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The Impact of Prairie Strips on Aphidophagous Predator Abundance and Soybean Aphid Predation in Agricultural Catchments

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Abstract

Reconstructing prairie vegetation in row crop-dominated agricultural landscapes may contribute to several ecosystem services, including the biological control of insect pests, such as the soybean aphid *Aphis glycines* Matsumura. The influence of the amount and configuration of reconstructed prairie vegetation on the delivery of ecosystem services was investigated in several small catchments at Neal Smith National Wildlife Refuge in Iowa. Treatments include catchments entirely in row crops under a no-till, corn—soybean (*Zea mays*L.—*Glycine max* [L.] Merrill) rotation, catchments with 10% of the land in prairie located at the base, and catchments with 10 or 20% of the land in multiple contour strips of prairie. During 2009 and 2011 growing seasons, we measured abundance and diversity of aphidophagous insect predators in response to treatment and habitat type (i.e., soybean, prairie). In 2011, we further studied the biological control of soybean aphids by artificially infesting uncaged and caged plants to prevent exposure from predators. While aphidophagous predators were more abundant in prairie, populations of key aphid predators did not significantly differ among treatments. Biological control of the soybean aphid did not differ among treatments or with distance from prairie. Our results suggest that prairie strips, in addition to providing soil and water quality benefits, may increase the populations of beneficial insects, but may not directly impact biocontrol. We propose several hypotheses to explain why we did not observe more soybean aphid predation with the increased abundance of aphidophagous predators in catchments containing prairie.

Keywords

Agricultural and Biosystems Engineering, Natural Resource Ecology and Management, biological control, ecosystem service, habitat manipulation, natural enemy, STRIPS

Disciplines

Agriculture | Bioresource and Agricultural Engineering | Entomology

Comments

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The Impact of Prairie Strips on Aphidophagous Predator Abundance and Soybean Aphid Predation in Agricultural Catchments

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ABSTRACT Reconstructing prairie vegetation in row crop-dominated agricultural landscapes may contribute to several ecosystem services, including the biological control of insect pests, such as the soybean aphid *Aphis glycines* Matsumura. The influence of the amount and configuration of reconstructed prairie vegetation on the delivery of ecosystem services was investigated in several small catchments at Neal Smith National Wildlife Refuge in Iowa. Treatments include catchments entirely in row crops under a no-till, corn–soybean (*Zea mays* L.–*Glycine max* [L.] Merrill) rotation, catchments with 10% of the land in prairie located at the base, and catchments with 10 or 20% of the land in multiple contour strips of prairie. During 2009 and 2011 growing seasons, we measured abundance and diversity of aphidophagous insect predators in response to treatment and habitat type (i.e., soybean, prairie). In 2011, we further studied the biological control of soybean aphids by artificially infesting uncaged and caged plants to prevent exposure from predators. While aphidophagous predators were more abundant in prairie, populations of key aphid predators did not significantly differ among treatments. Biological control of the soybean aphid did not differ among treatments or with distance from prairie. Our results suggest that prairie strips, in addition to providing soil and water quality benefits, may increase the populations of beneficial insects, but may not directly impact biocontrol. We propose several hypotheses to explain why we did not observe more soybean aphid predation with the increased abundance of aphidophagous predators in catchments containing prairie.

KEY WORDS biological control, ecosystem service, habitat manipulation, natural enemy, STRIPS

As demands for food, feed, fiber, and fuel increase with a growing and more affluent population, the need for agricultural landscapes to provide multiple benefits to sustainability goals has become a prominent global discussion (Tilman et al. 2002, von Braun 2007, Godfray et al. 2010). While the primary objective of agricultural landscapes is crop and livestock production, these lands could also be managed to provide additional benefits, such as biological control, improved air, soil, and water quality, biodiversity, and rural vitality, among others (Organisation for Economic Cooperation and Development [OECD] 2001), in other words, provide both agricultural goods and ecosystem services—the services that humans derive from nature. As shown by Boody et al. (2005), agricultural landscapes can be designed to achieve such multifunctional goals. The strategic integration of perennial plant communities in and around annual crop production systems is particularly effective in achieving

multifunctional goals (Asbjornsen et al. 2013). While this principle generally holds true, the composition, amount, and configuration of perennial vegetation substantially affect the type and quantities of ecosystem services derived, particularly to crop production (Schulte et al. 2006). Here, we address the specific case of designing agricultural landscapes in the U.S. Corn Belt for the combined goals of crop production, habitat for aphidophagous predator populations, and biocontrol of an agricultural pest, the soybean aphid (*Aphis glycines* Matsumura).

The soybean aphid is a significant pest of soybeans (*Glycine max* [L.] Merrill) in North America (Ragsdale et al. 2011). Although the aphid and its host plants, soybean and common buckthorn (*Rhamnus cathartica* L.), are native to Asia, the soybean aphid was found in North America in 2000. Current management of the soybean aphid in its expanded range involves scouting and applying foliar insecticides when populations reach an economic threshold (Ragsdale et al. 2007). Fifty-seven taxa of predators and parasitoids have been documented attacking soybean aphids in the United States, suggesting the opportunity to manage this pest through biological control. In the Midwestern United States, 18 life stages of different insects, primarily predators, have been identified as potential natural enemies (Rutledge et al. 2004, Schmidt et al.

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2008). Coccinellids, syrphids, and the predatory hemipteran, *Orius insidiosus*, are the most abundant predators found in soybean fields (Schmidt et al. 2008, 2011). Although soybean aphid parasitoids are present in North America, they are only a minor component of the natural enemy community (Ragsdale et al. 2011).

