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Coccinellid immigration to infested host patches influences suppression of *Aphis glycines* in soybean

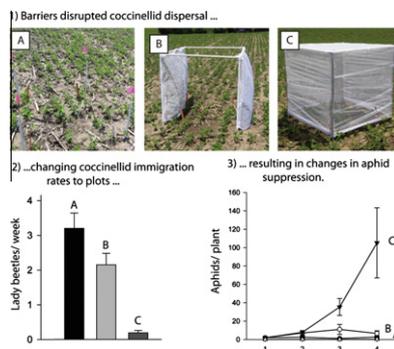
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HIGHLIGHTS

- ▶ We manipulated coccinellid immigration rates and measured effects on *Aphis glycines* populations.
- ▶ With low aphid pressure, ambient coccinellid immigration suppressed *A. glycines*.
- ▶ Reducing immigration resulted in large increases in *A. glycines* populations.
- ▶ With high aphid pressure, coccinellid and foliar predators together suppressed aphids.

GRAPHICAL ABSTRACT



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ABSTRACT

Generalist natural enemies may be well adapted to annual crop systems in which pests and natural enemies re-colonize fields each year. In addition, for patchily-distributed pests, a natural enemy must disperse within a crop field to arrive at infested host patches. As they typically have longer generation times than their prey, theory suggests that generalist natural enemies need high immigration rates to and within fields to effectively suppress pest populations. The soybean aphid, *Aphis glycines* Matsumura, is a pest of an annual crop and is predominantly controlled by coccinellids. To test if rates of coccinellid arrival at aphid-infested patches are crucial for soybean aphid control, we experimentally varied coccinellid immigration to 1 m² soybean patches using selective barriers and measured effects on *A. glycines* populations. In a year with low ambient aphid pressure, naturally-occurring levels of coccinellid immigration to host patches were sufficient to suppress aphid populations, while decreasing coccinellid immigration rates resulted in large increases in soybean aphid populations within infested patches. Activity of other predators was low in this year, suggesting that most of the differences in aphid population growth were due to changes in coccinellid immigration. Alternatively, in a year in which alate aphids continually colonized plots, aphid suppression was incomplete and increased activity of other predatory taxa contributed to adult coccinellid predation of *A. glycines*. Our results suggest that in a system in which natural enemy populations cannot track pest populations through reproduction, immigration of natural enemies to infested patches can compensate and result in pest control.

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1. Introduction

Natural enemies of crop pests exhibit a wide range of life history traits that influence their effectiveness as biological control

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agents. Modeling studies suggest that effective pest suppression may be obtained from either specialist natural enemies inflicting high mortality rates, or from generalist natural enemies with high immigration rates into an infested area (Chang and Kareiva, 1999). Additionally, each of these strategies may be better adapted to particular crop types. For example, specialist natural enemies may be well-adapted for perennial crops in which temporal stability

allows equilibrium to be achieved between natural enemy and pest populations, while generalists may be better suited for annual crops which both pests and natural enemies have to recolonize each growing season (Murdoch et al., 2006). Furthermore, because generalist natural enemies like coccinellids (Coleoptera: Coccinellidae) tend to have long generation times relative to those of their prey and thus cannot rapidly respond numerically to pest population dynamics (Dixon et al., 1997; Kindlmann and Dixon, 1999a, 1999b, 2001), generalists must exhibit high immigration rates to be effective (Murdoch et al., 2006). In fact, higher immigration rates have been demonstrated to decrease the predator/prey ratios necessary for effective pest suppression (van der Werf, 1995), and manipulating immigration rates of generalist predators has resulted in lower pest abundance and higher yields (Snyder and Wise, 1999).

Natural enemy immigration occurs at different temporal and spatial scales. In annual agriculture, many natural enemies overwinter outside of the crop and must first immigrate into crop fields after their establishment. Once in the crop habitat, they must then disperse and locate prey-infested patches within the field. In this manuscript, we focus on the process of patch-level immigration and its impact on populations of the soybean aphid, *Aphis glycines* Matsumura (Hemiptera: Aphididae), an invasive and economically damaging pest of soybean (*Glycines max* (L.) Merrill).

In the North Central U.S., soybean is typically grown in annual rotation with other crops and both *A. glycines* and many of its natural enemies must colonize the crop each season (Ragsdale et al., 2011). Furthermore, because *A. glycines* is patchily distributed in soybean fields (Costamagna and Landis, 2011), it is necessary for predators to locate and immigrate to aphid-infested patches within soybean fields. In North America, generalist predators provide the majority of natural control of *A. glycines*, and multiple studies indicate that if predators are reduced or excluded entirely, *A. glycines* quickly reach outbreak levels (Brosius et al., 2007; Costamagna and Landis, 2006; Costamagna et al., 2007; Desneux et al., 2006; Donaldson et al., 2007; Fox et al., 2005; Gardiner et al., 2009; Rhainds et al., 2007; Schmidt et al., 2007). Large, mobile predators play a particularly important role in *A. glycines* suppression. Both Gardiner and Landis (2007) and Costamagna et al. (2008) showed that small, less mobile predators like *Orius insidiosus* (Say) and various predatory larvae were unable to control *A. glycines*, while aphid populations were significantly lower when they were accessible by large predators like coccinellids. Furthermore, the large coccinellid beetles *Coccinella septempunctata* L. and *Harmonia axyridis* Pallas have been shown to be highly efficient *A. glycines* predators, having the highest per capita consumption rate of the *A. glycines* predators studied to date, and contribute to a majority of *A. glycines* predation in the North Central U.S. (Costamagna and Landis, 2007). In addition, these two species are dominant in soybean fields in Michigan. *H. axyridis* and *C. septempunctata* together accounted for 75% and 62% of total lady beetle captures in Michigan soybean fields in 2008 and 2009 (Woltz, unpub. data).

