

Landscape diversity enhances biological control of an introduced crop pest in the north-central USA

M. M. GARDINER,^{1,5} D. A. LANDIS,¹ C. GRATTON,² C. D. DiFONZO,¹ M. O'NEAL,³ J. M. CHACON,⁴ M. T. WAYO,¹
N. P. SCHMIDT,³ E. E. MUELLER,² AND G. E. HEIMPEL⁴

¹Department of Entomology, 204 Center for Integrated Plant Systems, Michigan State University,
East Lansing, Michigan 48824-1311 USA

²Department of Entomology, 1630 Linden Dr., 237 Russell Labs, University of Wisconsin, Madison, Wisconsin 53706 USA

³Department of Entomology, 177 Insectary, Iowa State University, Ames, Iowa 50011-3140 USA

⁴Department of Entomology, 219 Hodson Hall, 1980 Folwell Ave., University of Minnesota, St. Paul, Minnesota 55108 USA

Abstract. Arthropod predators and parasitoids provide valuable ecosystem services in agricultural crops by suppressing populations of insect herbivores. Many natural enemies are influenced by non-crop habitat surrounding agricultural fields, and understanding if, and at what scales, land use patterns influence natural enemies is essential to predicting how landscape alters biological control services. Here we focus on biological control of soybean aphid, *Aphis glycines* Matumura, a specialist crop pest recently introduced to the north-central United States. We measured the amount of biological control service supplied to soybean in 26 replicate fields across Michigan, Wisconsin, Iowa, and Minnesota across two years (2005–2006). We measured the impact of natural enemies by experimentally excluding or allowing access to soybean aphid infested plants and comparing aphid population growth over 14 days. We also monitored aphid and natural enemy populations at large in each field. Predators, principally coccinellid beetles, dominated the natural enemy community of soybean in both years. In the absence of aphid predators, *A. glycines* increased significantly, with 5.3-fold higher aphid populations on plants in exclusion cages vs. the open field after 14 days. We calculated a biological control services index (BSI) based on relative suppression of aphid populations and related it to landscape diversity and composition at multiple spatial scales surrounding each site. We found that BSI values increased with landscape diversity, measured as Simpson's *D*. Landscapes dominated by corn and soybean fields provided less biocontrol service to soybean compared with landscapes with an abundance of crop and non-crop habitats. The abundance of Coccinellidae was related to landscape composition, with beetles being more abundant in landscapes with an abundance of forest and grassland compared with landscapes dominated by agricultural crops. Landscape diversity and composition at a scale of 1.5 km surrounding the focal field explained the greatest proportion of the variation in BSI and Coccinellidae abundance. This study indicates that natural enemies provide a regionally important ecosystem service by suppressing a key soybean pest, reducing the need for insecticide applications. Furthermore, it suggests that management to maintain or enhance landscape diversity has the potential to stabilize or increase biocontrol services.

Key words: *Aphis glycines*; biological control; ecosystem services; introduced crop pests; landscape diversity; natural enemies; predators; soybean aphid.

INTRODUCTION

Insects provide vital ecosystem services including decomposition, pollination, and biological control of crop pests (Losey and Vaughan 2006). In agroecosystems, the diversity and abundance of natural enemies that provide biological control in crop fields are influenced by the structure and composition of the surrounding landscape (Marino and Landis 1996, Colunga-Garcia et al. 1997, Bommarco 1998, Elliott et al. 1999, Thies et al. 2003, Schmidt and Tscharrntke 2005,

Tscharrntke et al. 2005). Landscape variables such as habitat complexity, quality, and patchiness as well as an organism's dispersal capability all impact the ability of a landscape to support biological control in agricultural croplands (Elliott et al. 1999, Thies et al. 2003, Schmidt and Tscharrntke 2005). Moreover, agricultural crop fields are ephemeral habitats in which anthropogenic disturbances such as tillage, pesticide application, and harvesting require arthropods to frequently recolonize crops (Wissinger 1997). The surrounding landscape provides the local species pool of arthropods for this recolonization and thus may influence the level of biological control in frequently disturbed crop fields (Lee et al. 2001).

Manuscript received 1 August 2007; revised 5 March 2008; accepted 15 April 2008; final version received 8 May 2008.
Corresponding Editor: S. M. Altizer.

⁵ E-mail: gardin18@msu.edu

Invasions of exotic species can significantly alter the abundance and distribution of herbivores within a landscape. Landscapes vary in their suitability for invasive species, and understanding how landscape structure influences pest suppression is critical to successfully managing invaders in their nonnative range. In the summer of 2000, the soybean aphid, *Aphis glycines* (see Plate 1) Matsumura, was first detected in the United States, and has now spread throughout 23 soybean growing states and three Canadian provinces (Venette and Ragsdale 2004). Feeding by *A. glycines* on the leaves, stems, and pods of the soybean plant causes reductions in photosynthetic rate (Macedo et al. 2003), plant growth, and seed yield of soybean plants (Ragsdale et al. 2007). Soybean aphid is consumed by a diversity of natural enemies that can provide strong top-down regulation of its populations (Costamagna and Landis 2007) and result in a trophic cascade of increased crop yields (Costamagna et al. 2007a). Although several parasitoids can be found attacking soybean aphid, generalist predators currently dominate the natural enemy community (Costamagna et al. 2008).

A complex of native and exotic generalist predators attack and feed on soybean aphid in North America. These include *Harmonia axyridis* Pallas (see Plate 1), *Coccinella septempunctata* L., *Hippodamia variegata* (Goeze), *Hippodamia convergens* Guérin-Méneville, and *Coleomegilla maculata* DeGeer (Coleoptera: Coccinellidae), *Orius insidiosus* Say (Hemiptera: Anthocoridae), *Chrysoperla carnea* (Stephens) (Neuroptera: Chrysopidae), *Aphidoletes aphidomyza* (Rondani) (Diptera: Cecidomyiidae), *Leucopis* spp. (Diptera: Chamaemyiidae), and Syrphidae (Diptera) (Fox et al. 2004, 2005, Desneux et al. 2006, Costamagna and Landis 2007). Generalist predators have been shown to significantly reduce soybean aphid populations (Fox et al. 2005, Desneux et al. 2006, Costamagna and Landis 2007); however, the level of suppression is not consistent between studies. For example, Desneux et al. (2006) reported low overall aphid populations (less than 10 per plant) varying only 1.1–3.5 fold in the presence/absence of predators. In contrast, Costamagna and Landis (2007) reported aphid populations of several thousand per plant, varying 6.8-fold in the presence/absence of predators. These studies were conducted in landscapes that vary tremendously in complexity, from diverse landscapes in Michigan (Fox et al. 2004, Costamagna and Landis 2007) to corn- and soybean-dominated landscapes in Indiana (Desneux et al. 2006). It is likely that differences in the efficacy of biological control are due to variation in landscape composition surrounding soybean fields across the north-central region.