Increasing habitat structural complexity is generally expected to correspond with increases in natural enemy abundance (Landis et al. 2000). Through a meta-analysis of insect community data, Langelotto and Denno (2004) found increasing in-field habitat structural complexity, in the form of no-tillage, intercropping, and polyculture, generally correspond with increases in natural enemy abundance. Nearby noncrop vegetation, including remnant native vegetation and planted flowering refuges, may harbor an abundant and diverse community of arthropod natural enemies by providing alternative sources of food and shelter. In the United Kingdom, flowering field boundaries, which increase structural complexity by adding new functional groups of plants to a crop-dominated landscape, have been shown to increase predator abundance in crop fields and decrease aphid populations relative to controls (Hickman and Written 1996, Collins et al. 2002).

Not only has the conversion of native vegetation to cropland in the U.S. Corn Belt reduced landscape complexity, leaving diverse areas highly fragmented, but crop rotation and intercropping are less commonly practiced (Samson and Knopf 1994, Brown and Schulte 2011, Wright and Wimberly 2013). Such agricultural homogenization negatively affects natural enemy populations and reduces the biological control of insect pests (Kruess and Tscharntke 1994). For example, Gardiner et al. (2009a,b) observed the amount of noncrop vegetation influences the composition of the natural enemy community within Midwest soybean fields and the biological control of soybean aphids. Specifically, greater amounts of forested habitat surrounding soybean fields correlated with greater abundance of exotic coccinellids (i.e., *Harmonia axyridis* (Pallas) and *Coccinella septempunctata*) within soybean fields (Gardiner et al. 2009a). Native lady beetles (e.g., *Cycloneda munda*, *Hippodamia convergens*) responded negatively to forested landscape, and positively to grasslands. Soybean fields within landscapes with greater complexity, and more perennial habitat experienced greater biological control of the soybean aphid (Gardiner et al. 2009b).

Efforts to improve soybean aphid biological control by reintroducing habitat for natural enemies has had mixed results. The production of soybean with a cover crop (Koch et al. 2012, Lundgren et al. 2013) or living mulch (Schmidt et al. 2007) has improved the biological control of soybean aphids, but the abundance of aphidophagous predators was not consistently increased by these within-field efforts. Their impact on the soybean aphid may not be fully realized, in part because the habitat provided was not optimized for the needs of the natural enemies of soybean aphids.

Perennial plants may provide habitat for increasing natural enemies of the soybean aphid. Furthermore, using native plants as a resource for conserving beneficial insects may be facilitated by their adaptation to environmental conditions of the target area; they are also less likely to become invasive (Frank et al. 2008). Fiedler and Landis (2007) noted that select native plants commonly found in prairies provide flowering resources that are attractive to beneficial insects, including insect predators. The flowering period of the species evaluated by Fiedler and Landis (2007) varied through the season, which when planted in a mixture can provide a season long, attractive habitat for natural enemies (Gill et al. 2014). This flowering period overlaps with the colonization period of the soybean aphid in Iowa (Ragsdale et al. 2011). The reconstructed native prairie vegetation evaluated in our study was designed to achieve a mix of locally adapted ecotypes for prairie species conservation and water and soil conservation compatible with a corn-soybean rotation. We investigated if this prairie provided a season-long floral resource for aphidophagous insects as predicted from the results of Fiedler and Landis (2007).

We evaluated whether a perennial plant community strategically integrated within crop fields to achieve soil and water conservation benefits also increased predatory arthropods and an ecosystem service they provide to adjacent cropland. We tested a series of hypotheses to address the effects of prairie strips on the community of predaceous arthropods that feed on soybean aphids and soybean aphid predation rates within the adjacent soybean cropland. We hypothesized that the abundance of soybean aphid predators would differ between crop and prairie areas. Specifically, we predicted that soybean aphid predators would be more abundant in prairie strips than adjacent crops. We also expected that the higher abundance of aphidophagous insects in prairie strips would translate into more abundant soybean aphid predators in cropped portions of agricultural catchments with greater amounts of prairie. Therefore, we tested a second hypothesis that abundance would differ in soybean of agricultural catchments with different amounts and configurations of prairie. We not only compared abundance of predators in cropped portions, but also their abundance in the entire catchment, and therefore tested a third hypothesis that the abundance of soybean aphid predators would differ among catchment treatments. We expected that predators would be more abundant in catchments with the greatest amounts of prairie.

We also tested several hypotheses that focused on the impact these predators may have on the biological control of the soybean aphid. We tested a fourth hypothesis that aphid predation rates would differ among catchment treatments, with increased predation rates corresponding with increases in the amount of prairie within catchments. We assume that the perennial plants within the prairie will serve as a source of predators that will colonize the adjacent annual cropland. We predicted that when prairie is interspersed in strips as opposed to those placed only

at the base, a greater abundance of predators will occur throughout the cropped portions of the catchments. Our last hypotheses focused on the distance from the edge of the prairie in a single catchment. This fifth hypothesis tested if predation rates differ with distance from the edge of the prairie. We predicted that predation rates will increase with proximity to prairie.

Finally, our sixth hypothesis tested if the concentration of nitrogen within plants differs by location in the catchment. In general, aphids are phloem-feeding insects whose growth is limited by nitrogen (Dixon 1998). Variation in soybean aphid population growth has been attributed to differences in plant nutrients (Myers and Gratton 2006, Schmidt et al. 2007). Strips of prairie embedded in the catchments used in this study affected the movement of nitrogen through the cropland (Liebman et al. 2012), which may in turn alter the quality of soybean as a host for aphids. Therefore, we explored if plant nutrient content varied by location within a catchment, with plants closer to the prairie buffer strip having a greater concentration of nitrogen, contributing to variation in aphid abundance in addition to predation.