Most coccinellid beetles have long generation times relative to aphids, suggesting an inability to suppress aphid prey through reproduction alone (Dixon et al., 1997; Kindlmann and Dixon, 1999a, 1999b, 2001). Furthermore, although *H. axyridis* and *C. septempunctata* overwintered adults are active in spring foraging in crops like alfalfa and wheat (Colunga-Garcia and Gage, 1998; LaMana and Miller, 1996), there is very little production of larvae in soybean fields before mid-summer when *A. glycines* populations are rapidly increasing. This is because coccinellids require minimum prey densities to oviposit (Seagraves, 2009), tend to oviposit near aphid colonies, and lay more eggs when more prey are available (Hodek and Honek, 1996). For example, in surveys of 34 soybean fields throughout the soybean-producing region of Michigan

in 2009, lady beetle larvae were not detected in soybean fields until 20 July even though aphids were present by the first week of June (Woltz unpub. data). Thus, we predict that early-summer predation of *A. glycines* on small soybean plants due to adult coccinellids regularly arriving at and predating aphid-infested patches within soybean fields will be crucial to overall *A. glycines* suppression.

Here, we measure the importance of patch-level coccinellid immigration for suppressing aphid populations by experimentally varying coccinellid immigration to 1 m² soybean patches by using selective barriers. We hypothesize that: (1) our manipulations would create a gradient of coccinellid immigration within the plots and that (2) decreases in early summer growing season lady beetle immigration would result in increases in aphid populations within plots.

2. Materials and methods

2.1. Site

This study was conducted during the summers of 2010 and 2011 on and around the Kellogg Biological Station, Long Term Ecological Research Site (KBS LTER; 42.405714N, 85.377658W). Agriculture in this region consists of a mix of annual field crops (corn, soy, and wheat) and perennial forage crops (pasture and perennial mixes for hay). Deciduous forests and old field successions make up the primary non-crop land cover in the area. Study fields were planted between 10 and 24 May in 2010 and between 9 May and 2 June in 2011. Sampling took place weekly from 16 June to 9 July in 2010, and from 5 to 26 July in 2011. Sampling was later in 2011 because a rainy spring delayed soybean herbicide applications in this region and thus our access to fields. During the first week of the 2010 experiment, soybean plants ranged from the two to five trifoliolate growth stage (V2–5) (Higley and Boethel, 1994), while during the first week of the 2011 experiment, soybean plants ranged from the four to six trifoliolate growth stage (V4–6).

2.2. Plot establishment

This study was replicated in $n = 8$ soybean fields in each year. Each field contained three treatment types manipulating patch-level immigration, crossed with two sampling types for a total of 6 plots per field and 48 plots per year. Predators and *A. glycines* were monitored in 1 m × 1 m plots in which the immigration of coccinellids to host patches was differentially manipulated by use of selective barriers. Selective cages and barriers can be used to manipulate the movement of key coccinellids through plots without altering levels of other predators or abiotic conditions (Costamagna et al., 2007; Gardiner and Landis, 2007; Gardiner et al., 2009). In a previous experiment, we observed that 1 m × 1 m plots surrounded by 4-sided 40 cm tall polyethylene plastic fences (i.e. fully open tops) reduced the number of adult coccinellids entering the plot. This occurred even though prey density was significantly higher on plants inside of plots (Landis and van der Werf, 1997). Upon encountering such vertical barriers, adult coccinellids frequently climb upward to the top edge, and typically initiate a short flight (D. Landis pers. obs.). While some subsequently land inside the enclosed plot, many do not, and thus even simple barriers can be used to manipulate the density of transient adult coccinellids. Plots were placed at least 10 m from the edge of each field and a minimum of 20 m from other plots. Coccinellids are strong fliers capable of dispersing long distances (Hodek et al., 1993). In our previous studies, we have found that

coccinellids in soybean fields are captured on sticky traps at similar rates at distances of 25, 50, and 100 m away from field edges. Therefore, the distance of our treatment plots from the field edge or from each other should not influence the potential numbers of coccinellids entering each plot. The same design was used in each field, and barrier treatments and sampling types were randomly assigned to each location. Plots were centered on a soybean row such that each contained 3 rows of soybean plants grown 38.1 cm apart. All fields received commercial levels of fertilizer and weed control but no insecticides were applied.

Three treatments were used to manipulate coccinellid immigration within the 1 m × 1 m plots (Fig. 1). The “open” treatment had no barriers to immigration of coccinellids, and plot corners were simply demarcated with stakes. In a second treatment, “2-sided” barriers were erected on opposite sides of the plot, leaving the top and two sides open. A 1 m³ PVC frame was erected around each plot and secured into the soil. The east and west facing sides of the 1 m³ frame were wrapped in coarse mesh netting (2 mm openings) that allowed smaller predators to pass through, but prevented coccinellids from entering (Costamagna et al., 2007). The mesh extended from the top of the frame sides to 2 cm above the ground, allowing ground-dwelling predators (Carabidae, Aranae, etc.) to freely enter and exit the plots (Fig. 1). The effect of wind on coccinellid flight is debated (Hodek and Honek, 1996). At our site the dominant wind direction is west to east, thus our barriers consistently blocked coccinellids traveling with or against the wind irrespective of row orientation. Finally, in a third treatment, “5-sided,” the 1 m³ PVC frame was covered on all four sides and the top with coarse mesh netting (2 mm openings) also raised 2 cm above the ground. Previous research has shown little or no effect of predator exclusion cages on microclimate within cages (Fox et al., 2004; Hopper et al., 1995; Schmidt et al., 2003), little or no effect of cages on soybean growth (Fox et al., 2004), biomass, or yield (Costamagna et al., 2008), and little or no effects on soybean aphid growth separate from changes in predator density (Costamagna et al., 2008; Fox et al., 2004).

