Landscape structure and habitat management differentially influence insect natural enemies in an agricultural landscape

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ABSTRACT

Increasing evidence suggests that landscape composition is an important driver of beneficial insect populations and resulting ecosystem services. Additionally, local-scale manipulations such as planting floral strips are used at the field-level to provide resources for beneficial insects to increase their services. It has been proposed that the benefits of local manipulations will depend on the landscape context, with greater benefits in simplified landscapes and smaller benefits in landscapes with an abundance of non-crop resources. To test this, we used soybean aphid, *Aphis glycines*, and its coccinellid predators as a model system to elucidate the effects of habitat management and landscape on biocontrol services in soybean. We selected pairs of soybean fields in landscapes of varying composition and planted buckwheat, *Fagopyrum esculentum*, strips adjacent to one field in each pair. We measured coccinellid abundance and biocontrol in each field. Coccinellid abundance was higher in buckwheat than in control field margins in all landscapes, and coccinellid abundance in soybean was positively related to amount of semi-natural vegetation in the landscape. We found no evidence of an interaction between landscape and local variables, and biocontrol services were high in all contexts. For soybean aphid suppression, landscape factors are the key drivers of predator abundance.

1. Introduction

Landscape complexity and local management of agricultural lands can influence the diversity of plants, animals, and microorganisms (Altieri, 1999; Tscharntke et al., 2005) which in turn affect the provision of ecosystem services such as nutrient cycling, water regulation, and pest suppression provided by beneficial insects (Altieri, 1999; Schlapfer et al., 1999; Tilman et al., 2002; Kremen, 2005). Biological control of crop pests is an ecosystem service valued at US$ 4.5 billion/yr in the United States alone (Losey and Vaughan, 2006), and it can reduce the need for costly chemical pesticides and associated environmental and human health concerns (Meehan et al., 2011). In order to support this valuable ecosystem service, various on-farm management practices have been developed to increase natural enemy diversity and abundance. For example, planting non-crop habitats adjacent to crop fields can provide natural enemies with additional food resources and refuge from disturbance (Landis et al., 2000), and may decrease the negative impacts of farming on local biodiversity (Concepcion et al., 2008). However, recent studies demonstrating the influence of landscape-scale factors on biocontrol services have led some to

hypothesize that the landscape context may constrain the ability of local management actions to influence community dynamics and biocontrol services (Concepcion et al., 2008; Tscharntke et al., 2012).

Landscape composition influences natural enemy communities through the provision of food and shelter resources. Complex landscapes with large amounts of semi-natural habitat may benefit natural enemies by providing undisturbed areas that offer shelter from crop disturbances, overwintering refuges, alternative hosts and prey, and additional nectar resources (Thies et al., 2003; Bianchi et al., 2006). As such, the amount of non-crop or semi-natural habitat in a landscape has been positively related to the abundance of a variety of predators, including spiders (Drapela et al., 2008; Schmidt et al., 2008), carabid beetles (Purtauf et al., 2005), coccinellid beetles (Gardiner et al., 2009), and opiliones (Gardiner et al., 2010). A meta-analysis of 46 landscape-scale studies in agroecosystems showed positive relationships between the amount of natural or non-crop habitat in the landscape and natural enemy abundance and diversity, predation and parasitism (Chaplin-Kramer et al., 2011).

Landscape-mediated increases in natural enemy abundance and diversity can in turn lead to higher predation and parasitism rates, and thus greater pest control. Thies and Tscharntke (1999) found that high rates of plant damage by the rape pollen beetle, *Meligethes aeneus* (Fabricius), and low rates of parasitism and

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larval mortality were correlated with landscape simplicity, while parasitism by two key parasitoid species increased with landscape heterogeneity. In a study by Gardiner et al. (2009), biocontrol of soybean aphid, *Aphis glycines* Matsumara, was greater in diverse compared to agriculturally dominated landscapes, and in landscapes with greater amounts of non-crop habitat. Similarly, the percentage of non-crop area in the landscape has been positively related to parasitism-induced mortality of true armyworm *Pseudaleta unipuncta* (Haworth) (Marino and Landis, 1996) and negatively related to pest damage by rape pollen beetles (Thies et al., 2003).

At the field or farm scale, local habitat can also be manipulated to provide natural enemies with resources to optimize their performance, a practice known as habitat management (Landis et al., 2000). Floral resource strips are commonly used to increase natural enemy efficacy by providing them with resources such as nectar, pollen, or alternative prey (Landis et al., 2000). Efforts to increase biocontrol with floral strips have met with mixed success, with some studies showing no effect on predator abundance within fields (Bigger and Chaney, 1998; Koji et al., 2007) and others leading to increased predator or parasitoid abundance and reduced pest pressure in crop fields (Hickman and Wratten, 1996; Langer and Hance, 2004; Lee and Heimpel, 2005). Because the surrounding landscape supplies the natural enemies that may respond to floral resource strips, it is possible that the ability of habitat management to influence pest control depends on the landscape context in which a particular crop field is situated. Tscharntke et al. (2005) suggested that local management practices may only increase biocontrol services in partially simplified landscapes, presumably because complex landscapes already supply natural enemies with necessary resources, while landscapes almost entirely cleared for agriculture may not support sufficient natural enemy populations to allow significant effects of habitat management. Thus, the increase in biocontrol services due to local management is expected to be the greatest in landscapes of an intermediate complexity. Recent studies to test this hypothesis have shown conflicting patterns, with landscape simplicity having positive (e.g. Haenke et al., 2009) or negative (e.g. Winqvist et al., 2011) effects on the benefits of local management practices.

Our goal was to examine the potential interaction between landscape traits and habitat management in a typical field crop agroecosystem of the U.S. Midwest. To do so, we used the soybean aphid and its coccinellid (lady beetle) predators as a model system to elucidate the effects of habitat management and landscape on biocontrol services in soybean fields. Coccinellids are a primary predator of soybean aphid in the north central U.S., with large species like *H. axyridis* and *C. septempunctata* having the highest per capita consumption and accounting for the majority of soybean aphid predation (Costamagna and Landis, 2007). Coccinellid abundance has been correlated with landscape features such as diversity and proportion of non-crop habitat (Gardiner et al., 2009) and may respond to floral resources (Harmon et al., 2000). Many coccinellids are known to feed on pollen of a variety of flowering plant species, including some aphidophagous species commonly found in soybean fields in north central U.S., like *C. septempunctata*, *P. quatourdecimpunctata*, and *C. maculata* (Hodek and Honek, 1996). Pollen is an important protein source for carnivorous coccinellids when insect prey are scarce (Hodek and Honek, 1996). Buckwheat is a commonly used flowering resource in habitat management studies because of its demonstrated attractiveness to natural enemies (Fiedler et al., 2008). Additionally, buckwheat strips can serve as a source of alternative prey, like non-pest aphids and the eggs and larvae of lepidopterans and herbivorous beetles.