Given strong local variation in the level of soybean aphid suppression, the goal of this study was to determine if, and at what scales, landscape diversity and composition may explain biological control of *A. glycines* in agricultural landscapes. Our hypothesis was that landscapes composed of a high proportion of non-

crop habitat such as grasslands and forests would provide overwintering habitat and alternative prey resources to natural enemies. Such landscapes would in turn increase the abundance of generalist predators and result in greater suppression of the soybean aphid. Our objectives were to (1) measure the impact of predator assemblages on soybean aphid populations across the north-central United States and (2) determine if the level of biological control detected in soybean fields was related to the diversity and composition of the surrounding landscape.

METHODS

Field sites

Between June and August of 2005 and 2006, we examined the abundance of aphids and arthropod natural enemies at 26 sites distributed among four states (Iowa, Michigan, Minnesota, and Wisconsin) in the north central United States as part of a larger multistate study of soybean aphid management (Fig. 1). Sites were selected to study how landscape variation across a large portion of the soybean growing region affected biological control of soybean aphid. Within each year, a minimum distance of 30 km separated each field site. Across years, we maintained the relative regional distribution of sites, but sampled different fields. The average distance between soybean fields sampled in subsequent years was 1.6 km (range 0.2–4.6 km; Fig. 1). Field size averaged 16.0 ha (range 13.6–48.1 ha). In each replicate field, a randomized complete-block design with 4–6 blocks and either four (2005) or five (2006) treatments was established in 0.4-ha (2005) or 0.2-ha (2006) plots. Multiple experiments occurred within these fields, and this study was conducted in plots which were not treated with insecticide.

Natural enemy impact experimental design

Following the methods of Costamagna et al. (2007a), we used cages to exclude natural enemies from selected plants, contrasting the population growth of aphids in the presence or absence of these antagonists. When an average population of 10 aphids per plant was reached in the overall field, cages were erected in the center of each plot (four per site), each enclosing a single plant. Each caged plant was paired with an uncaged plant, 1 m away in the same row, hereafter referred to as “open” plants. Aphids were either added or removed to start each plant with 10 aphids of mixed age classes. In some locations, aphid populations never reached an average level of 10 aphids per plant. In these sites we manually redistributed aphids from the field to the experimental plants to initiate the study. Cages consisted of a 0.4 m diameter \times 1 m tall tomato wire support covered by a sleeve of fine-mesh white no-see-um netting (openings of 0.65×0.17 mm; Kaplan Simon, Braintree, Massachusetts, USA). The mesh sleeve was tied at the top and attached to a metal “T” post; it was secured at the bottom by burying the edges in the soil. The numbers of

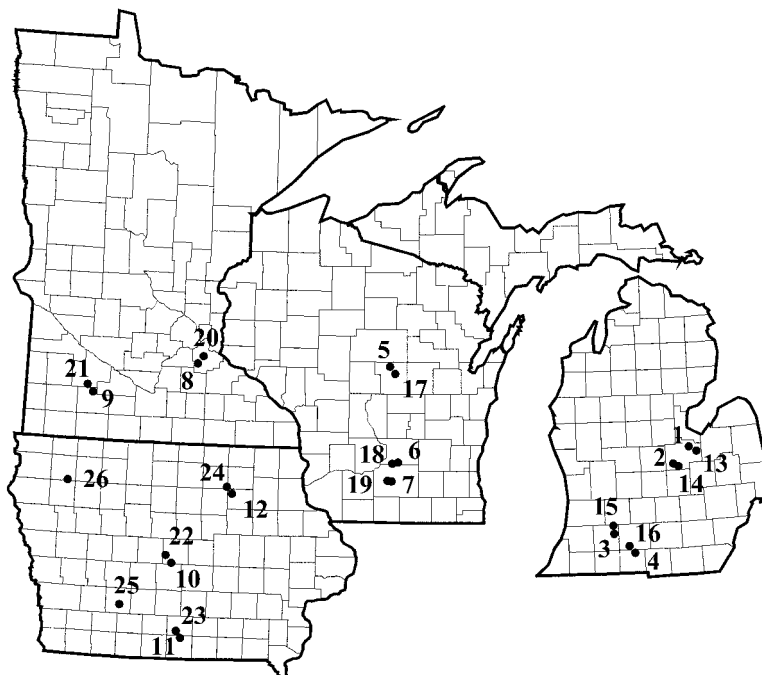


FIG. 1. Location of 26 soybean fields sampled in 2005 (fields 1–10) and 2006 (fields 11–26) in the north-central United States. The predator exclusion cage study was completed in all sites. Fields 2, 9, and 25 were excluded from the AIC_c analysis of BSI (biological control services index) and Coccinellidae abundance due to incomplete data.

apterous and alate aphids were recorded weekly on both the open and caged plants using nondestructive field counts 7 and 14 days post establishment.

Assessment of cage effects

Cage studies must address possible effects on microclimate and test organism behavior. Using similar cages, Costamagna and Landis (2007) found that a “sham” cage treatment (exclusion cages with windows to allow access by natural enemies) and a no-cage treatment did not differ significantly in aphid population growth after 7 or 14 days. Another potential concern is that exclusion cages could prevent dispersal of alate aphids and artificially elevate aphid populations. To minimize this possibility, we limited our study to 14 days. After 7 days, alate number was low and similar (1.4 ± 0.1 and 1.9 ± 0.1 alate aphids per plant, mean \pm SE) in the exclusion cage and open treatments, respectively. At 14 days, the exclusion cage treatment had an average of 20.7 ± 1.4 alates per plant whereas the open plant had 1.8 ± 0.1 alates per plant. To examine the impact of cages with a high number of alates on our results, we analyzed a subset of the data excluding all cages that had more alates than were found on open plants (10% of cages). Exclusion of these data from analysis (not shown) did not affect the outcome.

Soybean aphid and natural enemy sampling

Destructive whole-plant counts were used to estimate *A. glycines* abundance at weekly intervals from early

June until late August. In each plot, five randomly selected plants were removed from the ground and the numbers of apterous and alate aphids were counted on each plant. We present the date of first aphid detection and the date when the economic threshold of 250 aphids per plant (Ragsdale et al. 2007) was reached for each site (Table 1).