Each field contained two sets of each treatment. One set used as “sampling plots” in which predators were sampled without replacement. The other set was used as “observation plots” in which aphid populations were monitored. This allowed us to eliminate any effects of predator removal on aphid abundance. At the initiation of the experiment, every soybean plant in each plot was visually inspected and all insects found were removed.

2.3. Predator monitoring

To determine the efficacy of our barrier treatments for manipulating immigration to plots, coccinellids and other aerially-dispersing predators (chrysopids (Neuroptera: Chrysopidae), hemerobeids (Neuroptera: Hemerobediae), lampyrids (Coleoptera: Lampyridae), cantharids (Coleoptera: Cantharidae), and dolichopodids (Diptera: Dolichopodidae)) were measured within sampling plots with 23 cm × 28 cm unbaited yellow sticky cards (PHERO-CON AM, Great Lakes IPM, Vestaburg, MI). All coccinellids on the cards were counted and identified to species in the field. The traps were placed in the center of each sampling plot suspended from step-in plastic fence posts at plant canopy height and were replaced weekly (Fig. 1A–C). We also measured activity-density of ground-dwelling predators to test our assumption that they would not be affected by the barrier treatments. Ground-dwelling predators including carabids (Coleoptera: Carabidae), staphylinids (Coleoptera: Staphylinidae), elaterids (Coleoptera: Elateridae), formicids (Hymenoptera: Formicidae), spiders (Aranae) and harvestmen (Opiliones), were collected in 11 cm diameter pitfall traps filled with 1:1 propylene glycol:water solution. Pitfall traps were collected and reset each week. Foliar-dispersing predators, those residing on the foliage and likely to disperse short distances from plant to plant, were assessed with weekly visual plant surveys. Each week the 5 plants surveyed for aphids within each plot were also inspected for syrphid larvae (Diptera: Syrphidae), coccinellid larvae, chrysopid eggs and larvae, and anthocorid (Hemiptera: Anthocoridae) adults and nymphs.

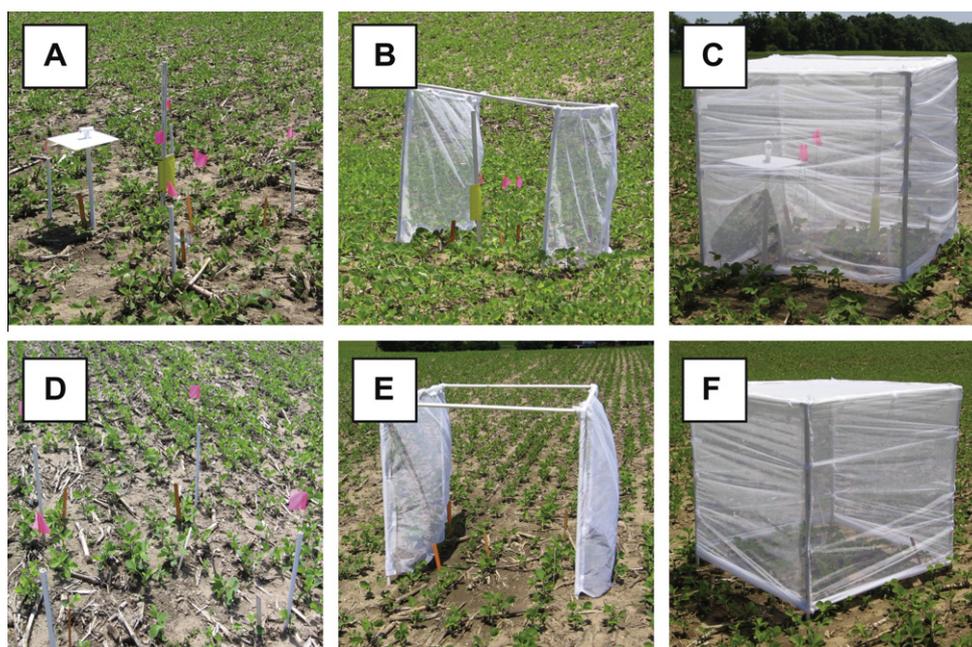


Fig. 1. Predator activity-density and aphid abundance were measured in 1 m² plots. Barriers to coccinellid immigration were constructed with 2 mm opening mesh netting and were raised 2 cm above the ground to allow full access by small and ground-dwelling predators. Open plots (A and D) had no barriers to immigration. 2-Sided plots (B and E) had barriers erected on the east and west sides of plot. 5-Sided plots (C and F) had barriers on all sides. Each field contained two sets of plots. In sampling plots (A–C), predators were sampled without replacement. In observation plots (D–F), aphid populations were monitored without disturbing predator populations.