In this study, we hypothesized that: (1) coccinellid abundance will increase in response to habitat management; (2) predators will significantly suppress soybean aphid populations; (3) biocontrol
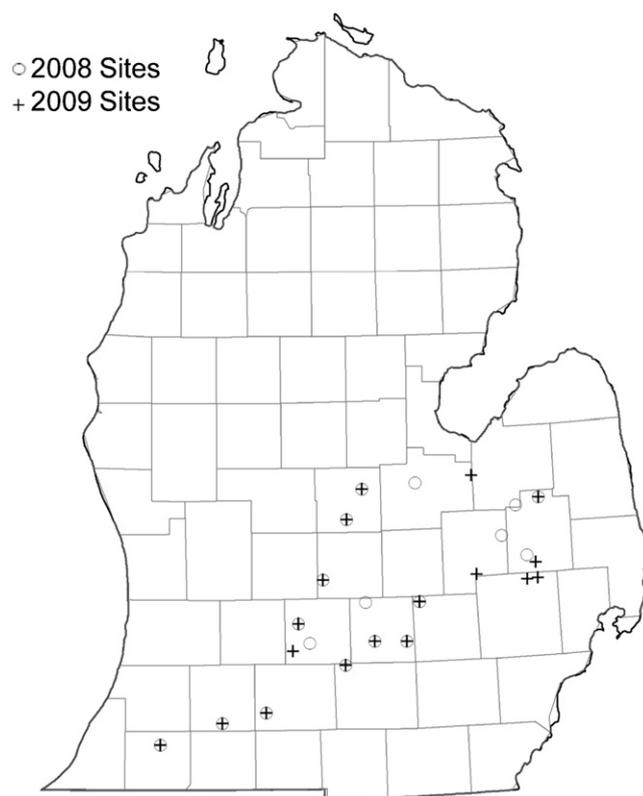

Fig. 1. Site locations of paired soybean fields across southern Michigan sampled for aphids and natural enemies in 2008 and 2009. Sites on the same or nearby farms from year to year appear to overlap at this scale (crossed circles), but samples were collected in a different set of fields in each year.

services will be positively related to habitat diversity within landscapes; and (4) the degree to which habitat management improves biocontrol services will depend on characteristics of the surrounding landscape. To test these hypotheses, we manipulated floral resources adjacent to soybean fields situated in landscapes of varying complexity and composition and measured resultant changes in levels of biocontrol services.

2. Methods

2.1. Site design

This study was replicated in 17 sites across a gradient of landscape diversity in southern Michigan (Fig. 1 and Tables A.1 and A.2) during the summers of 2008 and 2009. Within a year, each site consisted of two soybean fields, located from 0.5 to 1.8 km apart. In each site, a control field was bordered by a fencerow or grassy field margin, and a treatment field was adjacent to a floral resource strip of annual buckwheat (*Fagopyrum esculentum* cv. Mancan). Hereafter, the control field margin and the buckwheat strip will collectively be referred to as field edges. Within each field, sampling was replicated in four 30 m × 20 m plots (Fig. 2). In 2008, plots in control fields were set up at least 40 m away from all edges and any non-soybean vegetation. In the buckwheat fields in 2008 and in both fields in 2009, the plots were set up 15 m away from the buckwheat strip or field margin and at least 40 m away from any non-soybean vegetation on all other sides.

2.2. Buckwheat establishment and control margin characteristics

Buckwheat strips were 5 m wide × 200 m in length (Fig. 2). The strips were planted using a 19 cm row spacing at a rate of 70 kg/ha
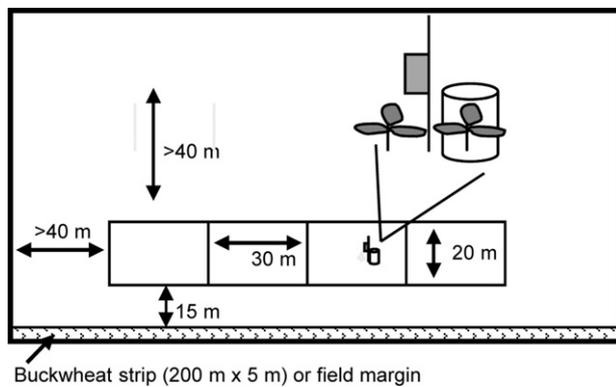
Fig. 2. Schematic of sampling design showing relative locations of plots and buckwheat strip or control field margin. Inset: a yellow sticky trap and a pair of caged and uncaged soybean plants for the biocontrol experiment were located in the center of each plot.

using a Great Plains Seed Drill (Salina, Kansas) along field edges chosen by land owners. In each year, the majority of strips (12 in 2008, 11 in 2009) were planted along fencerows, with the remaining strips planted along woodlots (2 in 2008), driveways or roads (2 in 2008, 5 in 2009), or directly between two crop fields (1 in each year). Strips were planted between 19 May and 6 June in 2008, and between 3 June and 7 July in 2009 (Tables A.3 and A.4). The strips were planted later in 2009 due to heavy rains in May. After reaching full bloom, buckwheat height and density were measured at 10 random locations within each strip.

Control field margins were chosen to match the cardinal direction of the paired buckwheat strip at each site, except in a few cases where field dimensions made this infeasible. Control field margins were similar to the edges next to which buckwheat strips had been planted (10 at fencerows, 1 next to a woodlot, 3 next to driveways or roads, 1 between crop fields and 2 next to larger patches of mown grass). Vegetation of control field margins consisted of grasses and weedy herbs generally between half a meter and a meter in height.