During the two weeks of the natural-enemy impact experiment, the diversity and abundance of natural enemies was estimated using two different sampling techniques (Schmidt et al. 2008). To measure aerially dispersing natural enemy populations, a single unbaited yellow sticky card (PHEROCON AM, Great Lakes IPM [Integrated Pest Management], Vestaburg, Michigan, USA) was placed in each plot at all study sites. In the center of each plot, a metal “T” fence post was erected with holes every 10 cm vertically. A 0.6 cm diameter dowel was placed through a hole to suspend a 22.9×27.9 cm sticky card just above the plant canopy. Sticky traps were collected at 7 and 14 days, and all adult Coccinellidae, Anthocoridae, Nabidae, Chrysopidae, Hemerobiidae, and Syrphidae (in 2006 only) were counted. We also visually inspected plants on days 7 and 14 to measure the diversity and abundance of natural enemies foraging in soybean. In 2005, five randomly selected plants were inspected per plot and all adult and immature Coccinellidae, *Orius insidiosus* (Anthocoridae), Nabidae, Chrysopidae, Hemerobiidae, Syrphidae, *Aphidoletes aphidimyza* (Cecidomyiidae), Araneae, Aphelinidae, and Braconidae were counted. In 2006,

TABLE 1. Study sites with dates of first soybean aphid (*Aphis glycines*) detection, period of predator exclusion cage study, dates when aphid threshold was reached in the open field and exclusion cages, plant stages during cage study, and Simpson's *D* values for the 1.5-km landscape radius surrounding each soybean field.

State	Site number	Year	Aphid detection	Cage study	Threshold, field†	Threshold, exclusion‡	Plant stage§	Simpson's <i>D</i>
MI	1	2005	29 Jun	6 Jul–20 Jul	13 Jul	20 Jul	R2–R3	5.42
MI	2	2005	8 Jun	13 Jul–20 Jul	20 Jul	13 Jul	R2–R3	...
MI	3	2005	14 Jun	20 Jun–5 Jul	1 Aug	5 Jul	V2–V5	5.09
MI	4	2005	14 Jun	20 Jun–5 Jul	18 Jul	5 Jul	V4–R2	6.40
WI	5	2005	20 Jun	11 Jul–25 Jul		25 Jul	R2–R3	3.85
WI	6	2005	16 Jun	30 Jun–14 Jul		14 Jul	R1–R2	3.27
WI	7	2005	17 Jun	17 Jun–1 Jul		17 Jun	V5–R1	3.27
MN	8	2005	16 Jun	14 Jul–27 Jul	27 Jul	27 Jul	R2–R3	4.22
MN	9	2005	30 Jun	21 Jul–28 Jul	28 Jul		R2–R3	...
IA	10	2005	7 Jul	11 Jul–25 Jul	29 Aug	25 Jul	R2–R4	3.24
IA	11	2005	13 Jul	13 Jul–28 Jul		28 Jul	R2–R3	3.51
IA	12	2005	19 Jul	26 Jul–10 Aug	16 Aug	10 Aug	R3–R5	2.31
MI	13	2006	14 Jun	6 Jul–19 Jul		19 Jul	R1–R2	6.06
MI	14	2006	19 Jun	31 Jul–14 Aug		14 Aug	R2–R3	5.78
MI	15	2006	13 Jul	19 Jul–2 Aug		2 Aug	R3	6.53
MI	16	2006	19 Jun	7 Aug–21 Aug		21 Aug	R3	5.20
WI	17	2006	29 Jun	20 Jul–3 Aug			R3–R5	7.06
WI	18	2006	9 Jun	14 Jul–28 Jul			V7–R2	2.42
WI	19	2006	7 Jul	21 Jul–4 Aug		4 Aug	R2–R4	3.89
MN	20	2006	5 Jun	17 Jul–31 Jul		31 Jul	R2–R5	2.98
MN	21	2006	5 Jul	17 Jul–31 Jul	25 Jul	31 Jul	R2–R3	3.41
IA	22	2006	15 Jun	25 Jul–8 Aug			R4–R5	3.11
IA	23	2006	19 Jul	26 Jul–9 Aug			R4–R5	3.61
IA	24	2006	10 Jul	24 Jul–7 Aug		7 Aug	R4–R5	2.32
IA	25	2006	10 Aug	10 Aug–24 Aug	30 Aug		R4–R6	...
IA	26	2006	14 Jul	11 Aug–25 Aug			R5–R6	2.25

Notes: State abbreviations: MI, Michigan; WI, Wisconsin; MN, Minnesota; IA, Iowa. For the two threshold columns, blank cells indicate that the economic threshold was not exceeded. For the Simpson's *D* column, ellipses indicate incomplete data.

† Date when overall field exceeded the economic threshold of 250 aphids per plant.

‡ Date when plants in exclusion cages exceeded the economic threshold.

§ Based on Higley and Boethel (1994).

|| Simpson's *D* for 1.5 km radius, where $D = 1/\sum (p_i)^2$ and p_i is the proportion of habitat in the i th land-cover category.

we reduced the number of locations sampled by visual plant counts to one site per state and inspected 10 randomly selected plants per plot.

Landscape analysis

Field geospatial data were collected using a handheld GPS receiver using Wide Area Augmentation System (WAAS) correction. The spatial coordinate for the center of each site was used to obtain ortho-rectified digital aerial imagery (Appendix A). We digitized the habitats surrounding each study site to a radius of 3.5 km using ARC GIS 9.1 (ESRI 2005). These aerial images differed temporally, representing images captured between 1998 and 2006. Land use changes between the image date and study period were recorded by ground-verification in June–August annually, with corrections made during the digitization process. At the same time we also determined the specific land cover present within all areas of each landscape (Appendix B). Some locations included polygons that were not visible from a roadway and permission to access private lands could not be obtained. These polygons were given a value of zero and were excluded from further analysis. The area of each site that could not be identified varied from 0% to 2%. The smallest polygons identified included field plots on university research farms and

small patches of fallow field (<5 m²); the largest were contiguous urban areas, lakes, and forests (<11.9 km²).

Landscape diversity was measured using Simpson's Index, *D* (Simpson 1949). Simpson's Index is typically used to examine the variance of species abundance distributions; here we applied it to examine variance in the proportion of area covered by each of 22 land use categories. This index was calculated for each of the landscapes at each of the spatial scales examined. The equation for Simpson's Index is: $D = 1/\sum (p_i)^2$ where p_i is the proportion of habitat in the i th land-cover category (*D* increases as diversity increases). Using methods modeled after Thies et al. (2003) we measured landscape diversity at seven spatial scales ranging from 0.5 km to 3.5 km radii (at 0.5-km intervals) from the field center.