Materials and Methods

Experimental Design. This study is part of the Strategic Trials of Row crops Integrated with Prairie Strips (STRIPS) project, established in 2007 by a team of scientists in conjunction with the Neal Smith National Wildlife Refuge (NSNWR) near Prairie City, IA. The STRIPS project studies ecological and social phenomena associated with the experimental integration of prairie vegetation in agricultural landscapes. Our overarching hypothesis is that the strategic placement of prairie in agricultural landscapes will produce disproportionate improvements in ecosystem functioning without compromising the social and economic viability of agroecosystems (Schulte 2011).

While other components of the STRIPS project address water quality and flow, soil erosion, carbon and nitrogen cycling, plant, bird, and arthropod pollinator diversity, we tested the hypothesis that the amount and configuration of prairie will affect the diversity of aphidophagous insect predators and biocontrol of the soybean aphid. The experimental units consisted of catchments ranging between 0.5 and 3.2 ha in size and 6.1–10.5% in slope. Width of prairie strips ranged from 3.1 to 78.2 m, depending on the size of the catchment and its placement at upslope or foot slope. The catchments were managed for production of corn and soybeans in a rotation that began with soybean in 2009. No data related to this study were collected in 2010, as the experiment was planted to corn. Crops were produced using conventional practices consistent with the region, including no-till and synthetic fertilizers. Pesticides were limited to the herbicide glyphosate; insecticides were not used during either the corn or soybean phase of the rotation. Each catchment received one of four treatments: 1) all row crops, 2) 90% row crops and 10% of the catchment

in prairie located at the base, 3) 90% row crops and 10% of the catchment in prairie distributed in multiple contour strips, and 4) 80% row crops and 20% of the catchment in prairie distributed in multiple contour strips (Fig. 1 and Table 1). These treatments were assigned to catchments within a randomized incomplete block design: two blocks contained three catchments and one block contained six catchments.

In 2007, prairie vegetation was established in catchments according to the experimental design. A seed mixture of 32 species selected from other established prairies at the NSNWR was planted in July; the prairie vegetation was mowed in June and August in 2008, June 2009, and October 2010 to control weeds. According to Hirsh et al. (2013), the reconstructed prairie contained 103 species in 2009 and 118 species in 2011, including natives and exotics, annuals, perennials, and biennial, composed of both dicot and monocot plants. In 2011, of these plants, 22 contributed >1% of the relative ground cover on average, totaling 85% of the relative ground cover; 96 other species made up the other 15% relative ground cover. Of the 22 dominant species, seven—comprising 26.8% of the relative ground cover—have been cited for enhancing natural enemy abundance. Of the 96 other species, five—comprising 0.9% of the relative ground cover—were recognized by Fiedler and Landis (2007) as attractive to natural enemies of insect pests (Appendix 1).

Aphidophagous Arthropod Community. The soybean aphid predator community was sampled with a sweep net to test our first three hypotheses. Each sample consisted of 20 sweeps while walking forward with a 30.5-cm-diameter canvas sweep net. Each sweep net sample was placed into individual top-closure polyethylene bags, labeled according to its respective date, site, sample number, and stored at -20°C for future identification. In 2009, sampling was conducted monthly from May to September. At each sampling date, three randomly located samples were taken in each prairie strip and at three random locations within the fifth row of the soybeans from the base of each catchment. In 2011, following the same methods as 2009, sweep net sampling was conducted using three replications of 20 sweeps within the crop and prairie portion of each catchment except for June when only 10 sweeps per vegetation type were made. In 2011, the insect community was sampled on a monthly basis from June through September, and a weekly basis in July, using a sweep net in the prairie and crop field. Sampling was intensified in July to monitor for changes that may have occurred when the soybean aphid predation studies were conducted. In catchments with multiple prairie or crop strips, one prairie buffer strip was randomly selected and the crop strip above the selected prairie strip was sampled at each sample date. In the statistical analyses completed for sweep net data, data from all months were summed for a season-long total, so that the month-to-month variation in our sampling procedure did not affect the final analysis. The taxonomic categories for insects collected in 2009 and 2011 vary, as methods were slightly different. Specifically, spiders were not iden-