2.3. Aphid counts

Soybean aphid abundance was estimated at weekly intervals using destructive whole plant counts. Five randomly selected soybean plants in each plot were removed and the number of alate and apterous aphids counted. Vegetative and reproductive growth stages for each plant were recorded (Higley and Boethel, 1994).

2.4. Coccinellid counts

Aerially dispersing coccinellids were measured in soybean fields and field edges with 23 cm × 28 cm unbaited yellow sticky cards (PHEROCON AM, Great Lakes IPM, Vestaburg, MI). All coccinellids on the cards were counted and identified to species in the field. In 2008, traps were placed in the center of each plot in all study sites and at two locations within each buckwheat strip. Traps were suspended at 120 cm height from plastic step-in fence posts (Zareba Systems, Lititz, PA) and replaced every week from 1 June to 15 August. In 2009, four traps were placed in each field, one in the center of each plot, and three sticky traps were placed in the field edge of both treatment and control fields. The traps in the center of each plot were located 25 m away from the field edge, and were suspended from step-in plastic fence posts at plant canopy height and were replaced every week from 8 June to 26 August.

2.5. Biocontrol study

The effect of biocontrol services on soybean aphid populations was determined by contrasting soybean aphid population growth in the presence and absence of generalist predators, using methods modified from Gardiner et al. (2009). Predators were excluded using cages erected from 7 July to 19 July in 2008 (Table A.5) and from 9 July to 12 Aug in 2009 (Table A.6). In each plot a single soybean plant was enclosed in either a 0.84 m tall, 0.30 m diameter (2008) or a 1.07 m tall, 0.36 m diameter (2009) wire tomato support cage. The cages were covered with fine-mesh white netting (openings of 0.65 mm × 0.17 mm; Skeeta, Bradenton, FL) sewn into sleeves of 137 cm circumference. The bottom of the mesh sleeve was buried in the soil, and the top was tied to a metal "T" post. Each caged plant was paired with an uncaged plant of the same vegetative and reproductive growth stage, located 1 m away in the same row.

Each caged and uncaged plant was infested with 5 aphids in 2008 and 10 aphids in 2009. In both years the aphids were of mixed age classes representing natural colonies in the field. The aphids were transferred using a fine paintbrush from soybean plants in predator exclusion cages established in the soybean fields earlier in the season to rear aphids. Fields in each site were infested with aphids reared in that particular site, except where a field contained insufficient populations. The number of aphids on each caged and uncaged plant was counted at 7 d and 14 d after infestation using non-destructive sampling in the field. Apterous and alate aphids were counted separately, and cages containing more than 10 alates were excluded from analyses to limit the influence of alates that would have normally dispersed to other plants remaining and reproducing within the cages.

Biocontrol services were measured as an index describing the difference in aphid population size with and without naturally occurring predators as a proportion of the exclusion treatment in each site (Gardiner et al., 2009). The Biocontrol Services Index (BSI) was calculated as the difference between the number of aphids on the open plant and on the caged plant, divided by the number of aphids on the caged plant, all at fourteen days after initial infestation.

$$BSI = \frac{Ac - Ao}{Ac}$$

Ac, number of aphids on caged plant at 14 d
Ao, number of aphids on open plant at 14 d

BSI values range from 0 to 1, with 1 representing total aphid suppression and 0 representing no aphid suppression. Negative BSI values created in cases where $Ao > Ac$ were reset to 0. Values of BSI were calculated for each plot in each year, and a field average was calculated.

All cage study results in 2008 are based on 11 sites. Three sites were excluded from the cage study due to the unsuccessful establishment of their buckwheat strips. Three additional sites were excluded from the analysis of cage data due to an inability to successfully establish rearing and experimental cages at the site. All cage study results in 2009 are based on 12 sites. Two sites were not included in the cage study due to the very late blooming of the buckwheat strips in those sites. Two sites were excluded from the analysis because large numbers of alate aphids in the fields during the week of the cage study increased the numbers on the open plants. Two additional sites were excluded due to difficulties in establishing aphid populations due to competing pest populations.

2.6. Landscape analysis

Landscapes were assessed by considering all landcover types surrounding each field using the methods of Gardiner et al. (2009). GPS coordinates were collected from the center of each field using a handheld GPS receiver. The GPS coordinates were used to obtain ortho-rectified digital aerial photos for each field from the Michigan Spatial Data Library. Habitats around each field were digitized to a 2.0 km radius using ARC GIS 9.2 (2008) or 9.3 (2009; ESRI Redlands, CA). This range represents a reasonable foraging area of large species of adult ladybeetles. Flights of approximately 1.8–2.0 km or greater are considered migratory (i.e. entering or leaving overwintering habitat) for *Hippodamia convergens* (Hodek et al., 1993), a lady beetle species of similar size and diet preferences as the dominant coccinellid predators of soybean aphid. Shorter distances can be considered within the realm of "trivial flights," or short-distance flights for foraging, which is the type of dispersal relevant for biocontrol in crop fields. Habitat types within field sites were ground-verified each summer and landscape changes were corrected during digitization. During ground-truthing, the specific land cover within all habitat polygons in each landscape was determined by assigning landscape categories to each polygon. Landscape categories included field crops (primarily corn, soy, wheat, and forage crops) and non-crop habitat types (primarily woodlots, old field, and residential areas) (Table A.7). Categories were added for any additional land cover types discovered during ground-truthing. Total area of each habitat category for each site was calculated in ARC GIS 9.2 or 9.3 at four scales: 0.5, 1.0, 1.5, and 2.0 km from the center of the focal field.

Proportion of semi-natural habitat and Simpson's Diversity Index (D) (Simpson, 1949) were used independently as metrics of landscape heterogeneity. Semi-natural habitat included wooded habitats such as forests, woodlots, and fencerows, as well as grassy habitats such as old field and Conservation Reserve Program lands. Simpson's index – typically used as a measure of species diversity – is used here as a measure of habitat diversity within each landscape, according to the methods of Gardiner et al. (2009).

$$D = \sum \frac{n_i(n_i - 1)}{N(N - 1)}$$

n_i, area of land covered by ith land-cover category
N, total area covered by land categories in each circle

Simpson's index is less sensitive than other diversity measures to category richness, in this case habitat richness (Magurran, 2004). Therefore, Simpson's index effectively describes the variance in relative abundance of habitat types without being skewed by the presence of rare habitats (Magurran, 2004).