2.4. Aphid monitoring

Naturally occurring aphid populations within each study field were monitored weekly using whole plant counts. During the first week of sampling, the centermost plant in all plots was infested with 10 greenhouse-reared (2010) or field-collected (2011) aphids of mixed age classes representing natural incipient colonies. Aphid abundances were counted weekly on the infested plant and on 4 additional randomly selected plants within each plot. Apterous and alate aphids were counted separately to account for the different modes in which aphid populations could be increasing in the plots. Briefly, aphid densities can increase through reproduction, triggering the production of large numbers of winged alate dispersal morphs. Alternatively, the appearance of alate aphids at low aphid densities suggests the arrival of new colonizers from other infested patches, fields, or hosts. Plot counts were stopped after 4 (2010) or 5 (2011) weeks due to a build-up of alates in the 5-sided treatment.

Aphid populations within fields were monitored weekly by randomly placing a 1 m² quadrat within the soybean field. Five quadrat samples were taken each week in each field. Five random plants within each quadrat were inspected for apterous and alate *A. glycines*, coccinellid adults and larvae, lacewing larvae, syrphid larvae, and anthocorid adults and nymphs. The vegetative growth stage of each surveyed plant was determined according to Higley and Boethel (1994) and recorded. Finally, the number of soybean plants within each quadrat was recorded.

2.5. Statistical analysis

For all of the insect taxa, neither data nor residuals were normal and variance was heterogenous and increased with the mean. Therefore, insect data were analyzed using generalized linear models, which estimate parameters with less bias than modeling transformed data (O'Hara and Kotze, 2010) and avoid complications of making inferences in the untransformed scale (Venables and Ripley, 2004). We analyze data for each taxon separately for each year. Soybean aphid dynamics are known to vary dramatically from year to year (e.g. Rhainds et al., 2010) and we did not wish to average over this important variation. We report results for all tests for which levels are different at $\alpha < 0.1$, using Tukey's adjustment for multiple comparisons.

2.5.1. Predator counts

The activity-density of coccinellids, lampyridae (2011 only), six taxa of ground-dwelling predators (formicids, carabids, staphylinids, elaterids, spiders, and harvestmen), and anthocorids (2011 only), were analyzed using separate generalized linear mixed models (PROC GLIMMIX; SAS 9.2). With the exception of anthocorids, individuals per trap for each taxon were modeled with a negative binomial distribution, a common distribution for over-dispersed count data. Data from each year were analyzed separately. The log-normal distribution was the best fit for the average number of anthocorids (combined adults and nymphs) per plant in each plot in 2011, the only foliar-dispersing predator abundant enough to analyze statistically. Other predator taxa were not captured frequently enough to allow for statistical comparisons between treatments. Captures rates for all taxa (untransformed mean \pm S.E.) are summarized in the results.

For each taxon we analyzed statistically, we treated treatment, week and their interaction as fixed effects and field as a random block. Laplace estimation was used to estimate means and Wald F - and t -tests were used for hypothesis testing (Bolker et al., 2009). Least square means comparisons were constructed on the linked scale. Because of difficulty in model convergence for coccinellid data, non-significant effects were dropped from the model

and least square means comparisons were run on models containing only significant effects.

2.5.2. Aphid abundance

Aphid counts from observation and sampling plots were modeled with a negative binomial distribution using a repeated measures generalized linear model (PROC GENMOD; SAS 9.2). Plot was the subject of the repeated measures across weeks. Repeated measures were used in the case of aphid abundance because we followed the same population of aphids within a plot over time. In contrast, predator data were drawn from random samples of the broader population and are not expected to be correlated from week to week. Data from each year were analyzed separately.

3. Results

3.1. Adult coccinellid captures

A total of 231 and 355 adult coccinellids were collected on sticky traps in 2010 and 2011. Four exotic and five native species of adult coccinellids were captured in both years (Table 1). Three exotic species accounted for 84% and 85% of all coccinellids collected in 2010 and 2011, respectively. *H. axyridis* accounted for 38% and 47%, *Propylea quatuordecimpunctata* accounted for 34% and 20%, and *C. septempunctata* accounted for 11% and 18%. No other coccinellid species accounted for more than 6% of total captures in either year. We successfully manipulated adult coccinellid immigration into plots in both years. In 2010, adult coccinellid immigration into plots differed by treatment ($F_{2,103} = 2.82$, $p = 0.06$; Fig. 2), but not by week ($F_{3,103} = 1.02$, $p = 0.39$), and the treatment by week interaction was not significant ($F_{6,103} = 0.65$, $p = 0.69$). Trap catches averaged 3.1 ± 0.41 coccinellids per week in the open treatment, 2.1 ± 0.40 coccinellids per week in the 2-sided treatment, and 0.42 ± 0.24 in the 5-sided treatment. There were significantly more adult coccinellids in the open treatment than in 5-sided treatments ($t_{112} = 6.79$, $p < 0.0001$), and significantly more in 2-sided than in 5-sided ($t_{112} = 5.77$, $p < 0.0001$). There was a trend toward higher adult coccinellid captures in open than in 2-sided plots, but this difference was not significant at Tukey-adjusted levels. The three most common species followed these patterns of having captures that were highest in the open, intermediate in the 2-sided, and lowest in the 5-sided plots (Table 1).