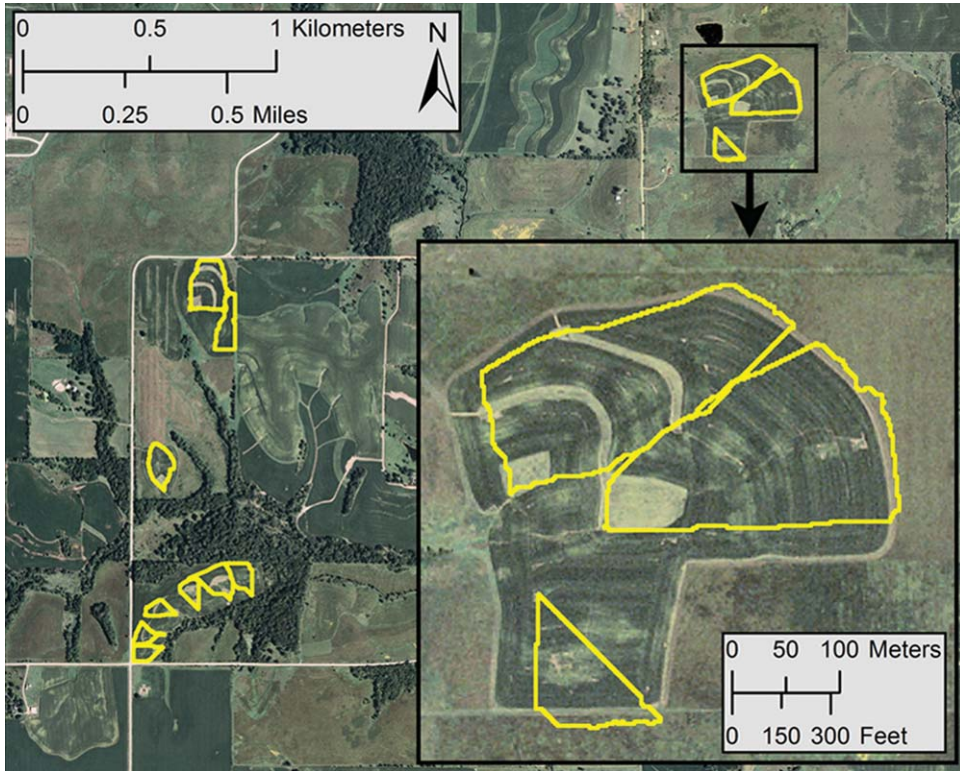


Fig. 1. Three blocks of experimental catchments composing a study area within NSNWR, a diverse landscape of reconstructed prairie, cropland, and forest. Catchments (i.e., experimental units) are highlighted in yellow. Strips of prairie in catchments differ in the quantity and arrangement, making up the different treatments applied to catchments; treatments described in detail in Table 1. Inset: Block 2, showing three of four experimental treatments from north to south; ten, foot, crop.

tified to family or species in 2009, and they were identified when possible in 2011.

Soybean Aphid Predation. In 2011, we tested hypotheses related to soybean aphid predation. To test these hypotheses, we used methods developed by Gardiner et al. (2009b), in which the population growth of aphids is compared between caged and uncaged soybean artificially infested with aphids. We used a cage designed by Schmidt et al. (2007). Similarly designed cages have been used to account for the impact of predators on soybean aphid populations

(Fox et al. 2005, Costamagna and Landis 2006, McCaville et al. 2011). These authors demonstrated that the cage design did not significantly affect temperature and thus aphid development, such that differences in aphid population between caged and uncaged plants are due to natural enemies. Pairs of soybean plants were randomly selected throughout each experimental unit and one plant of each pair was covered with a cage. Tomato cages were placed around a single plant and covered with white no-see-um netting whereas uncaged treatments had no cage and no net-

Table 1. Characteristics of experimental catchments associated with the STRIPS Project at NSNWR

Treatment	Size (ha)	Slope (%)	Treatment	Abbreviation
Block 1-1	0.53	7.5	10% prairie at foot slope	Foot
Block 1-2	0.48	6.6	10% prairie on contour in two strips	Ten
Block 1-3	0.47	6.4	20% prairie on contour in two strips	Twenty
Block 1-4	0.55	8.2	20% prairie on contour in two strips	Twenty
Block 1-5	1.24	8.9	10% prairie on contour in two strips	Ten
Block 1-6	0.84	10.5	100% soybeans	Crop
Block 2-1	3.00	7.7	10% prairie on contour in three strips	Ten
Block 2-2	3.19	6.1	10% prairie at foot slope	Foot
Block 2-3	0.73	9.3	100% soybeans	Crop
Block 3-1	1.18	10.3	10% prairie at foot slope	Foot
Block 3-2	2.40	6.7	20% prairie on contour in three strips	Twenty
Block 3-3	1.24	6.6	100% soybeans	Crop

ting. At the soil line, a trench was dug around the cage and the netting was placed in the trench and buried, ensuring full closure by the cage.

Because the study site had not experienced an infestation of soybean aphid by July 2011, we artificially infested the caged and uncaged plants under study with adult soybean aphid from a colony collected in a field in Ames, IA. On 8 July 2011, 10 aphids were introduced to each plant using a probe. Soybean aphids (apterous and alates of all life stages) were counted once a week following infestation, with the last sampling date on 27 July 2011. On the first and second week following infestation, some of the soybean aphid populations were naturally reduced to zero. When this occurred, the soybean plants in the study were reinfested with 10 aphids at the next sampling date so we could continue the study. The plants paired with the reinfested plants were reduced from their current population back to 10 to restart the experiment. Soybean aphid populations were counted for 3 wk following infestation and reinfestation to monitor population changes; both winged and wingless aphids were combined for analysis. One data point of counted winged aphids was lost; thus, we are underestimating winged aphids on one instance.

Two pairs of caged and uncaged soybean plants were randomly selected in each catchment, totaling 24 pairs (48 total plants) of soybean plants. The location of each caged plant was determined by first randomly selecting a quadrant of each catchment using the random number function in Microsoft Excel, then a number of paces was selected using the random number function to determine how many paces into the quadrant horizontally and then up or down into the quadrant vertically to place each caged plant. Uncaged plants were placed in the same row as the caged plant, approximately one meter away. Soybean plants around the caged and uncaged plants were removed if they made contact with the selected plant.

Of the 12 experimental catchments included in the overall study, one was selected to test our hypothesis that soybean aphid predation varied with proximity to prairie. For this experiment, we selected a catchment that was the most isolated from the other catchments (>500 m) to avoid influence by prairie vegetation from adjacent catchments. The catchment selected for the study had prairie located only at the base of the field (i.e., the foot treatment). Unlike the previously described experiments in which the catchment was considered the experimental unit, each pair of caged and uncaged soybean plants was considered an experimental unit for this study; the proximity of each pair to prairie was considered the treatment. Two sets of five pairs of caged and uncaged plants were established within the catchment; five pairs within the soybean row immediately adjacent to the prairie and five pairs at a row \approx 50 m from the edge of the prairie. Transects were established approximately perpendicular to the contour of the land. At each transect, position pairs of caged and uncaged plants were \approx 0.5 m apart. Pairs along the row of soybeans adjacent to the prairie were \approx 2 m apart, and pairs in the row

50 m into the field were \approx 20 m apart, with differences in distances due to the funnel shape of the catchment. At each pair of soybean plants, soybean aphid infestation and monitoring followed the methods outlined above.