Statistical analysis

A repeated-measures mixed-model analyses of variance (ANOVA) (PROC MIXED in SAS version 9.1) was used to compare the average aphid populations on the caged and open plants in the 26 locations sampled. Fixed factors included in the model were: cage treatment, week, and the cage treatment × week interaction. Cage treatment replicate nested within site was included as a random effect and week was the repeated variable. Differences in aphid abundance

between treatments were assessed by comparing least-squares means. Aphid counts were log-transformed prior to analysis to meet the assumptions of normality and homogeneity of variances (SAS Institute 1999).

To relate biological control services to landscape variables, we calculated the relative aphid suppression found in each site by expressing the change in aphid numbers on open and caged plants as a proportion of aphid abundance in the absence of predators for any given site. The resulting Biocontrol Services Index (BSI), varied from 0 to 1, with values increasing as the level of aphid predation increases:

$$\text{BSI} = \frac{\sum_{p=1}^4 (A_{c,p} - A_{o,p})}{A_{c,p}}$$

where A_c is the number of aphids on the caged plant on day 14, A_o is the number of aphids on the open plant on day 14, p is the plot, and n is the number of replicates for a given site.

In one case a negative BSI value was calculated due to higher aphid populations on the open plant than in the corresponding exclusion cage treatment. Because this indicated a lack of effective biological control, this site was given an index value of zero.

To evaluate the relationship between predator abundance, BSI, and landscape variables, we performed a principal components analysis (PCA). The 22 land use categories were combined into eight variables included in the PCA analysis: four crop variables (proportion of corn, soybean, wheat, and other crops), and four non-crop variables (proportion of forest, grasslands, urban, and water) (Appendix B). Principal component axes were extracted using the correlations among variables and the resulting factors were not rotated. We restricted our analysis to the first two eigenvectors, which together explained between 43.8% and 56.1% of the variability in the landscape data. This was done for each spatial scale (radii of 0.5–3.5 km). The PCA analysis was completed using JMP version 7 (SAS Institute 2007).

To assess the influence of the principal components and landscape diversity (D) on BSI and coccinellid abundance (the average number of adult Coccinellidae collected from sticky cards across the two weeks of sampling), we compared all possible models containing these variables using Akaike's Information Criterion, adjusted for sample size (AIC_c) (Burnham and Anderson 2002). The AIC_c analysis was conducted at each spatial scale of analysis (0.5–3.5 km). At radii of 1 km and larger, eight models were compared: Intercept only, Diversity (Simpson's D), PC1, PC2, Diversity + PC1, Diversity + PC2, PC1 + PC2, and Diversity + PC1 + PC2. At a 0.5 km radius, the interpretation of PC2 was not consistent with larger spatial scales and was not included in model analysis. For each analysis, we present the maximum log-likelihood estimate, the Akaike weights, and AIC_c differences (Δ_i). For each response

variable, we present the model with the minimum AIC_c value, which has the best support for the data and any other models with an AIC_c difference of less than 2 (Burnham and Anderson 2002). Models with a Δ_i in this range are termed "competing models" (Ribic and Sample 2001) and are considered to also have substantial support for the data (Burnham and Anderson 2002). We calculated adjusted r^2 for the minimum AIC_c model and competing models to evaluate how well the models explained the variation in the data. We also calculated partial correlations for all variables in models with more than one predictor. Partial correlations were used to assess the importance of individual independent variables after adjusting for additional variables in the model. The AIC_c analysis and adjusted r^2 were determined using R version 2.1.1 (R Development Core Team 2005). Partial correlations were obtained using PROC CANCORR in SAS version 9.1 (SAS Institute 1999). Three sites were excluded from this analysis. In 2005, only the 7-d count was collected at site 2 and 9; therefore BSI values could not be calculated for these sites. In 2006, ground-verification of the landscape data was not collected for site 25 (Fig. 1).

Sites that are geographically close may be more similar than sites that are farther apart (Legendre 1993). Therefore, before interpreting the results of our AIC_c analysis for either BSI or Coccinellidae abundance, we determined if the residuals from the best-fit or competing models were spatially autocorrelated by examining sample variogram plots. For both response variables, we did not detect spatial autocorrelation among our 23 sites.

RESULTS

Aphid populations in 2005 and 2006

In 2005, *Aphis glycines* arrival in soybean was detected beginning in mid-June in Michigan, Minnesota, and Wisconsin. Soybean aphid was detected about one month later in the Iowa sites, beginning on 7 July (Table 1). Of the 12 sites sampled, eight reached the economic threshold of 250 *A. glycines* per plant in the field as a whole. The date at which threshold was reached in the field at large varied from mid-July to late August (Table 1). Populations in exclusion cages exceeded threshold in 11 of 12 sites 11.6 days earlier, on average, than the open field. In 2006 soybean aphid was detected beginning in mid-June through mid-July in all sites except site 25 in Iowa, where aphids were not found until 10 August. Only two of the 14 sites reached threshold in the field at large, whereas in exclusion cages eight sites exceeded threshold (Table 1).

Predator and parasitoid diversity across the region

Coccinellidae, Syrphidae, Chrysopidae, and Anthoridae were the most abundant predators collected on sticky cards (Fig. 2). Nine species of coccinellids were observed (Appendix C). Across the region, *Harmonia axyridis* comprised the greatest percentage of the