In 2011 adult coccinellid immigration into plots differed by treatment ($F_{2,84} = 8.01$, $p = 0.0007$; Fig. 2), but not by week ($F_{3,84} = 1.30$, $p = 0.28$), and the treatment by week interaction was not significant ($F_{6,84} = 0.57$, $p = 0.75$). There were 6.03 ± 1.04 adult coccinellids in the open treatment, 2.38 ± 0.33 in the 2-sided treatment, and 0.26 ± 0.10 in the 5-sided treatment. There were significantly more adult coccinellids in the open treatment than in 2-sided ($t_{86} = 4.16$, $p < 0.0001$) or in 5-sided ($t_{86} = 7.43$, $p < 0.0001$), and significantly more in 2-sided than in 5-sided ($t_{86} = 5.50$, $p < 0.0001$).

3.2. Ground-dwelling predators

Average captures for each ground-dwelling taxon are shown in Table 2. Of the six taxa examined, only carabidae varied between treatments in 2010 ($F_{2,99} = 3.13$, $p = 0.05$). Carabids were captured more frequently in 5-sided than in 2-sided plots ($t_{99} = 2.48$, $p = 0.04$). Captures in open plots were intermediate to the 5- and 2-sided plots and not statistically different from either. Several taxa varied between weeks (Formicidae: $F_{3,99} = 14.13$, $p < 0.0001$; Carabidae: $F_{3,99} = 3.36$, $p = 0.02$; Staphylinidae: $F_{3,99} = 20.27$, $p < 0.0001$; Elateridae: $F_{3,99} = 10.01$, $p < 0.001$; Opiliones:

Table 1
Means ± standard errors for all adult coccinellid species captured on sticky traps in 2010 and 2011.

Coccinellidae	2010			2011		
	Open	2-Sided	5-Sided	Open	2-Sided	5-Sided
Exotic species						
<i>Harmonia axyridis</i>	1.275 ± 0.277	0.700 ± 0.249	0.184 ± 0.184	3.450 ± 0.757	0.675 ± 0.191	0.026 ± 0.026
<i>Coccinella septempunctata</i>	0.350 ± 0.122	0.275 ± 0.134	0	1.275 ± 0.293	0.325 ± 0.083	0.026 ± 0.026
<i>Propylea quatuordecimpunctata</i>	1.000 ± 0.238	0.725 ± 0.175	0.211 ± 0.086	0.800 ± 0.130	0.900 ± 0.171	0.077 ± 0.043
<i>Hippodamia variegata</i>	0.050 ± 0.035	0.050 ± 0.035	0	0.275 ± 0.107	0.075 ± 0.042	0.026 ± 0.026
Native species						
<i>Cycloneda munda</i>	0.125 ± 0.053	0.150 ± 0.067	0	0.225 ± 0.091	0.200 ± 0.073	0.051 ± 0.036
<i>Coleomegilla maculata</i>	0.200 ± 0.073	0.125 ± 0.053	0.026 ± 0.026	0.050 ± 0.035	0.100 ± 0.060	0.051 ± 0.051
<i>Brachiacantha ursina</i>	0.075 ± 0.042	0.025 ± 0.025	0	0.050 ± 0.035	0.050 ± 0.035	0
<i>Hippodamia parenthesis</i>	0.050 ± 0.035	0.050 ± 0.035	0	0.075 ± 0.042	0.025 ± 0.025	0
<i>Hippodamia convergens</i>	0	0	0	0.050 ± 0.034	0.025 ± 0.025	0

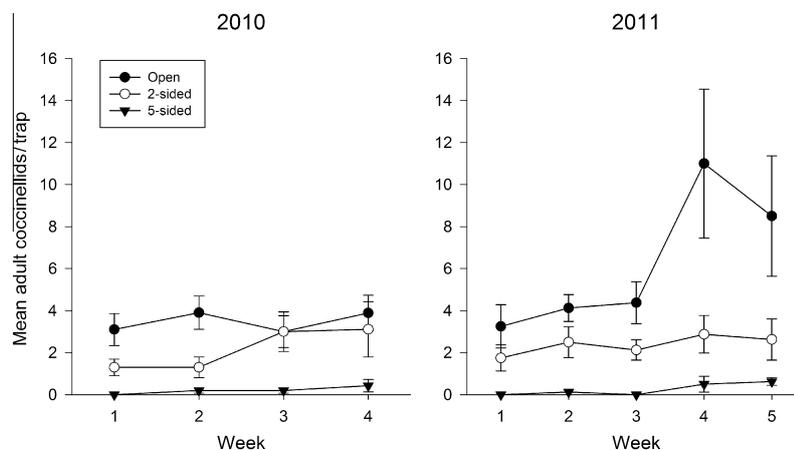


Fig. 2. Mean number of adult coccinellids captured in treatment plots in 2010 and 2011. In 2010, coccinellid immigration was higher in open and 2-sided than in 5-sided treatment plots. In 2011, coccinellid immigration rates were different in all treatments.

Table 2
Means ± standard errors for the most common ground-dwelling predator species captured in pitfall traps in 2010 and 2011.