Plant Nitrogen. We tested the hypothesis that the concentration of nitrogen in soybean plants varied by location within a catchment by sampling leaves from soybean plants along the soybean row closest to the prairie and also 50 m into the field. These plant samples were taken from the same catchment used in the previous section (i.e., Soybean aphid predation). Plant samples were dried, ground, and analyzed for total nitrogen, carbon, phosphorous, and potassium in each plant. The plants infested with aphids were not selected, as the goal was to survey the plant population in that area of the catchment, not the exact plants involved, which may have already been affected by aphids. We removed leaves once soybeans reached plant maturity.

Statistical Analysis. Arthropod abundance was analyzed on a per treatment basis as the season-long sum of all sweep net subsamples. Each sample consisted of an average of the three sweep net subsamples. For each sample, aphidophagous insects and arachnids were identified to family and to the lower taxonomic units when possible for members of the Coccinellid and Anthocorid families. Aphid populations are reported as an average of total aphids per plant. In the aphid population data, the sample was the average of the two subsamples, which were the two caged or noncaged plant data for each experimental unit. All statistical analyses described below were conducted in R (R Development Core Team 2010).

We used a paired two-tailed *t*-test to determine if the abundance of predators differed between prairies and soybeans. Our experimental design was composed of two nominal variables (prairie and crop) with one measurement variable (abundance of natural enemies), which makes a paired *t*-test ideal to test differences for each paired set of data calculated from individual catchments. For each catchment that contained prairie, the abundance of predators in prairies was subtracted from the abundance of predators in soybeans. Data from the crop only treatments were not used to test this hypothesis. This difference was calculated for each sampling date and then summed to calculate a season-long difference combining all four sampling dates in 2009 and seven sampling dates in 2011; differences were then compared with zero. Separate paired *t*-tests were conducted for each year for the following response variables: total predator abundance, the most abundant species in each year (*O. insidiosus*), exotic lady beetles, and native lady beetles.

To test our second hypothesis, we used analysis of variance (ANOVA) to determine if the placement and configuration of prairie in catchments affected the season-long total abundance of aphidophagous predators in the portion of the catchment planted with soybean. ANOVAs were conducted separately for

2009 and 2011 for *O. insidiosus*, exotic lady beetles, and native lady beetles.

Because measures of total abundance may be insensitive to changes in taxon abundance, we also used a community composition analysis to test hypotheses regarding whether vegetation type or treatment significantly affected the composition of the arthropod predator community. We attempted to use nonmetric multidimensional scaling (NMDS) ordination methods to visualize the arthropod predator community of each vegetation type, but nine dimensions were required to explain the majority of variance in our data. Instead, we used an Adonis analysis, which is similar to an ANOVA but applied to community composition data. Adonis is a permutational multivariate ANOVA for species composition data (Stevens and Oksanen 2011) conducted in the vegan package of R (Oksanen et al. 2011). Additionally, we conducted a SIMPER analysis (Clarke 1993) within the vegan package of R. Much like NMDS, SIMPER is an analysis based on distance measures, which determines which species contribute most to the dissimilarity matrix that is calculated from arthropod community data. This analysis can demonstrate which species impact the differences demonstrated between treatment community compositions; however, it may mis-represent the importance of a given species (Warton et al. 2012).

To test our hypothesis that the abundance of aphidophagous predators varied among the entire catchment (both prairie and crop), we used area-based weighting to combine insect abundance data collected from prairie strip and row-cropped portions of each catchment. The abundance measured in each habitat type was multiplied by the percent area of each habitat represented within a catchment and then summed. Data for each catchment were then summed across all months for a weighted season total. We used ANOVA to determine if the season-long total abundance of aphidophagous predators varied among the treatments.

For hypotheses concerning the biological control of the soybean aphids, we compared soybean aphid populations on caged and uncaged soybean plants. We calculated a biological services index (BSI) developed by Gardiner et al. (2009b) to quantify the amount of assumed predation observed per experimental unit using the following equation:

$$BSI = (A_c - A_o) / A_o$$

where A_c is the number of aphids on the caged plant and A_o is the number of aphids on the uncaged plant. In cases where the computed value was negative, the BSI was set to zero to indicate no biological control, because aphids cannot experience negative biological control. Thus, BSI values can range from zero to one, with higher values indicating higher levels of aphidophagous insect predation on soybean aphids. A biological services index for each pair of plants was calculated using the aphid populations from the last sampling date and averaged across subsamples within each catchment. We used ANOVA to test whether BSIs varied among the treatments (i.e., our fourth

hypothesis). Fixed effects tested in the model were block and treatment. An ANOVA was also used to test if BSI increased with proximity to prairie edge (i.e., our fifth hypothesis). A biological services index was computed from measured caged–uncaged plant pairs placed along transects at two distances from reconstructed prairie; the fixed effect tested was distance from prairie.

Results

Aphidophagous Arthropod Community. In 2009, 5,835 aphidophagous arthropods representing 13 taxa and two groups of unidentified categories were collected with sweep nets. In 2011, 2,013 aphidophagous arthropods representing 21 taxa and two unidentified coccinellid categories were collected with sweep nets, of which all were identified to family or species when possible (Table 2). In Table 2, numbers are first reported in season-long sum as well as on a per 1,000 sweep basis. We report on a per 1,000 sweep basis because sampling methodologies used in 2009 and 2011 used a different number of sweeps per sample.

In 2009, more predators were collected in the prairie (total: 3,933; average per 1,000 sweeps: 771.2) than the soybean fields (total: 1,902; average per 1,000 sweep: 660.4). The results of the *t*-tests of the season-long totals indicate prairies had more natural enemies than soybean fields, whereas the abundance of both exotic and native lady beetles were significantly lower in prairie than in soybeans (Table 3). The abundance of the most commonly collected predator, *O. insidiosus*, did not significantly differ between prairie and soybean.

