Press, Gainesville, FL.

Duelli, P., and M. K. Obrist. 2003. Regional biodiversity in an agricultural landscape: the contribution of seminatural habitat islands. Basic Appl. Ecol. 4: 129–138.

Dufrene, M., and P. Legendre. 1997. Species assemblages and indicator species: the need for a flexible asymmetrical approach. Ecol. Monogr. 67: 345–366.

Durães, R., W. P. Martins, and F. Z. Vaz-de-Mellos. 2005. Dung beetle (Coleoptera: Scarabaeidae) assemblages across a natural forest-cerrado ecotone in Minas Gerais, Brazil. Neotrop. Entomol. 34: 721–731.

Egan, J. F., and D. A. Mortensen. 2012. A comparison of land-sharing and land-sparing strategies for plant richness conservation in agricultural landscapes. Ecol. Appl. 22: 459–471.

French, B. W., N. C. Elliott, R. C. Berberet, and J. D. Burd. 2001. Effects of riparian and grassland habitats on ground beetle (Coleoptera: Carabidae) assemblages in adjacent wheat fields. Environ. Entomol. 30: 225–234.

Fry, J., G. Xian, S. Jin, J. Dewitz, C. Homer, L. Yang, C. Barnes, N. Herold, and J. Wickham. 2011. Completion of the 2006 National Land Cover Database for the Conterminous United States, PE&RS, Vol. 77: 858–864.

Fujita, A., K. Maeto, Y. Kagawa, and N. Ito. 2008. Effects of forest fragmentation on species richness and composition of ground beetles (Coleoptera: Carabidae and Brachinidae) in urban landscapes. Entomol. Sci. 11: 39–48.

Gotelli, N. J., and R. K. Colwell. 2001. Quantifying biodiversity: procedures and pitfalls in the measurement and comparison of species richness. Ecol. Lett. 4: 379–391.

Halme, E., and J. Niemalä. 1993. Carabid beetles in fragments of coniferous forest. Ann. Zool. Fenn. 30: 17–30.

Holland, J., and L. Fahrig. 2000. Effects of woody borders on insect density and diversity in crop fields: a landscape-scale analysis. Agric. Ecosyst. Environ. 78: 115–122.

Jonason, D., H. Smith, J. Bengtsson, and K. Birkhofer. 2013. Landscape simplification promotes weed seed predation by carabid beetles (Coleoptera: Carabidae). Landsc. Ecol. 28: 487–494.

Kagawa, Y., and K. Maeto. 2009. Spatial population structure of the predatory ground beetle *Carabus yaconinus* (Coleoptera: Carabidae) in the mixed farmland-woodland satoyama landscape of Japan. Eur. J. Entomol. 106: 385–391.

Kleijn, D., F. Berendse, R. Smit, and N. Gilissen. 2001. Agri-environment schemes do not effectively protect biodiversity in Dutch agricultural landscapes. Nature 413: 723–725.

Kotze, D. J., and M. J. Samways. 1999. Invertebrate conservation at the interface between the grassland matrix and natural Afromontane forest fragments. Biodivers. Conserv. 8: 1339–1363.

Kremen, C., N. M. Williams, R. L. Bugg, J. P. Fay, and R. W. Thorp. 2004. The area requirements of an ecosystem service: crop pollination by native bee communities in California. Ecol. Lett. 7: 1109–1119.

Landis, D. A., S. D. Wratten, and G. M. Gurr. 2000. Habitat management to conserve natural enemies of arthropod pests in agriculture. Annu. Rev. Entomol. 45: 173–201.

Leslie, T. W., G.-A. Hoheisel, D. J. Biddinger, J. R. Rohr, and S. J. Fleischer. 2007. Transgenes sustain epigeal insect biodiversity in diversified vegetable farm systems. Environ. Entomol. 36: 234–244.

Leslie, T. W., D. J. Biddinger, C. A. Mullin, and S. J. Fleischer. 2009. Carabidae population dynamics and temporal partitioning: response to coupled neonicotinoid-transgenic technologies in maize. Environ. Entomol. 38: 935–943.

Leslie, T. W., D. J. Biddinger, J. R. Rohr, and S. J. Fleischer. 2010. Conventional and seed-based insect management strategies similarly influence nontarget coleopteran communities in maize. Environ. Entomol. 39: 2045–2055.

Marino, P. C., and D. A. Landis. 1996. Effect of landscape structure on parasitoid diversity and parasitism in agroecosystems. Ecol. Appl. 6: 276–284.

Marshall, S. A. 2006. Insects: their natural history and diversity: with a photographic guide to insects of eastern North America. Firefly Books Inc., Buffalo, NY.

Marshall, E.J.P., T. M. West, and D. Kleijn. 2006. Impacts of an agri-environment field margin prescription on the flora and fauna of arable farmland in different landscapes. Agric. Ecosyst. Environ. 113: 36–44.

Matlack, G. R. 1993. Microenvironment variation within and among forest edge sites in the northeastern United States. Biol. Conserv. 66: 185–194.