Year/treatment	Carabidae	Elateridae	Staphylinidae	Formicidae	Spiders	Opiliones
2010						
Open	4.925 ± 1.035	1.450 ± 0.716	7.725 ± 1.799	9.250 ± 1.812	15.325 ± 2.403	9.700 ± 1.239
2-Sided	3.800 ± 1.016	1.200 ± 0.731	11.075 ± 3.094	7.000 ± 1.371	11.600 ± 2.079	10.575 ± 3.152
5-Sided	8.275 ± 1.894	0.525 ± 0.193	10.200 ± 2.421	6.950 ± 1.757	9.000 ± 1.512	10.575 ± 3.152
2011						
Open	4.350 ± 0.602	0.525 ± 0.179	3.400 ± 0.724	18.300 ± 1.687	17.050 ± 2.471	4.750 ± 1.247
2-Sided	5.500 ± 0.781	1.075 ± 0.466	3.675 ± 0.578	22.700 ± 4.389	18.775 ± 3.349	6.225 ± 1.037
5-Sided	8.650 ± 1.673	0.875 ± 0.355	6.750 ± 1.860	16.225 ± 2.927	20.700 ± 3.984	6.475 ± 1.159

$F_{3,99} = 2.53, p = 0.06$), generally increasing over time. No taxon showed a significant week by treatment interaction in 2010.

Only Carabidae and Opiliones varied between treatments in 2011 ($F_{2,98} = 3.92, p = 0.02$; $F_{2,98} = 6.60, p = 0.002$, respectively). Carabids were captured more frequently in 5-sided than open plots ($t_{98} = 2.76, p = 0.02$). Captures in 2-sided plots were intermediate to the 5-sided and open plots and not statistically different from either. Opiliones were captured more frequently in both 5- and 2-sided plots than in open plots ($t_{98} = 3.06, p = 0.008$; $t_{98} = 3.39, p = 0.003$, respectively), but did not differ between 5- and 2-sided plots. Spiders, opiliones, formicids and staphylinids varied between weeks ($F_{4,98} = 3.89, p = 0.006$; $F_{4,98} = 14.02, p < 0.0001$; $F_{4,98} = 10.96, p < 0.0001$; $F_{4,98} = 5.61, p = 0.0004$, respectively). Captures of all five of these taxa increased and decreased erratically between weeks, with no consistent patterns. Additionally, there

was a significant week X treatment interaction for formicids in 2011 ($F_{8,98} = 2.21, p = 0.03$), although no differences in treatments were consistent over time, and no individual comparisons were significant using adjusted p -values.

3.3. Foliar- and aerially-dispersing predators

Most foliar-dispersing predators were found in low abundances with no systematic differences between treatments (Table 3). Anthocorids in 2011 did not vary by week ($F_{3,122} = 2.16, p = 0.10$) or by treatments ($F_{2,122} = 2.11, p = 0.13$). However, there were significant interaction effects ($F_{6,122} = 2.67, p = 0.02$). There were more anthocorids per plant in 2-sided than in the open treatment in week 2 ($t_{122} = 2.17, p = 0.03$). In week 3, there were more anthocorids per plant in both open and 2-sided than in the 5-sided

Table 3Means \pm standard errors for foliar-dispersing predators observed on soybean plants in 2010 and 2011.

Year/treatment	Syrphid larvae	Coccinellid larvae	Anthocorid adults	Anthocorid nymphs	Chrysopid larvae
2010					
Open	0.031 \pm 0.010	0.006 \pm 0.004	0.006 \pm 0.004	0.028 \pm 0.011	0.006 \pm 0.00
2-Sided	0.088 \pm 0.043	0.003 \pm 0.003	0.006 \pm 0.004	0.009 \pm 0.005	0.016 \pm 0.00
5-Sided	0.250 \pm 0.105	0.003 \pm 0.003	0.016 \pm 0.007	0.019 \pm 0.011	0.013 \pm 0.00
2011					
Open	0.005 \pm 0.004	0.038 \pm 0.010	0.103 \pm 0.028	0.346 \pm 0.040	0.035 \pm 0.01
2-Sided	0.003 \pm 0.003	0.038 \pm 0.013	0.113 \pm 0.022	0.533 \pm 0.055	0.020 \pm 0.00
5-Sided	0	0.020 \pm 0.007	0.110 \pm 0.036	0.333 \pm 0.037	0.058 \pm 0.01

treatment ($t_{122} = 2.03$, $p = 0.04$; $t_{122} = 3.68$, $p = 0.0003$, respectively).

Lampyrids in 2011 varied by week ($F_{4,98} = 6.53$, $p = 0.0001$) and treatment ($F_{2,98} = 24.25$, $p < 0.0001$) but there was no interactive effect ($F_{8,98} = 1.43$, $p = 0.19$). There were more lampyrids captured in the open treatment than in either the 2- or 5-sided treatment ($t_{98} = 5.10$, $p < 0.0001$; $t_{98} = 5.54$, $p < 0.0001$, respectively). Other aerially-dispersing predators were collected in fairly low numbers relative to coccinellid captures, and in general, were highest in the open treatment and lowest in the 5-sided treatment (Table 4).

3.4. Aphid abundance

In 2010, natural aphid pressure in the study fields was very low, never reaching more than 1.72 aphids/plant in any field in any week. Within infested plots, aphid numbers varied between treatment ($\chi^2 = 109.02$, $p < 0.0001$), week ($\chi^2 = 98.23$, $p < 0.0001$), and their interaction ($\chi^2 = 142.47$, $p < 0.0001$). All plots had the same number of aphids when infested, with treatment differences developing over time (Fig. 3). In the first week there were no differences between aphid counts. In week 2 there were significantly more aphids in both 5- and 2-sided treatments than in the open treatment ($\chi^2 = 7.65$, $p = 0.006$; $\chi^2 = 4.22$, $p = 0.04$, respectively), but not between 5- and 2-sided. In week 3, all treatments had significantly different numbers of aphids. In week 4, there were significantly more aphids in the 5-sided treatment than in both the open and 2-sided treatments, but no difference between open and 2-sided treatments. By the fourth week, there were 105 ± 38 aphids/plant in the 5-sided treatment, but only 7 ± 3 aphids/plant in 2-sided treatments and 3 ± 1 aphids/plant in the open treatment.