Diversity decreases as D increases, therefore we calculated $-\ln D$ so that values intuitively increase with increasing diversity. The negative logarithm is preferable to other transformations such as the reciprocal of D, which can create variance problems (Magurran, 2004).

Because seminatural habitat and metrics of habitat diversity have been found to be highly correlated in other studies (e.g. Thies and Tscharntke, 1999; Steffan-Dewenter et al., 2002; Roschewitz et al., 2005b), we calculated Pearson correlation coefficients (PROC CORR, SAS 9.2) for the two landscape variables percentage of semi-natural habitat and $-\ln D$ at each landscape extent to determine the degree to which these two metrics measured different components of landscape structure.

2.7. Statistical analysis

2.7.1. Coccinellid abundance

To test the hypothesis that coccinellid abundance increases in response to habitat management, total coccinellid captures were compared between treatment and control fields, and between buckwheat strips and control field margins. Additionally, the response of coccinellid populations to landscape composition and the interaction between landscape and habitat management were determined. Weekly coccinellid counts were averaged for each field or field margin and analyzed separately for each year using analyses of variance (ANOVA) (PROC GLIMMIX, SAS 9.2). For each response variable (coccinellid abundance in soybean fields in 2008, coccinellid abundance in soybean fields in 2009, and coccinellid abundance in field edges in 2009), eight separate models were run considering either the effect of landscape diversity ($-\ln D$) or proportion of semi-natural habitat measured at 0.5, 1.0, 1.5, or 2.0 km. Fixed effects were treatment, landscape (either $-\ln D$ or semi-natural habitat), and the treatment by landscape interaction. Coccinellid abundance in field edges was log transformed prior to analysis to meet the assumptions of ANOVA. It was unnecessary to transform coccinellid abundance in soybean fields.

Additionally, individual coccinellid species abundance was compared between buckwheat strips and control field margins, as well as between the soybean fields adjacent to buckwheat fields and those without strips. Because of difficulty in meeting distributional assumptions with the data for any individual coccinellid species, nonparametric tests were used. Average summer abundance in each field or field edge were first ranked (PROC RANK, SAS 9.2), such that the field or edge with the highest abundance was given the highest rank. Then, ranks were compared using mixed model ANOVA (PROC GLIMMIX, SAS 9.2), with treatment as a fixed effect and site as a random effect. ANOVA on rank-transformed data does not depend on the distribution of the data, is resistant to outliers, and is robust to non-normality of errors. However, assumptions regarding homoscedasticity of variance still hold, thus we were only able to compare the relatively common species *H. axyridis*, *C. septempunctata*, *P. quatourdecimpunctata*, *H. variegata*, and *C. maculata* using this method.

2.7.2. Biocontrol study

To test the hypothesis that the presence of predators significantly depresses soybean aphid populations, numbers of aphids on caged and uncaged soybeans were compared. Aphid counts were $\log(x+1)$ transformed prior to analysis to meet the assumptions of homogeneity of variance, and were analyzed using a repeated measures mixed model ANOVA (PROC GLIMMIX, SAS 9.1). Fixed effects were treatment, cage status (i.e. plant caged or uncaged), week and their two- and three-way interactions. Random effects were site and all interaction terms involving site.

3. Results

3.1. Buckwheat establishment

In 2008, buckwheat strips were successfully established in 14 out of 17 sites (Fig. 3). Three sites were not included in the analysis because of low germination due to flooding or loss to hail. The average height of buckwheat in the 14 strips used in the 2008 study was 89 cm, ranging from 50 cm to 109 cm (Table A.3). The average density of buckwheat in the 14 strips was 12.2 stems/100 cm², ranging from 7.2 to 20.5 stems/100 cm². In 2009, 17 strips were successfully established. The average height of all buckwheat strips in 2009 was 57.4 cm, ranging from 20.5 to 93.1 cm (Table A.4). The average density of all buckwheat strips in 2009 was 7.4 stems/100 cm²,

Table 1

Effects of landscape and local habitat management on coccinellid abundance in 2008 soybean fields, 2009 soybean fields, and 2009 field margins. Separate analyses were run with (A) Simpson's diversity index – ln D, and with (B) proportion of semi-natural habitat in the landscape as the landscape descriptor variables. Results are shown for landscape values at the 2.0 km scale, but were consistent at all scales.

	A			B		
	F value	pr > *F*			*F* value	pr > *F*
2008 Soy fields						
Buckwheat treatment	$F_{1,24} = 2.72$	0.112	Buckwheat treatment		$F_{1,24} = 0.59$	0.451
Diversity ($-\ln D$)	$F_{1,24} = 1.15$	0.295	Semi-natural habitat		$F_{1,24} = 0.07$	0.798
Treatment*$-\ln D$	$F_{1,24} = 2.18$	0.153	Treatment*semi-natural		$F_{1,24} = 1.81$	0.191
2009 Soy fields						
Buckwheat treatment	$F_{1,30} = 0.19$	0.662	Buckwheat treatment		$F_{1,30} = 0.47$	0.496
Diversity ($-\ln D$)	$F_{1,30} = 0.14$	0.713	Semi-natural habitat		$F_{1,30} = 6.11$	0.019
Treatment*$-\ln D$	$F_{1,30} = 0.31$	0.580	Treatment*semi-natural		$F_{1,30} = 0.19$	0.667
2009 Field margins						
Buckwheat treatment	$F_{1,30} = 10.58$	0.003	Buckwheat treatment		$F_{1,30} = 10.78$	0.003
Diversity ($-\ln D$)	$F_{1,30} = 0.00$	0.889	Semi-natural habitat		$F_{1,30} = 0.25$	0.618
Treatment*$-\ln D$	$F_{1,30} = 0.03$	0.834	Treatment*semi-natural		$F_{1,30} = 0.40$	0.532

ranging from 1.4 to 16.8 stems/100 cm^2. Final buckwheat height did not change significantly with planting date in either year (2008: $F_{1,126} = 1.85$, $p = 0.176$; 2009: $F_{1,153} = 0.09$, $p = 0.762$), nor did density (2008: $F_{1,126} = 0.26$, $p = 0.613$; 2009: $F_{1,153} = 0.28$, $p = 0.600$).