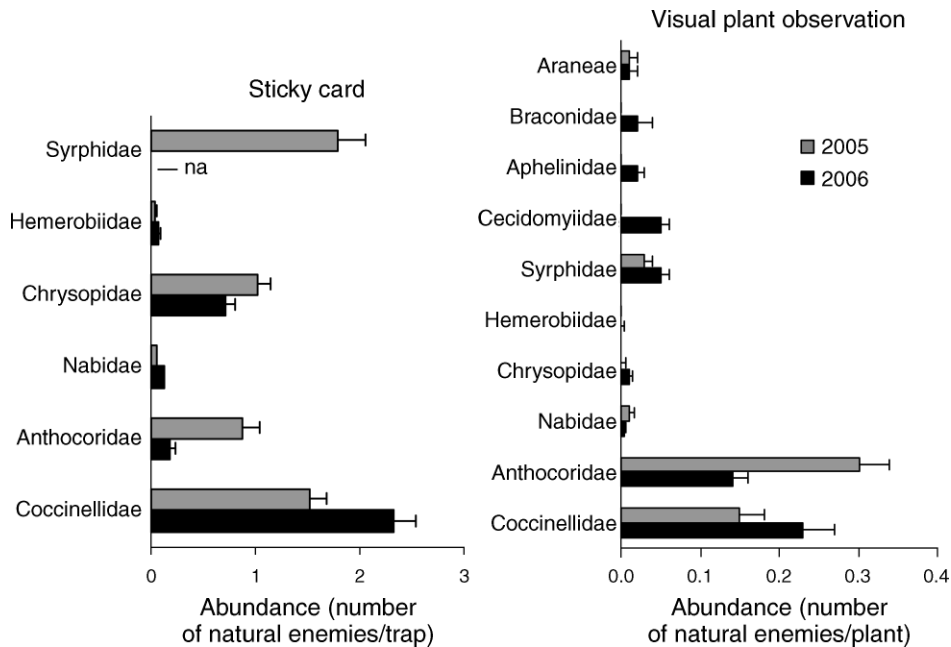


FIG. 2. Number of natural enemies (mean + SE) counted on sticky card traps (7-day cumulative) and during visual plant observations (illustrating natural enemies present on a plant at a single point in time) in 2005 and 2006. Syrphidae were not counted on sticky cards in 2005 (na = not available).

coccinellid population in both years (70% in 2005, 72% in 2006). Visual plant counts illustrated that Coccinellidae and Anthocoridae were the most abundant natural enemies found on soybean plants (Fig. 2). The most abundant lady beetle species found on soybean plants was *H. axyridis*, with adults and larvae comprising 47% and 88% of the coccinellid community in 2005 and 2006. Anthocoridae consisted solely of adult and nymphal *Orius insidiosus*.

Impact of predators on soybean aphid

Despite their apparent low abundance, natural enemies had a large impact on soybean aphid, with significantly higher aphid populations occurring on caged vs. open plant treatments. The relationship between these treatments across the two weeks of the experiment varied as indicated by a significant cage treatment \times week interaction ($F_{1,44} = 9.36$, $P = 0.003$; Fig. 3). However, the open treatment was significantly lower than the exclusion cage both 7 days ($P = 0.002$) and 14 days ($P < 0.0001$) after establishment.

Landscape diversity

The landscape surrounding each of our field sites varied from agriculturally dominated to forest and grassland dominated. Within the 3.5-km landscape radius surrounding each of the 23 sites, landscape diversity values (D) ranged from 2.43 to 6.40. Landscapes with low D values were dominated by corn and soybean fields, whereas landscapes with high D values included a diversity of crop and non-crop habitats. The

percentage of the landscape composed of annual cropland ranged from 20% to 91%. Landscapes with low to high percentages of annual cropland were found within each state (Michigan, 20–91%; Wisconsin, 29–71%; Minnesota, 44–73%; and Iowa 27–89%). Soybean and corn production covered between 4–38% and 9–57%

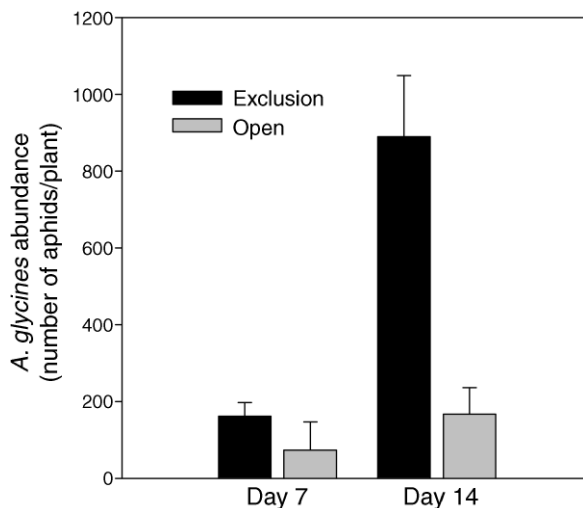


FIG. 3. Number of soybean aphids, *Aphis glycines*, per plant (mean + SE) in the cage (exclusion) and open-plant treatments. A significant week \times treatment interaction was found ($F_{1,44} = 9.36$, $P = 0.003$). Comparison of least-squares means for exclusion vs. open treatments at 7 days ($P = 0.002$) and 14 days ($P < 0.0001$) indicates that aphid populations were significantly higher in the absence of natural enemies.

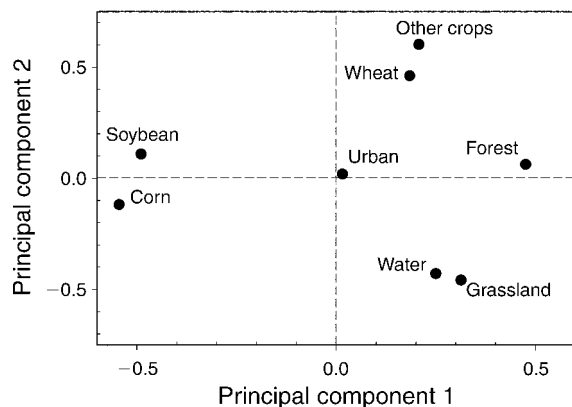


FIG. 4. PCA ordination for principal components 1 and 2 of landscape elements surrounding soybean fields sampled at a radius of 1.5 km.

of the 3.5-km landscape, respectively. The percentage of the landscape composed of forested habitat ranged from 1% to 42%.

Interpretation of principal components

Both principal components were interpreted as measures of landscape composition. Sites with positive loadings on PC1 were correlated with forested land cover, whereas sites with negative loading values were correlated with corn and soybean. Positive values of PC1 suggest a landscape dominated by forested habitats; negative values of PC1 indicate a landscape dominated by corn and soybean agriculture (Fig. 4). The interpretation of PC2 is scale dependent, with the correlation of the factor loadings consistent only at scales of 1 km and greater. Here positive scores were correlated with the variables other crops and wheat, indicating that landscapes with high loadings had a high proportion of locally important fruit, vegetable, ornamental, and small-grain crops. Negative values were correlated with the variables grassland and water, indicating landscapes with a high proportion of these more permanent habitat types (Fig. 4).

Model comparisons

Overall, BSI was best predicted by the Simpson's D at a spatial scale of 1.5 km (Table 2), having the lowest AIC_c score of any model at the seven spatial scales examined. The Simpson's D model was also the best predictor of BSI at 1, 2, 2.5, and 3 km, whereas the PC1 model had the lowest AIC_c scores at both 0.5 and 3.5 km. Competing models included Diversity + PC1 and PC1 (Table 2). There was a significant positive relationship between BSI and landscape diversity, indicating that the degree of soybean aphid suppression by natural enemies increased as the diversity of crop and non-crop habitats in the surrounding landscape increased (Fig. 5).