In 2011, aphids within the treatment plots increased over each week ($\chi^2 = 1319.91$, $p < 0.0001$), but there were no differences by treatment ($\chi^2 = 2.31$, $p = 0.31$) and no interactive effects ($\chi^2 = 6.50$, $p = 0.37$). However, in 2011 arrival of alate aphids in fields was higher than in 2010 (Fig. 3). In 2010, no naturally colonizing alate aphids were observed in any soybean fields, although there was some build-up of alatae in 2- and 5-sided treatments during weeks 3 and 4 (Table 5). In 2011, however, naturally-colonizing alatae were observed in every week, and were found in all treatments from week 2 onward (Table 5).

nizing alatae were observed in every week, and were found in all treatments from week 2 onward (Table 5).

4. Discussion

We set out to determine if the patch-level immigration of adult coccinellids influenced aphid suppression in soybean fields. Our treatments were effective at creating a range of coccinellid immigration to local host patches. In both years there were significantly fewer coccinellids captured in 5-sided than open treatments, with captures in 2-sided treatments intermediate to these. Lampyrids were also captured at higher rates in open than 2- or 5-sided plots. However, lampyrids are expected to make limited contributions to soybean aphid suppression because their capture rates in soybean fields tend to be lower than coccinellids, they are considered to be somewhat specialized predators of earthworms and snails (Debach and Rosen, 1991), and they have never been confirmed to feed on soybean aphid despite numerous surveys of predators in North American soybean fields (Ragsdale et al., 2011). In contrast to coccinellids and lampyrids, activity-density of other predatory taxa was not consistently influenced by treatment (e.g. anthocorids), was highest in the 5-sided treatment (e.g. opiliones and carabids), or was low in comparison to coccinellid activity-density.

Changing the patch-level immigration rate of coccinellids altered *A. glycines* dynamics, as populations showed trends toward higher numbers in the plots with the lowest coccinellid captures in both years. Aphid populations were highest in the 5-sided treatment in spite of increased activity-density of some ground-dwelling predators in these plots. Increased opiliones and carabid activity-densities in 5-sided plots may be a result of aggregation to higher prey resources as the bottoms of treatment barriers were open and allowed free access to these predators.

There are several possible explanations for the different aphid dynamics in 2010 and 2011 despite similar coccinellid immigration rates into the different treatment plots for the first three weeks of each year of the study. In both years, aphid populations in the open and 2-sided plots remained similar to ambient levels in the surrounding soybean fields. A steady influx of alate aphids from the surrounding field or landscape into the plots in 2011

Table 4Means \pm standard errors for aerially-dispersing predator species captured on sticky traps in 2010 and 2011.

Year/treatment	Coccinellidae	Chrysopidae	Hemeroptera	Lampyridae	Cantharidae	Dolichopodidae
2010						
Open	3.125 \pm 0.405	0.200 \pm 0.089	0.100 \pm 0.100	1.150 \pm 0.575	0.075 \pm 0.042	0.125 \pm 0.064
2-Sided	2.100 \pm 0.398	0.300 \pm 0.103	0.075 \pm 0.042	0.300 \pm 0.114	0.050 \pm 0.035	0
5-Sided	0.421 \pm 0.243	0.079 \pm 0.044	0	0.132 \pm 0.086	0	0
2011						
Open	6.025 \pm 1.041	0.075 \pm 0.042	0.075 \pm 0.042	3.800 \pm 0.712	0.075 \pm 0.055	1.000 \pm 0.275
2-Sided	2.375 \pm 0.330	0.075 \pm 0.042	0.025 \pm 0.025	1.200 \pm 0.249	0	0.375 \pm 0.106
5-Sided	0.256 \pm 0.095	0.026 \pm 0.026	0.026 \pm 0.026	1.051 \pm 0.345	0	0.128 \pm 0.066

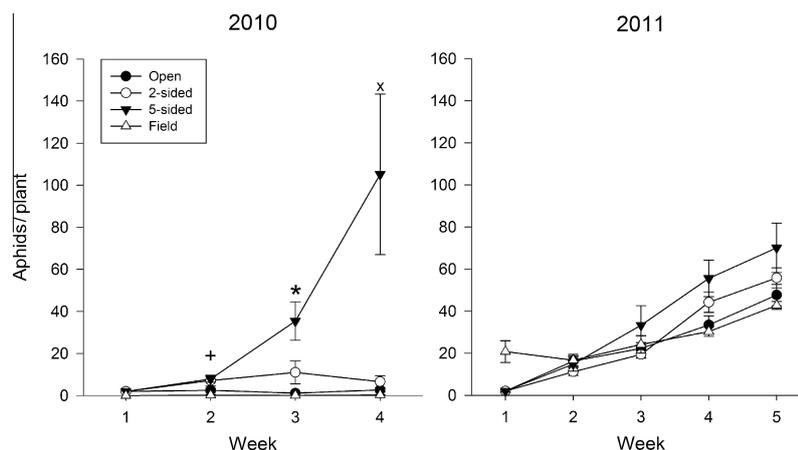


Fig. 3. Mean number of *A. glycines* observed per plant each week in soybean fields outside of plots and in open, 2- and 5-sided treatment plots in 2010 and 2011. Symbols indicate significantly more aphids in (+) 5-sided and 2-sided than in open plots, (*) between all treatments and (x) in 5-sided than in open or 2-sided plots.