3.2. Landscape analysis

The studied landscapes represented a gradient of landscape diversity, with landscapes ranging from forest-dominated to agriculturally dominated in both years. All landscapes were predominantly made up of corn, soy, wheat, forest, grassland, and residential areas, but proportions of each of these varied between landscapes (Tables A.8 and A.9). In 2008, diversity values ($-\ln D$) ranged from 1.19 to 1.91, while the percentage of semi-natural habitat ranged from 3 to 79% at the 2.0 km scale. In 2009, diversity values ranged from 0.83 to 1.95, with the percentage of semi-natural habitat ranging from 5 to 76% at the 2.0 km scale. Values were similar for smaller scales.

In 2008, the landscape variables $-\ln D$ and the proportion of semi-natural habitat were not correlated at any scale ($r^2 = -0.11$, $p = 0.59$; $r^2 = -0.05$, $p = 0.81$; $r^2 = 0.08$, $p = 0.69$; $r^2 = 0.05$, $p = 0.80$; in descending order of landscape extent). In 2009, these landscape variables were correlated at 2.0, 1.5, and 0.5 km. However, the correlations are low ($r^2 = -0.44$, $p = 0.009$; $r^2 = -0.33$, $p = 0.05$; $r^2 = 0.34$, $p = 0.05$, respectively) and they explain little variation in the two variables. Furthermore, the changing sign of the correlations and the lack of correlation at 1.0 km ($r^2 = -0.24$, $p = 0.18$), suggest that these two variables are not closely related within this set of landscapes.

3.3. Aphid counts

Soybean aphids naturally colonized all fields used in the study, but populations generally remained below the economic threshold of 250 aphids/plant (Ragsdale et al., 2007). In 2008, aphids were first detected on 2 June and aphids were discovered in all fields by 17 July (Table A.5). In 2009, aphids were initially detected during the first week of sampling (9–12 June) in 6 fields, and all fields were infested by 23 July (Table A.6). Only one field reached the economic threshold during the last week of sampling in 2009.

3.4. Coccinellid abundance

In 2008, 1412 coccinellids were collected and identified in soybean fields. Of these, 90% were exotic species, with 47% *H. axyridis*, 31% *C. septempunctata*, 10% *P. quatourdecimpunctata*, and 2% *H. variegata*. The most common native species were *C. maculata* and *H. parenthesis*, which made up 6% and 2% of the total capture, respectively. All other species made up 1% or less of captures. In 2009, 4276 coccinellids were collected and identified in soybean fields. The majority were exotic species, with 33% *C. septempunctata*, 28% *H. axyridis*, 18% *P. quatourdecimpunctata*, and 9% *H. variegata*. The most common native species were *C. maculata* and *H. parenthesis*, which made up 5% and 3% of the total capture, respectively. All other species made up 1% or less of captures.

Habitat manipulation altered predator abundance, with significantly more coccinellids found in buckwheat strips than in control field edges in 2009, the only year for which the comparison was made (Table 1 and Fig. 4). An average of 2.69 ± 0.42 lady beetles per card were found in the buckwheat strips, as compared to an average of 1.32 ± 0.21 per card in the control field margins.

Slightly more coccinellids were captured in fields with buckwheat strips than in control fields in both years, although the effect was not significant in either year (Table 1 and Fig. 4). Coccinellid abundance in fields was not affected by landscape diversity at any scale in either year, nor by the diversity by treatment interaction (Table 1). However, in 2009, lady beetles were more abundant in soybean fields surrounded by landscapes with greater proportions of semi-natural habitat measured at 1.5 and 2.0 km (Table 1 and Fig. 4). The treatment by landscape interaction for this effect was not significant at any scale. Statistical results for all effects were identical at the 1.5 and 2.0 km scales, while no effect of landscape was shown at smaller scales.
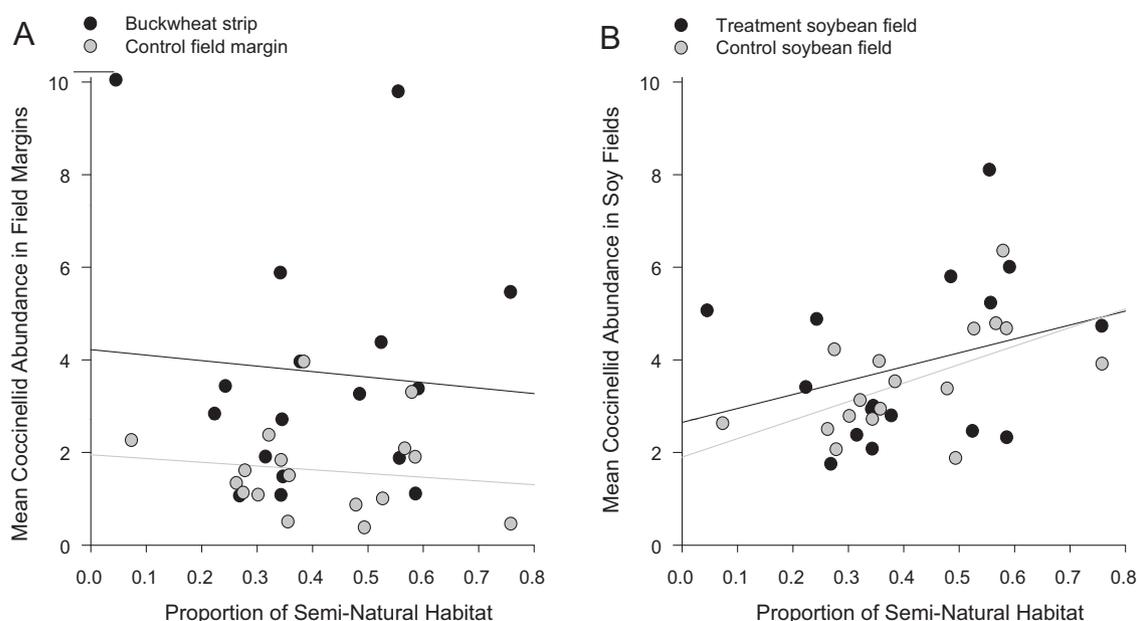

Fig. 3. An example buckwheat strip in full bloom in July 2009.