Overall Coccinellidae abundance was best predicted by the PC1 + PC2 model at a spatial scale of 1.5 km (Table 3). This model had the lowest AIC_c value and contained 45% of Akaike weight. The abundance of coccinellids was positively correlated with PC1 and negatively correlated with PC2, indicating that these predators were most abundant in soybean field in landscapes with an abundance of forests and, to a lesser extent, grasslands (Fig. 6). The Diversity and Diversity + PC2 models had the lowest AIC_c value at 0.5 and 1.0 km, respectively, whereas the PC1 model had the lowest AIC_c at spatial scales of 2 km and greater.

DISCUSSION

Biological control of pests is an important, yet infrequently measured, ecosystem service (Swinton et al. 2006). In this study, we found that the ability of a landscape to supply biocontrol services as manifested by suppression of the soybean aphid was a function of the diversity of the agricultural landscape, and that coccinellids, the primary predator of soybean aphid, responded to the presence of natural habitat within the landscape.

Impact of biological control

Previous authors have illustrated the importance of natural enemies in the suppression of aphid populations at the field scale (Dennis and Wratten 1991, Grasswitz

TABLE 2. Summary of model selection statistics for evaluating predation of *Aphis glycines* by generalist natural enemies, calculated as a biocontrol services index (BSI).

Radius (km)	Model	Log-likelihood	K_i	AIC_c	Δ_i	w_i	Adjusted r^2
0.5	$B_0 + B_1PC1^*$	-3.20	3	13.66	0.00	0.54	0.16
1.0	$B_0 + B_1D^{**}$	-1.44	3	10.14	0.00	0.50	0.28
1.5	$B_0 + B_1D^{**}$	-0.89	3	9.04	0.00	0.56	0.31
2.0	$B_0 + B_1D^{**}$	-1.60	3	10.46	0.00	0.48	0.27
2.5	$B_0 + B_1D^{**}$	-1.86	3	10.98	0.00	0.45	0.25
3.0	$B_0 + B_1D^*$	-2.69	3	12.64	0.00	0.30	0.19
3.0	$B_0 + B_1PC1^*$	-2.73	3	12.72	0.08	0.28	0.19
3.0	$B_0 + B_1D + B_2PC1^\dagger$	-2.08	4	14.32	1.68	0.13	0.20
3.5	$B_0 + B_1PC1^*$	-2.05	3	11.36	0.00	0.47	0.24

Notes: The first model listed at each spatial scale is the minimum AIC_c model, bold indicates the best overall model. Only models with a Δ_i of 2 or less are included as competing models. For details, see *Methods: Statistical analysis*. D is Simpson's diversity, where $D = 1/\sum (p_i)^2$ and p_i is the proportion of habitat in the i th land-cover category. Significance of variables is indicated as follows: * $P < 0.05$; ** $P < 0.01$.

† For this model, the partial correlations are $D = 0.23$, $PC1 = 0.23$.

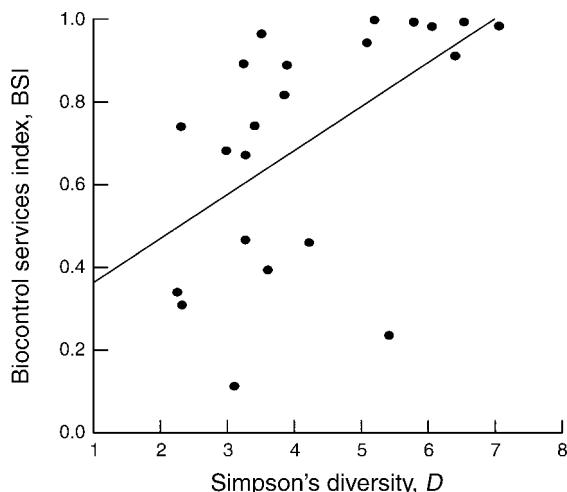


FIG. 5. Relationship between the biocontrol services index (BSI) and Simpson's diversity, D , at a radius of 1.5 km for 23 fields sampled for soybean aphid suppression, 2005–2006 ($y = 0.124x + 0.159$). BSI was calculated as the relative difference in aphid number between open and exclusion-cage treatments (see *Methods: Statistical analysis*).

and Burts 1995, Rutledge et al. 2004, Schmidt et al. 2004, Muller et al. 2005, Gardiner and Landis 2007). Schmidt et al. (2004) found that the exclusion of flying natural enemies led to 94% higher populations of the bird cherry–oat aphid, *Rhopalosiphum padi* (L.). Similarly, Fox et al. (2004), Costamagna and Landis (2007), Costamagna et al. (2007a), Desneux et al. (2006), and Donaldson et al. (2007) found that a diverse generalist natural enemy complex significantly reduced soybean aphid populations in individual soybean fields, whereas parasitoids are currently not major contributors (Costamagna et al. 2008). Because of the potential for rapid

population growth of aphids (Costamagna et al. 2007b), predation early in the season is key to preventing aphids from reaching threshold levels. Our study is the first to demonstrate that such phenomena are regionally important and result from the actions of natural enemy communities that vary with landscape composition.

Using exclusion cages, we found that communities of generalist predators are effective at suppressing *A. glycines* populations across a wide portion of the north-central United States. Suppression was found even though soybean production practices, time of first aphid infestation, and plant growth stage all varied widely during the study (Table 1). This reduction was not always effective in maintaining populations below the economic threshold, but without predation, aphid populations exceeded thresholds earlier in the season and more often than in the absence of predators. Since its detection in 2000, the soybean aphid has exhibited apparently cyclic outbreaks, with high populations in one year, typically followed by low populations in the following year. These cyclic outbreaks are probably attributable to the work of generalist predators that build populations in high aphid years and prevent outbreak populations in the following year. We conducted this study in a high (2005) and a low (2006) soybean aphid year and found that in both cases predators reduced the proportion of sites that exceeded threshold. Within 14 days, soybean aphid populations exceeded the threshold of 250 aphids per plant in 92% of exclusion cages sampled in 2005 and 57% in 2006, whereas in the presence of predators this dropped to 67% in 2005 and 14% in 2006. That is, the presence of predators would have reduced the need for insecticide treatment by 25–43% in 2005 and 2006, respectively. Remarkably, this study demonstrates that low numbers of natural enemies are required to achieve this suppres-

TABLE 3. Summary of model selection statistics for evaluating the abundance of Coccinellidae.