In 2011, more predators were collected in prairie strips (total: 1,171; per 1,000 sweeps: 464.8) than soybeans (total: 842; per 1,000 sweep: 445.1). Paired *t*-tests indicated that the season-long total of predators was greater in prairie than in soybean, whereas the abundance of *O. insidiosus*, exotic lady beetles, or native lady beetles did not significantly differ between the prairie and soybean (Table 3). In both 2009 and 2011, we did not observe a significant effect of the various treatments applied to the catchments on the total abundance of predators. At the level of the catchment, the various treatments did not affect the abundance of components of the predator community, including *O. insidiosus*, exotic, and native lady beetles (Table 4).

The results of the analysis of the predator community in 2009 indicate that block, treatment, vegetation type, and sampling date significantly affected the composition of the predator community (Block: $F_{2,105} = 3.86$, $P < 0.01$; Treatment: $F_{3,105} = 2.13$, $P < 0.01$; Vegetation: $F_{1,105} = 11.59$, $P < 0.01$; Date: $F_{3,105} = 16.09$, $P < 0.01$). Based on the SIMPER analysis of these data, Araneidae, *O. insidiosus*, *H. axyridis* adults, *H. axyridis* larvae, and *Toxomerus marginatus* were the most influential groups causing differences among treatments, with cumulative contributions of 61–77% depending on pairwise comparisons. Other important groups were Nabis spp., unidentified Syrphidae, and Dolichopodidae.

Table 2. Aphidophagous insects and spiders collected in 2009 and 2011 in prairies (mean per 1000 sweeps in parentheses)

Taxa	2009 sweep net ^a		2011 sweep net	
	Prairie	Soybean	Prairie	Soybean
Unidentified lady beetle larvae	0 (0)	6 (2.1)	0 (0)	7 (3.7)
Unidentified lady beetle adult	1 (0.2)	1 (0.4)	0	0
Native coccinellidae				
<i>Cycloneda munda</i>	23 (4.5)	42 (14.6)	7 (2.8)	8 (4.2)
<i>Cycloneda munda</i> larvae	4 (0.8)	5 (1.7)	0 (0)	0 (0)
<i>Hippodamia convergens</i>	7 (1.4)	14 (4.9)	6 (2.4)	1 (0.5)
<i>Hippodamia convergens</i> larvae	9 (1.8)	7 (2.4)	0 (0)	0 (0)
<i>Coleomegilla maculata</i>	1 (0.2)	2 (0.7)	6 (2.4)	10 (5.3)
<i>Hippodamia parenthesis</i>	9 (1.8)	1 (0.4)	4 (1.6)	7 (3.7)
<i>Coleomegilla maculata</i> larvae	8 (1.6)	7 (2.4)	1 (0.4)	8 (4.2)
<i>Adalia bipunctata</i> larvae	NA	NA	0 (0)	1 (0.5)
Exotic coccinellidae				
<i>Harmonia axyridis</i>	229 (44.9)	461 (160.1)	4 (1.6)	12 (6.3)
<i>Harmonia axyridis</i> larvae	16 (3.1)	337 (117.0)	1 (0.4)	14 (7.4)
<i>Coccinella septempunctata</i>	4 (0.8)	0 (0)	1 (0.4)	0 (0)
<i>Coccinella septempunctata</i> larvae	0 (0)	0 (0)	0 (0)	5 (2.6)
Other insects				
<i>Orius insidiosus</i>	960 (188.2)	394 (136.8)	301 (119.4)	408 (215.9)
Syrphidae adult	753 (147.7)	44 (15.3)	69 (27.4)	60 (31.7)
Nabidae	137 (26.9)	189 (65.6)	11 (4.4)	31 (16.4)
Dolichopodidae	134 (26.3)	65 (22.6)	0 (0)	0 (0)
Chrysopidae Adult	37 (7.25)	19 (6.6)	23 (9.1)	4 (2.1)
Hemerobiidae Adult	7 (1.4)	5 (1.7)	1 (0.4)	5 (2.6)
Chrysopidae and Hemerobiidae larvae	47 (9.2)	NA	84 (29.2)	17 (9.0)
Spiders				
Unidentified spiders	1497 (293.5)	189 (65.6)	13 (5.2)	20 (10.6)
Thomisidae	NA	NA	400 (158.7)	67 (35.4)
Salticidae	NA	NA	105 (41.7)	47 (24.9)
Opiliones	57 (11.18)	30 (40.4)	23 (9.1)	8 (4.2)
Arenidae	NA	NA	79 (31.3)	22 (11.6)
Tetragnathidae	NA	NA	47 (18.7)	41 (21.7)
Oxyopidae	NA	NA	23 (9.1)	11 (5.8)
Lycosidae	NA	NA	4 (1.6)	15 (7.9)
Limnysiidae	NA	NA	3 (1.2)	8 (4.2)
Phidromidae	NA	NA	3 (1.2)	3 (1.6)
Dictynidae	NA	NA	2 (0.8)	2 (1.1)
Total	3933 (771.2)	1902 (660.42)	1171 (464.8)	842 (445.1)

^a Results from 2009 and 2011 are not comparable due to differences in sampling methods.

In 2011, block, vegetation type, and sampling date had a significant effect on the predator community (Block: $F_{2,141} = 2.58, P < 0.01$; Vegetation: $F_{1,141} = 13.94, P < 0.01$; Date: $F_{6,141} = 4.90, P < 0.01$). In 2011, the impact of treatment on arthropod community trended toward significance, but not at the $P = 0.05$ level ($F_{3,141} = 1.44, P = 0.06$). A graphical analysis of the community data explained some of the differences detected (Fig. 2): overall, fewer spiders were collected in June than September. During August, <10%

of the predators captured in prairie were spiders, but during that same period, at least 70% of the predators in the crop were spiders. Based on the SIMPER analysis in 2011, >50% of the dissimilarity between the communities was accounted for by spiders (Thomisidae and Salticidae) as well as *O. insidiosus*. The other groups that contributed to dissimilarity were Araneidae, Tetragnathidae, and Syrphidae (adult). These groups contributed to another 12–20% of the dissimilarity depending on the specific pairwise comparison.