Fig. 4. (A) Coccinellid abundance in field margins was consistently and significantly higher in buckwheat strips than in control field margins across a gradient of semi-natural habitat within landscapes. (B) Coccinellid abundance in soybean fields in 2009 increased significantly with the proportion of seminatural habitat in the surrounding landscape at 2.0 km. The effect did not differ between fields adjacent to or without buckwheat strips.

Within buckwheat strips, 81% of lady beetles captured were exoticspecies (*C. septempunctata* 28%, *H. variegata* 25%, *P. quatourdecimpunctata* 20%, *H. axyridis* 8%). The native pink lady beetle *C. maculata* made up an additional 9% and the orange spotted lady beetles *Brachiacanthus* sp. made up an additional 4% of the lady beetles found in buckwheat strips. In contrast, there were more *H. axyridis* (17%) and fewer *H. variegata* (3%) in the control field margins. Proportions of other lady beetles were similar (*C. septempunctata* 24%, *P. quatuordecimpunctata* 34%, *C. maculata* 4%, *Brachiacanthus* sp. 8%). However, the abundance of lady beetles in field margins did not vary with landscape diversity or amount of semi-natural habitat in the landscape in either year (Table 1).

While rank comparisons showed no difference in species abundance between treatment and control fields in 2008 (Table 2), several coccinellid species were significantly more abundant in buckwheat strips than in control field edges in 2009 (Table 3). Using rank abundance, three common exotic species *C. septempunctata*, *H. variegata*, and *P. quatordecimpunctata*, as well as the common native species *C. maculata*, were more commonly found in buckwheat strips. *C. maculata* was also found to be more abundant in fields next to buckwheat strips than in fields next to control field margins. In contrast, no species was found to be more abundant in control field margins, and only *H. axyridis* was more common in control soybean fields.

3.5. Biocontrol study

Exclusion of natural enemies resulted in dramatically increased soybean aphid populations in both years (Fig. 5). Across fields and sites, the number of aphids on caged plants from which predators were excluded was significantly higher than on uncaged plants which were exposed to predators (2008: $F_{1,10} = 251.33$, $p < 0.0001$; 2009: $F_{1,10} = 114.03$, $p < 0.0001$). After 14 days, there were 38 fold more aphids per plant on caged than uncaged plants in 2008, and 53 fold more aphids per plant on caged than uncaged plants 2009. Buckwheat treatment did not significantly affect the size of the difference in aphid populations on caged and uncaged plants in either year (2008: $F_{1,10} = 1.62$, $p = 0.2313$; 2009: $F_{1,10} = 0.62$, $p = 0.4509$), nor were any of the interactions involving treatment significant in either year. The differences in aphid populations between caged and uncaged plants were greater at 14 days than at 7 days in both years (Fig. 5), as indicated by a significant week by cage status interaction (2008: $F_{1,10} = 61.06$, $p < 0.0001$; 2009: $F_{1,10} = 30.03$, $p = 0.0003$).

We found very high suppression of aphids by the existing predator populations in both years in almost all fields. BSI values in 2008 ranged from 0.77 to 1, with an average value of 0.954 ± 0.01 and 22 of 23 fields had BSI values greater than 0.90 (Table 4). BSI values in 2009 ranged from 0.66 to 0.99, with an average value of

Table 2
Mean ± S.E. of coccinellid beetles of each species found in soybean fields or field margins during 2008. No comparisons between treatment and control fields were significant in this year.

Coccinellids	Buckwheat strip	Treatment field	Control field
Exotic species			
Harmonia axyridis	0.32 ± 0.04	0.64 ± 0.05	0.52 ± 0.04
Coccinella septempunctata	0.87 ± 0.10	0.41 ± 0.03	0.35 ± 0.03
Hippodamia variegata	0.007 ± 0.005	0.02 ± 0.01	0.02 ± 0.01
Propylea quatuordecimpunctata	0.24 ± 0.03	0.15 ± 0.02	0.10 ± 0.01
Native species			
Coleomegilla maculata	0.11 ± 0.03	0.07 ± 0.01	0.07 ± 0.01

Additionally, the native species *Hippodamia convergens*, *Hi. parenthesis*, *Brachiacantha ursina*, *Cycloneda munda*, *Hyperaspis binotata*, and *Adalia bipunctata* were all collected at mean abundances of less than 0.02 in each habitat in 2008.

Table 3
Mean ± SE of coccinellid beetle species found in each field or field margin during 2009. Individual counts were rank transformed and compared using ANOVA. Asterisks (*) indicate a significant difference in abundance between buckwheat strips and control field margins, or between treatment and control fields (***$p < 0.01$, **$p < 0.05$, *$p < 0.1$).

Coccinellids	Buckwheat strip	Control field margin	Treatment field	Control field
Exotic species				
Harmonia axyridis	0.31 ± 0.03	0.27 ± 0.03	1.07 ± 0.08	1.09 ± 0.07
Coccinella septempunctata	1.07 ± 0.09	0.38 ± **0.05***	1.36 ± 0.08	1.18 ± 0.07
Hippodamia variegata	0.96 ± 0.13	0.04 ± **0.01***	0.50 ± 0.05	0.21 ± 0.02
Propylea quatuordecimpunctata	0.78 ± 0.08	0.54 ± **0.05***	0.71 ± 0.06	0.71 ± 0.05
Native species				
Coleomegilla maculata	0.35 ± 0.06	0.06 ± 0.01***	0.24 ± 0.03	0.16 ± **0.02***

Additionally, the native species *Hippodamia parenthesis, Hi. convergens, Hi. tredecimpunctata, Hi. glacialis, Brachiacantha ursina, Cycloneda munda, Hyperaspis undulata, Hy. binotata, Hy. proba, Hy. bigeminata*, and *Psyllobora vigintimaculata* were all collected at mean abundances less than 0.16 in each habitat 2009.

Table 4
Biocontrol services index values for aphid suppression by natural enemies for each soybean field in 2008 and 2009.