Radius (km)	Model	Log-likelihood	K_i	AIC _c	Δ_i	w_i	Adjusted r^2	Partial correlations
0.5	$B_0 + B_1D^*$	-33.47	3	74.20	0.00	0.54	0.19	
0.5	$B_0 + B_1D + B_2PC1$	-32.49	4	75.20	1.00	0.27	0.23	$D = 0.41, PC1 = 0.32$
0.5	$B_0 + B_1PC1$	-34.39	3	76.04	1.84	0.18	0.12	
1.0	$B_0 + B_1D^{**} + B_2(PC2)^{**}$	-30.33	4	70.82	0.00	0.40	0.35	$D = 0.58, PC2 = -0.54$
1.0	$B_0 + B_1PC1^{**} + B_2(PC2)$	-30.81	4	71.78	0.96	0.25	0.32	$PC1 = 0.55, PC2 = -0.39$
1.0	$B_0 + B_1PC1^*$	-32.71	3	72.68	1.86	0.16	0.24	
1.5	$B_0 + B_1PC1^{**} + B_2(PC2)^*$	-30.09	4	70.34	0.00	0.45	0.36	$PC1 = 0.56, PC2 = -0.46$
1.5	$B_0 + B_1(D) + B_2PC1^{**}$	-30.92	4	72.00	1.66	0.20	0.32	$D = -0.40, PC1 = 0.60$
2.0	$B_0 + B_1PC1^{**}$	-32.61	3	72.48	0.00	0.32	0.24	
2.0	$B_0 + B_1(D) + B_2PC1^{**}$	-31.27	4	72.70	0.22	0.29	0.29	$D = -0.33, PC1 = 0.58$
2.0	$B_0 + B_1PC1^{**} + B_2(PC2)$	-31.59	4	73.34	0.86	0.21	0.27	$PC1 = 0.54, PC2 = -0.29$
2.5	$B_0 + B_1PC1^*$	-32.96	3	73.18	0.00	0.46	0.22	
2.5	$B_0 + B_1PC1^* + B_2(PC2)$	-32.34	4	74.84	1.66	0.20	0.22	$PC1 = 0.52, PC2 = -0.23$
3.0	$B_0 + B_1PC1^*$	-33.74	3	74.74	0.00	0.42	0.17	
3.0	$B_0 + B_1PC1^* + B_2(PC2)$	-33.11	4	76.38	1.64	0.18	0.17	$PC1 = 0.46, PC2 = -0.23$
3.5	$B_0 + B_1PC1$	-34.24	3	75.74	0.36	0.33	0.13	
3.5	$B_0 + B_1PC1 + B_2(PC2)$	-33.28	4	76.72	0.98	0.20	0.16	$PC1 = 0.42, PC2 = -0.28$
3.5	B_0	-36.36	2	77.32	1.58	0.15		

Notes: The first model listed at each spatial scale is the minimum AIC_c model. Bold indicates the best overall model. Competing models with a Δ_i of 2 or less are included. D is Simpson's diversity, where $D = 1/\sum (p_i)^2$ and p_i is the proportion of habitat in the i th land-cover category. Significance of variables is indicated as follows: * $P < 0.05$; ** $P < 0.01$. Variables in parentheses indicate a negative relationship with Coccinellidae abundance.

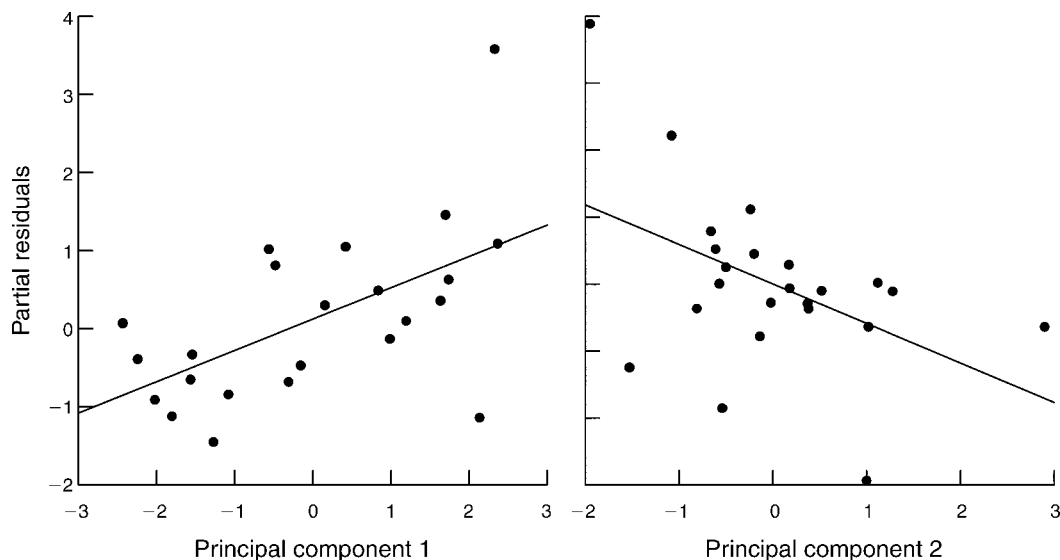


FIG. 6. Coccinellidae abundance in 23 soybean fields sampled for soybean aphid suppression was best explained by a model containing both PC1 and PC2 at a radius of 1.5 km ($y = 0.392x_1 - 0.361x_2 + 2.0638$). Partial residual plots illustrate a positive correlation with PC1 and a negative correlation with PC2, indicating that landscapes with an abundance of forests or grasslands support larger lady beetle populations in soybean fields compared with agriculturally dominated landscapes.

sion. Through this and other studies (Costamagna and Landis 2007, Costamagna et al. 2008), we now understand that small but consistent predation early in the season is they key to preventing aphids from reaching threshold levels.