Table 5
Average number of alate aphids observed per plant in each week in each plot in 2010 and 2011.

Week ^a	2010				2011			
	Field	Open	2-Sided	5-Sided	Field	Open	2-Sided	5-Sided
1	0	0	0	0	0.385 ± 0.112	0	0	0
2	0	0	0	0	0.060 ± 0.022	0.100 ± 0.042	0.088 ± 0.044	0.088 ± 0.044
3	0	0	0	0.025 ± 0.025	0.040 ± 0.016	0.063 ± 0.027	0.025 ± 0.018	0.013 ± 0.013
4	0	0	0.050 ± 0.039	4.675 ± 4.178	0.060 ± 0.018	0.013 ± 0.013	0.025 ± 0.018	0
5	0	0	–	–	0.141 ± 0.036	0.225 ± 0.073	0.063 ± 0.027	0.200 ± 0.156
6	0	–	–	–	0.135 ± 0.025	–	–	–
7	0	–	–	–	0.085 ± 0.026	–	–	–
8	–	–	–	–	0.217 ± 0.044	–	–	–

^a Week 1 started on 16 June in 2010 and on 5 July in 2011.

could be responsible for weekly population increases within the plots. Few alates were found in 2010, and only in plots with high densities of aphids, suggesting that these alates were produced within those plots, as aphids typically produce dispersal morphs in response to crowding (Dixon, 1985). In contrast, in 2011 alates were found in our treatment plots and in the surrounding field in every week after our initial infestation, even in plots with low densities of aphids, suggesting that these alates represented additional migrants to the plots. The reproduction of the alates within our plots would have boosted populations beyond what would be expected from reproduction from our original 10 aphids alone. Additionally, while the abundance of foliar-dispersing predators was low and variable in both years, abundances were generally higher in 2011. The increase of these predators across all treatments in 2011 may have contributed to the lack of significant differences in aphid populations in this year, while helping to hold populations in all treatments below economic threshold. However, due to their low consumption rates (Costamagna and Landis, 2007), it is unlikely that these foliar-dispersing predators such as *O. insidiosus* and coccinellid and chrysopid larvae were primarily responsible for *A. glycines* suppression in either year. Finally, the higher captures of opiliones and carabids in 5- and 2-sided plots in 2011 may have offset reductions in coccinellid immigration into these two treatment plots and be at least partially responsible for the lack of significant differences in aphid abundance between the treatments in this year. One species of opiliones has been observed feeding on soybean aphid in North America (Allard and Yeorgan, 2005) and nine species of carabids captured in soybean fields fed on soybean aphid in laboratory no-choice trials (Hajek et al., 2007; Hannam et al., 2008; Rutledge et al., 2004).

Coccinellid captures on sticky traps were within the range typically seen in Michigan soybean fields (e.g. Woltz et al., 2012). With low ambient aphid populations in the field in 2010, a coccinellid immigration rate of approximately 2–3 individuals captured in a plot per week was sufficient to prevent *A. glycines* population increase in both open and 2-sided treatments. This seemingly low activity-density of coccinellids implies that high numbers of coccinellids are not necessary to suppress soybean aphid populations if individuals are regularly moving through and predating in aphid-infested patches. In a study of the spatial dynamics of soybean aphid infestations in soybean fields, Costamagna and Landis (2011) found that areas of high *A. glycines* density in one week typically became areas of low density in subsequent weeks, suggesting that predators regularly located patches with increasing aphid density and drove populations back to average field levels. In contrast, in a year like 2011 with higher external aphid pressure from alates regularly colonizing soybean fields, coccinellid immigration alone may not be sufficient to counter the influx of new aphids and aphid densities may rise. Under such conditions, the densities of foliar-dispersing predators such as anthocorids and coccinellid and chrysopid larvae are likely to increase, increasing their contribution to aphid suppression. The changing roles of various predators under different levels of ambient aphid pressure are an interesting question that warrants further study.

Previous studies have shown that adult coccinellids aggregate in patches of high prey density (Hodek and Honek, 1996), a behavior resulting from decreased emigration from host patches (Krivan, 2008). However, for patches with low aphid densities, we have shown that the immigration of coccinellid beetles to aphid infested patches is important for *A. glycines* suppression. Similar results have been found in other systems. For example, experimentally

decreasing carabid and lycosid immigration into squash plots resulted in higher pest densities and lower squash yield (Snyder and Wise, 1999). Furthermore, although coccinellid emigration from a patch is related to characteristics such as prey density, the presence of potential predators or competitors, immigration into a patch is random with respect to the quality of that patch (Krivan, 2008). Rather, rates of immigration into a particular patch are determined by coccinellid decisions to leave nearby patches (Grez and Prado, 2000) as well as their overall densities in the landscape. Because coccinellid immigration rates to patches within soybean fields should be higher when their overall density in the landscape is higher, management actions to increase coccinellid immigration to aphid colonies must take place outside of the crop. Increasing evidence suggests that landscape composition at scales of multiple kilometers influences the activity-density of coccinellids in crop fields, likely because the presence and abundance of particular habitats determines the provision of resources necessary for coccinellid survival and reproduction (Gardiner et al., 2009; Woltz et al., 2012).

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