McCune, B., and M. J. Mefford. 1999. PC-ORD: Multivariate analysis of ecological data. MjM Software, Gleneden Beach, OR.

McGravey, K. W., and J. G. Lundgren. 2011. Ground beetles (Coleoptera: Carabidae) of the Midwestern United

Downloaded from http://ee.oxfordjournals.org/ by guest on December 31, 2016

States: a review and synthesis of recent literature. Terr. Arthropod Rev. 4: 63–94.

Menalled, F. D., P. C. Marino, S. H. Gage, and D. A. Landis. 1999. Does agricultural landscape structure affect parasitism and parasitoid diversity? Ecol. Appl. 9: 634–641.

Millar, R. B., M. J. Anderson, and G. Zunun. 2005. Fitting nonlinear environmental gradients to community data: a general distance-based approach. Ecology 86: 2245–2251.

Niemalä, J. 2001. Carabid beetles and habitat fragmentation: a review. Eur. J. Entomol. 98: 127–132.

Ober, K. 2011. Rapid diversification and evolution in ground beetles. Am. Entomol. 57: 46–48.

Payton, M. E., M. H. Greenstone, and N. Schenker. 2003. Overlapping confidence intervals or standard error intervals: what do they mean in terms of statistical significance? J. Insect Sci. 3: 34.

Petersen, M. K. 1999. The timing and dispersal of the predatory beetles *Bembidion lampros* and *Tachyporus hypnorum* from hibernating sites into arable fields. Entomol. Exp. Appl. 90: 221–224.

Pielou, E. C. 1966. The measurement of diversity in different types of biological collections. J. Theor. Biol. 13: 131–144.

Pluess, T., I. Opatovsky, E. Gavish-Regev, Y. Lubin, and M. H. Schmidt-Entling. 2010. Non-crop habitats in the landscape enhance spider diversity in wheat fields of a desert agroecosystem. Agric. Ecosyst. Environ. 137: 68–74.

Ponti, L., C. Ricci, F. Veronesi, and R. Torricelli. 2005. Natural hedges as an element of functional biodiversity in agroecosystems: the case of a Central Italy vineyard. Bull. Insectol. 58: 19–23.

Purtauf, T., I. Roschewitz, J. Dauber, C. Thies, T. Tscharntke, and V. Wolters. 2005. Landscape context of organic and conventional farms: Influences on carabid beetle diversity. Agric. Ecosyst. Environ. 108: 165–174.

Saska, P., M. Vodde, T. Heijerman, P. Westerman, W. van der Werf. 2007. The significance of a grassy field boundary for the spatial distribution of carabids within two cereal fields. Agric. Ecosyst. Environ. 122: 427–434.

Steffan-Dewenter, I., U. Munzenberg, C. Burger, C. Thies, and T. Tscharntke. 2002. Scale-dependent effects of landscape context on three pollinator guilds. Ecology 83: 1421–1432.

Sunderland, K. D. 2002. Invertebrate pest control by carabids, pp. 165–214. *In* J. M. Holland (ed.), The agroecology of carabid beetles. Intercept, Andover, United Kingdom.

ter Braak, C.J.F., and P. Šmilauer. 2002. CANOCO reference manual and CanoDraw for Windows user's guide: software for canonical community ordination, 4.5 edition. Microcomputer Power, Ithaca, NY.

Toft, S., and T. Bilde. 2002. Carabid diets and food value, pp. 81–110. *In* J. M. Holland (ed.), The agroecology of carabid beetles. Intercept, Andover, United Kingdom.

Tooley, J., and G. E. Brust. 2002. Weed seed predation by carabid beetles, 215–230. *In* J. M. Holland (ed.), The agroecology of carabid beetles. Intercept, Andover, United Kingdom.

Tscharntke, T., and A. Kruess.. 1999. Habitat fragmentation and biological control, pp. 190–205. *In* B. A. Hawkins and H. V. Cornell (eds.), Theoretical approaches to biological control. Cambridge University Press, Cambridge, United Kingdom.

Tscharntke, T., A. M. Klein, A. Kruess, I. Steffan-Dewenter, and C. Thies. 2005. Landscape perspectives on agricultural intensification and biodiversity – ecosystem service management. Ecol. Lett. 8: 857–874.

Watson, J. C., A. T. Wolf, and J. S. Ascher. 2011. Forested landscapes promote richness and abundance of native bees (Hymenoptera: Apoidea: Anthophila) in Wisconsin apple orchards. Environ. Entomol. 40: 621–632.

Winqvist, C., J. Bengtsson, T. Aavik, F. Berendse, L. W. Clement, S. Eggers, C. Fishcer, A. Flohre, F. Geiger, J. Liira, et al. 2011. Mixed effects of organic farming and landscape complexity on farmland biodiversity and biological control potential across Europe. J. Appl. Ecol. 48: 570–579.

Received 10 April 2013; accepted 15 November 2013.

Downloaded from http://ee.oxfordjournals.org/ by guest on December 31, 2016