Table 3. Paired t-test results from 2009 and 2011 testing for differences in the abundance of all aphidophagous insect predators, the most abundant taxon (*O. insidiosus*), and exotic and native lady beetles between prairie and soybean habitats

Null hypothesis	t-value ^a	P value	More abundant
2009 total abundance in prairie = soy	3.13	0.014*	Prairie
2009 <i>Orius</i> abundance in prairie = soy	1.77	0.115	NA
2009 exotic lady beetle abundance in prairie = soy	6.92	0.0001*	Soy
2009 native lady beetle abundance in prairie = soy	7.14	<0.0001*	Soy
2011 total abundance in prairie = soy	3.82	0.005*	Prairie
2011 <i>Orius</i> abundance in prairie = soy	0.02	0.986	NA
2011 exotic lady beetle abundance in prairie = soy	-1.37	0.208	NA
2011 native lady beetle abundance in prairie = soy	0.00	1.000	NA

^a Degrees of freedom for all tests show are 8.

* Signifies statistical significance rejecting null hypothesis below $P = 0.05$.

Table 4. ANOVA results from 2009 and 2011 testing for differences among treatments in the abundance of all aphidophagus insect predators, the most abundant taxa (spiders and *O. insidiosus*), and exotic and native lady beetles in portions of agricultural catchments in soybean production

Hypothesis	F-value	df	P value
2009 total abundance same in all treatments	0.0214	3, 44	0.8843
2009 total spider abundance same in all treatments	0.0018	3, 44	0.9662
2009 exotic lady beetle abundance same in all treatments	0.2489	3, 44	0.6203
2009 native lady beetle abundance same in all treatments	0.1737	3, 44	0.6789
2011 total abundance same in all treatments	0.3281	3, 80	0.8050
2011 <i>Orius</i> abundance same in all treatments	0.1374	3, 80	0.9374
2011 exotic lady beetle abundance same in all treatments	1.3411	3, 80	0.2669
2011 native lady beetle abundance same in all treatments	0.2523	3, 80	0.5595

These results suggest that these species or families were the most influential in determining the differences between treatments identified by the Adonis analysis.

In 2009, we did not observe an effect of the treatment on the season-long area-weighted total abundance of predators ($F_{3,8} = 0.38, P = 0.77$; Fig. 3a). A similar result was observed in 2011 ($F_{3,8} = 0.85, P = 0.50$; Fig. 3b). We observed slight differences in the weighted totals among treatments, but none were significant.

Soybean Aphid Predation. The aphid populations on caged and uncaged soybean plants were significantly different ($F_{1,22} = 16.26, P < 0.01$), indicating that the cages were successful in excluding predators.

Occasionally we observed predators within the caged plants (5 out of 72 observations), but not at levels sufficient to reduce aphid populations. Overall, aphid populations within caged plants averaged $2,338.7 \pm 752.5$ aphids compared with 208.7 ± 89.5 aphids on uncaged plants.

Overall, we measured BSI values indicative of significant aphid mortality due to predators (Fig. 4). Despite greater abundance of aphid predators in prairies, we did not detect a higher BSI among the treatments ($F_{3,8} = 0.29, P = 0.83$, Fig. 4). Although treat-

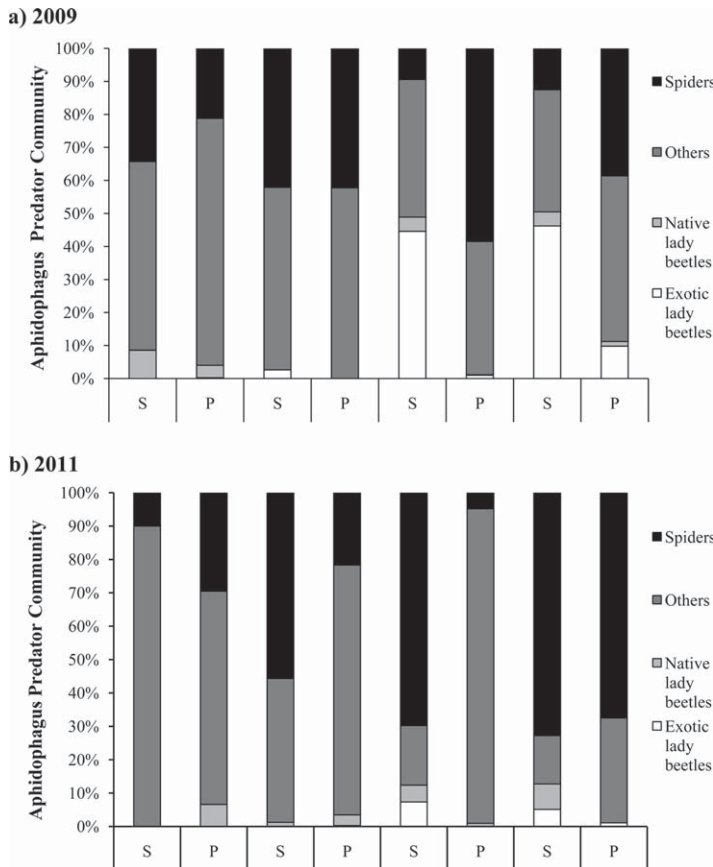


Fig. 2. Composition of the aphidophagus predator community during (a) 2009 and (b) 2011 collected once a month with a sweep net in either soybean (S) or prairie (P).