Site	2008 BSI		Site	2009 BSI	
	Treatment	Control		Treatment	Control
Breckenridge	0.993	0.973	Breckenridge	0.846	0.983
Cassopolis	0.901	0.943	Cassopolis	0.991	0.902
Fowlerville	0.948	0.995	Charlotte		0.968
Ithaca	1.000	1.000	Grand Blanc	0.663	0.830
Lapeer	0.990	0.959	Ithaca	0.974	0.927
Leroy	0.972	0.983	Mason	0.985	0.970
Mason	0.932	0.965	Oxford	0.991	0.998
Richfield	0.992	0.958	Silverwood	0.990	0.997
Saginaw	0.976	0.941	Springport	0.995	0.993
Stockbridge	0.776	0.979	Vermontville	0.992	0.983
Vermontville		0.924	Vicksburg	0.943	0.992
Vicksburg	0.922	0.918	Westphalia	0.997	0.968
Average	0.942 ± 0.002	0.959 ± 0.008		0.937 ± 0.031	0.968 ± 0.008

0.954 ± 0.02 and 20 of 23 fields had BSI values of greater than 0.90 (Table 4). We did not conduct landscape analyses on BSI because of a lack of variation in BSI to be explained by any other variables.

4. Discussion

4.1. Landscape effects on local management to improve services

In this study, predators had a significant negative impact on soybean aphid populations and lady beetle abundance increased both in habitat management strips and with the proportion of semi-natural habitat in the landscape, but we found no interaction between landscape context and local habitat management on coccinellid abundance. In contrast, other studies have found that the degree to which local management can influence communities is dependent upon the degree of heterogeneity in the surrounding landscape. Local management was more effective for increasing richness and abundance in simplified, crop-dominated landscapes than in diverse landscapes for a variety of taxa (e.g. pollinators (Carvell et al., 2011); bees (Holzschuh et al., 2007; Rundlof et al.,
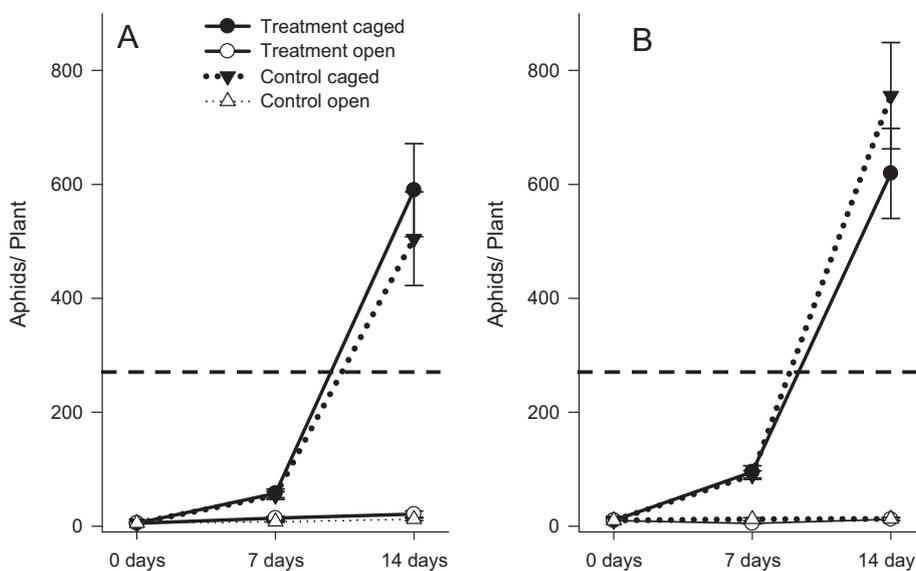

Fig. 5. Average number of aphids per soybean plant exposed to and excluding predators in treatment and control fields, at 7 and 14 days after infestation in (A) 2008 and (B) 2009. The horizontal dashed line indicates the economic threshold for soybean aphid of 250 aphids/plant. In both years, natural enemies dramatically suppressed soybean aphid populations, and the differences in aphid populations between caged and uncaged plants were greater at 14 days than at 7 days. However, buckwheat treatment did not significantly affect the size of the difference in aphid populations on caged and uncaged plants in either year.

2008); butterflies (Rundlof and Smith, 2006); birds (Geiger et al., 2010; Smith et al., 2010); aphidophagous syrphids (Haenke et al., 2009); and plants (Roschewitz et al., 2005a)). In contrast, Winqvist et al. (2011) demonstrated the opposite effect, with organic farming methods increasing biocontrol over conventional methods only in the most diverse landscapes. Additionally, other studies have shown little impact of local management at all, with taxon diversity and abundance responding primarily to landscape composition alone (Purtauf et al., 2005; Schmidt et al., 2005). These contrasting results may indicate that these relationships are highly taxon- and context-dependent. Indeed, even within a single study, different taxa exhibited opposite responses to landscape and local management (Concepcion et al., 2008), while a recent meta-analysis showed that the arthropod response to local management was influenced by landscape context for populations in cropland habitats but not within grassland habitats (Batáry et al., 2011).

4.2. Effects of local management on coccinellid beetles

The habitat management treatment successfully attracted coccinellid beetles, with significantly more lady beetles in buckwheat strips than in grassy field margins or fencerows. However, this increase in coccinellid abundance at the field edges was not reflected in higher abundance in adjacent soybean fields. Other studies have similarly demonstrated predators taking advantage of managed habitats without clear effects on adjacent fields. For example, a guinea grass border did not affect the abundance of predators within maize or the density of spotted stem borer, *Chilo partellus*, in spite of attracting abundant predators to the strip (Koji et al., 2007). In contrast, Walton and Isaacs (2011) found significantly higher abundance of both syrphid flies and predatory wasps in blueberry fields adjacent to native wildflower plantings than next to mown grass strips. In other cases, increased natural enemy abundance from floral resource strips have resulted in higher parasitism rates (Langer and Hance, 2004) and lower pest abundance in adjacent fields (Hickman and Wratten, 1996). Inconsistencies in these patterns could be a result of varying predator biology or landscape context.

4.3. Landscape effects on coccinellid beetles

In 2009, abundance of coccinellids in soybean fields increased with proportion of semi-natural habitat in the surrounding landscape. Similar positive effects of semi-natural habitat on natural enemies have been found for a variety of predatory and parasitic taxa (Chaplin-Kramer et al., 2011). Lady beetles require undisturbed habitat for overwintering, and *H. axyridis*, one of the two most abundant species collected in our study, is known to overwinter in wooded areas. The abundance of potential overwintering sites in landscapes with large proportions of semi-natural habitat could have led to higher overwinter survival of coccinellids in those landscapes, leading to larger populations emerging in the spring. Additionally, lady beetles in the north central U.S. emerge from overwintering in March and April, before field crops such as corn and soy are planted in May or June. Thus, lady beetles are dependent upon other food sources in the spring before foraging on soybean aphid in the summer. Aphids in semi-natural habitat, such as those feeding on grasses or legumes in old fields, could provide an abundant food source in the spring, allowing lady beetles in these landscapes to build up larger populations by the time field crops are planted in summer.