Ability of the landscape to supply biocontrol services

Although we observed a significant impact of biological control across this four-state region, there was also significant among-sites variation in the amount of aphid suppression, which was strongly influenced by the diversity of the surrounding landscape. Agricultural landscapes have changed dramatically with agricultural intensification, resulting in larger, more contiguous fields and non-crop areas reduced in area and frequency (Bianchi et al. 2006). We found that low-diversity landscapes dominated by soybean and corn production had reduced biological control of soybean aphid compared with diverse landscapes dominated by non-crop habitats. In a review, Bianchi et al. (2006) found that increased landscape complexity reduced pest pressure in 45% of the studies. Effects included reductions in pest density (Ostman et al. 2001, den Belder et al. 2002) and reduction in crop injury (Thies and Tschardtke 1999, Thies et al. 2003). Pest pressure increased with landscape complexity in 15% of the cases examined (Raffy and Tran 2005, Roschewitz et al. 2005), whereas the two were unrelated in 40% of the studies (Galecka 1966, Holland and Fahrig 2000, Klug et al. 2003, Thies et al. 2005). It is likely that some of this variation is tied to differences in the impact of landscape complexity on specific natural enemy populations. A more detailed understanding of how natural enemies

respond to landscape structure may help us to understand these outcomes.

Response of natural enemies to landscape diversity and composition

Tschardtke et al. (2005) addressed the potential impact of agricultural intensification on the disruption of ecosystem services including biological control, stating that simple landscapes may support lower abundance of natural enemies, reduced enemy biodiversity perhaps lacking a key species, or by restricting movement of natural enemies within the landscape. In this study we found that coccinellids were more abundant in soybean fields in landscapes with an abundance of forests and grasslands. These landscapes were more diverse and supported greater biocontrol of soybean aphid as measured by the BSI compared with landscapes dominated by agricultural habitat. Coccinellid species have been shown to be key predators of soybean aphid (Costamagna and Landis 2007, Gardiner and Landis 2007) as well as other pest aphids. Thus, to promote biological control in agricultural landscapes, it may be desirable to maintain a diversity of these habitats to favor these natural enemies.

The influence of landscape diversity on natural enemies has been addressed in several systems (Bommarco 1998, Elliott et al. 1999, Thies et al. 2003). Predator diversity and abundance typically increase with landscape diversity, proportion of non-crop habitat, and degree of connectedness between non-crop habitat patches, while decreasing with crop field size. For example, Elliott et al. (1999) found that uncultivated land and habitat patchiness were both associated with increasing abundance and richness in predator commu-



PLATE 1. Multicolored Asian lady beetle (*Harmonia axyridis*) adults attacking soybean aphid (*Aphis glycines*) on soybean. Photo credit: Kurt Stepnitz.

nities in wheat fields. Similarly, Thies et al. (2003) found that parasitism of the rape pollen beetle was positively correlated with percentage of non-crop habitat.

Landscape spatial scale

In this study, we examined the impact of landscape variables on biological control at seven spatial scales, with landscape radii varying from 0.5 km to 3.5 km. Analysis of landscape features at a radius of 1.5 surrounding focal soybean fields explained the highest proportion of the variation in both biological control of soybean aphid (BSI) and coccinellid abundance. Although we know relatively little about the movement of coccinellids, it is possible that a landscape of this size encompasses their ecological neighborhood (Addicott et al. 1987), containing the diversity of habitats utilized by these species. During early summer when aphid populations in croplands are low, these predators are likely to be very transient, moving between fields in search of prey. Landscapes of a similar grain size have proved important in predicting both herbivory and natural enemy abundance in other systems. For example, Thies et al. (2003) measured the functional spatial scale at which the rape pollen beetle, *Meligethes aeneus* F. and its parasitoids were affected by landscape. They tested the

effects of landscape on trophic-level interactions using simple (<3% non-crop habitat) to complex (>50% non-crop habitat) landscapes, and analyzed them at eight spatial scales, (concentric circles 0.5–6 km in diameter) and found that herbivory and parasitism were most strongly correlated with percentage of non-crop area at a diameter of 1.5 km. Schmidt and Tschardtke (2005) found that sheetweb spider abundance in wheat fields was correlated with non-crop area at a slightly larger spatial scale (landscape circles with a radius of 1–3 km).

Implications

Our study is the first to demonstrate that the biocontrol service provided by generalist predators in north-central U.S. soybean fields is dependent on the diversity and composition of the surrounding landscape. Biological control of *A. glycines* is reduced in simple landscapes dominated by corn and soybean production. Members of the Coccinellidae, an important family of natural enemies of *A. glycines*, were also found to decline in soybean fields located in agriculturally dominated landscapes. Therefore, maintaining overall landscape diversity, and especially perennial grassland and forested habitats, in the landscape will favor suppression of soybean aphid. Moreover, these habitats

may also enhance biocontrol services in other crops because the generalist natural enemies found in soybean fields are also important antagonists of many other herbivores. Our results suggest that such non-crop habitats do not need to directly border agricultural fields to promote biocontrol services; we found that occurrence of these habitats within ~1.5 km explained the highest percentage of the variation in both biological control and coccinellid abundance.

Finally, understanding the impact of shifting production practices on biocontrol services in agricultural landscapes is of critical importance. For example, in many parts of the north-central United States, corn and soybean were typically rotated annually. Recently, corn acreage has been on the rise in response to increased demand for corn ethanol, with harvested areas rising by 15 million acres (46 538 849 ha) between 2006 and 2007 (USDA-NASS 2008). Increasing pressure to produce biofuel crops on agricultural lands could have a negative effect on biocontrol services in these landscapes particularly if corn production increases, reducing landscape diversity and displacing habitats associated with greater predator abundance. This could have a negative effect on biocontrol services as the pressure to produce biofuels on cropland increases.

ACKNOWLEDGMENTS

This research is the result of a multistate collaborative effort funded by the USDA CSREES Risk Avoidance and Mitigation Program, grant number 2004-51101-02210. We thank Mike Jewett, Chris Sebolt, Aleksandra Kalenak, Nick Longbucco, Kevin Johnson, Ryan Alderson, Chuck Stallman, Steve Scott, Amanda Nodelman, Scott Kostohryz, Robert Moore, Joe Kaser, Aaron Carpioux, Erin Wayo, and Michelle Beckner for their help collecting field data. We thank the Michigan State University Statistical Consulting Center, Robert Tempelman, Ashton Shortridge, and Sasha Kravchenko for help with statistical analysis. Funding support also provided by a Pioneer Hi-Bred International graduate student fellowship and C. S. Mott fellowship in sustainable agriculture to M. M. Gardiner.

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APPENDIX A

Sources of aerial image data used in soybean aphid predation studies, 2005–2006 (*Ecological Archives* A019-007-A1).

APPENDIX B

Simpson's diversity (*D*) and PCA categories (*Ecological Archives* A019-007-A2).

APPENDIX C

Coccinellidae species collected from yellow sticky card traps during the 14-d predator exclusion experiment (*Ecological Archives* A019-007-A3).