In other studies, seminatural habitat has been used as a metric of landscape heterogeneity, as in European landscapes it has been repeatedly found to be highly correlated with Shannon habitat diversity (e.g. Thies and Tscharntke, 1999; Steffan-Dewenter et al., 2002; Roschewitz et al., 2005b). In our study, however,

Simpson's Diversity, a similar metric, was not strongly correlated with seminatural habitat at any scale. This could be because European landscapes are functionally different than landscapes in the north central U.S. Alternatively, the landscapes examined in this study may represent a greater maximum amount of seminatural habitat. In the European studies cited, maximum semi-natural habitat was usually around 30–50%, whereas in this study seminatural habitat was as high as 79%. It is possible that the relationship between habitat diversity and seminatural habitat breaks down at high levels of seminatural habitat because of dominance of one or two habitat types. A landscape may have a large proportion of seminatural habitat and low diversity if, for example, it is dominated by a single seminatural landcover type such as forest. In our study, semi-natural habitat was a better predictor of coccinellid abundance than habitat diversity. This may be because a single type of seminatural habitat can still provide multiple resources, such as nesting and overwintering habitats, temporary refuges, alternative prey and floral resources (Bianchi et al., 2006).

In contrast to the effect on lady beetles in crop fields, there was no effect of semi-natural habitat on coccinellid abundance within the buckwheat strips. Haenke et al. (2009) found that the abundance and species richness of syrphid flies in flower strips was positively related to the amount of cropland in the surrounding landscape, presumably because the addition of floral resources was more rewarding in crop-dominated landscapes than in diverse landscapes with abundant resources. This suggests that coccinellids used the flowering buckwheat strips regardless of the availability of other resources in the surrounding landscapes.

4.4. Effects of predators on soybean aphid density

Predators provided high levels of biological control of soybean aphid in all sites. Regardless of landscape conditions or habitat management, soybean aphid populations exposed to ambient predator densities were greatly suppressed compared to the predator exclusion treatment. In light of the fact that the abundance of the major predators of soybean aphid in this system, coccinellid beetles, was positively related to the proportion of semi-natural habitat in the landscape surrounding study fields, it is somewhat surprising that biocontrol services were not similarly lower in crop dominated landscapes and higher in landscapes with more semi-natural habitats. The high levels of biocontrol in all landscapes suggests that even the lowest abundance of coccinellids was sufficient to control soybean aphid. This result stands in stark contrast to those of Gardiner et al. (2009) who found that both coccinellid abundance and soybean aphid suppression were correlated with habitat diversity and abundance of non-crop habitat in surrounding landscapes. This may indicate a shift in this system from 2005 to 2006 when Gardiner et al. (2009) collected their data to 2008–09 when the data for this paper were collected. Elton (1958) postulated that changes within biological communities that lead to increased competition and predation or parasitism of exotics may be responsible for the transition of some exotic species from highly invasive to merely naturalized members of the community. In a similar fashion, the predominant predators of the soybean aphid, *H. axyridis* and *C. septempunctata*, may have become a greater proportion of the existing natural enemy community in response to the abundant food source provided by soybean aphids (Heimpel et al., 2010), thereby helping to suppress further aphid outbreaks. As further evidence, soybean aphid and *H. axyridis* populations were initially cyclic, with aphid outbreak years (2001, 2003, and 2005), followed by high populations of *H. axyridis* in 2002, 2004, and 2006 (Knapp et al., 2012). However, no soybean aphid outbreaks have occurred in Michigan since 2005 and aphids and *H. axyridis* have not cycled since then, possibly indicating that a new equilibrium has been reached in this system. Alternatively, management changes within soybean

fields could have limited the ability of soybean aphid populations to increase unchecked throughout the growing season. Modeling studies indicate that in order to prevent soybean aphid outbreaks, it is important for natural enemies to consume insipient aphid colonies before they become well established and produce alates (Costamagna and Landis, 2011). In the past, initial soybean aphid colonization of Midwestern soy fields occurred early in the season when coccinellids have had limited time to increase from their overwintering populations. Increased use of soybean seed treated with systemic insecticide in recent years (Magalhaes et al., 2008) may delay aphid population growth in soybean fields, giving natural enemy populations time to increase on alternative hosts and prey before soybean aphids become well-established.

5. Conclusions

In this study, landscape characteristics and local habitat affected soybean aphid natural enemies in different ways. At a local scale, coccinellid abundance increased within the managed habitats. Thus, within the same landscapes they were more commonly captured in flowering buckwheat strips than in typical field edge habitat such as grassy margins or fencerows. In contrast, overall coccinellid population levels in equivalent habitats (i.e. paired soybean fields) were influenced by the abundance of semi-natural habitat at the landscape scale. This makes sense in light of the large distances over which coccinellid species such as *H. axyridis* and *C. septempunctata* disperse and forage. Furthermore, we found no evidence of an interaction between local management and landscape diversity or semi-natural habitat in this study. Coccinellid response in soybean fields to landscape-scale semi-natural habitat was not affected by the presence of adjacent buckwheat strips, indicating that for this pest, landscape characteristics override the effect of enhanced local resources. This suggests that to manage for increased biocontrol services of soybean aphid will require a focus on manipulating overall landscape structure rather than local resources.

However, as the studies reviewed above suggest, the influences of landscape characteristics on the relationship between local habitats and natural enemy populations are likely system-specific and dependent upon the biology of the natural enemies in question. Soybean aphid is not the only pest of soybean in these landscapes and other crops have additional pest-natural enemy associations that may be successfully managed at local scales. A greater understanding of these complex relationships will enable growers and researchers to develop more effective management systems suited to specific landscapes, prevailing pests, and their natural enemy communities. Thus, we may anticipate that in the future a combination of local and landscape management practices may be required to maximize overall pest suppression in the larger agroecosystem.

Acknowledgements

Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at doi:10.1016/j.agee.2012.02.008.

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