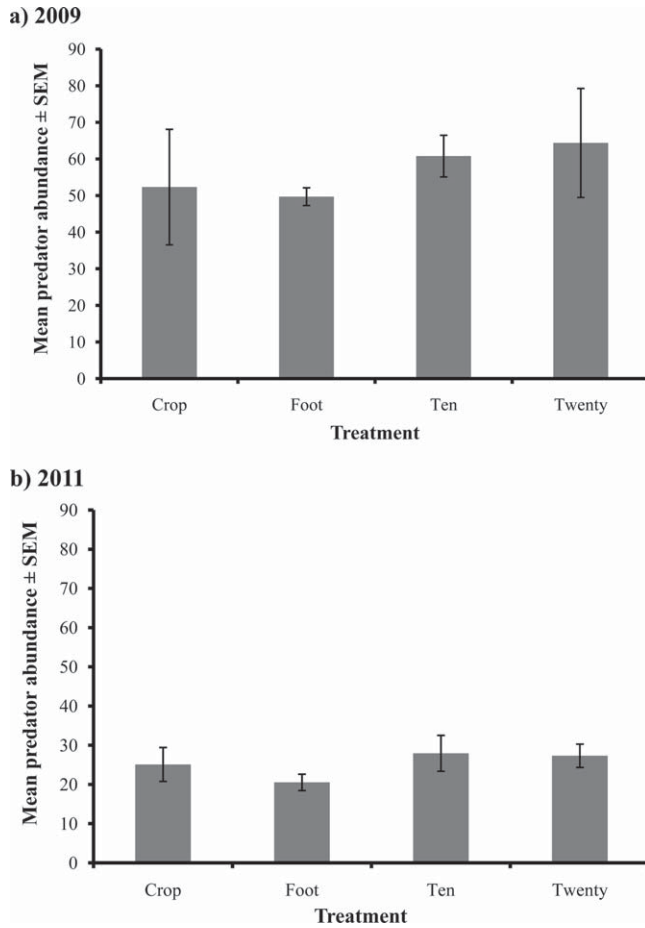


Fig. 3. Predator abundance (mean ± SEM) did not vary within catchments growing soybean with varying amounts of prairie (i.e., treatments) in (a) 2009 and (b) 2011. Predator abundances are weighted based on the amount of prairie and soybean within each catchment treatment; description of treatment structure is detailed in Table 2.

ment had no observable effect on BSI, the treatment that had the most area in prairie (i.e., 20% of catchment) had the highest BSI; conversely, the lowest BSI was measured in the treatment composed of all soybean and no prairie (i.e., crop).

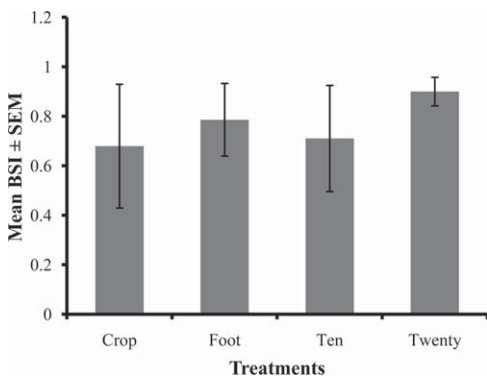


Fig. 4. BSI, an estimate of the biological control of the soybean aphid did not vary by treatment in 2011.

Based on distance from prairie, we measured an average BSI of 0.76 ± 0.07 among caged and uncaged plants directly adjacent to prairie and of 0.89 ± 0.05 among plant pairs at a location surrounded by soybean, 50 m distant from prairie; hence, significant biological control of the soybean aphid in both locations. No effect of distance on BSI was detected after 3 wk of aphid population growth ($F_{1,8} = 0.52, P = 0.49$).

Plant Nitrogen. In comparing aphid populations between caged and uncaged plants along transects proximal and distant to prairie, was significantly higher in the crop field (Fig. 4). Aphid populations on caged plants, which we expect to be more affected by the bottom-up effect of plant nutrients, were higher 50 m into the crop field, averaging $4,267 \pm 1,845$ (SEM) aphids per plant, compared with populations only 1 m from the prairie strip, averaging $1,524 \pm 1,185$ (SEM) aphids per plant. Although the difference in nitrogen between plants from the two locations was not statistically different at the $P = 0.05$ level, the general trends showed plant ammonium levels were higher in plants

adjacent to prairie ($856 \text{ ppm} \pm 45$) than in 50 m into the crop field ($701 \text{ ppm} \pm 37$; $F_{1,18} = 3.49$, $P = 0.08$); plant nitrate levels were higher in plants from in the field ($575 \text{ ppm} \pm 88$) than those adjacent to the prairie ($324 \text{ ppm} \pm 36$; $F_{1,18} = 2.78$, $P = 0.11$); and total plant nitrogen was highest from plants in the field ($3.2\% \pm 0.02$) as compared with those adjacent to the prairie ($3.09\% \pm 0.04$; $F_{1,18} = 3.21$, $P = 0.09$).

Discussion

We tested a series of hypotheses to determine if adding prairie to catchments committed to row-cropped could increase the abundance and diversity of predator insects such that biological control of soybean aphids would be increased in the crop land. Of these hypotheses, we only observed significant differences in the abundance of aphidophagous predators between prairie and crop areas; season-long abundance was higher in prairie areas compared with crop areas in both 2009 and 2011 (Table 3). From the Adonis analysis, we observed insect communities that were distinct between habitat types, and in 2009 by treatment.

Although predator abundance was higher in prairies, this did not translate into an increase in biological control (i.e., no change in the B.S.I.). While prairie did not directly impact biological control of soybean aphids, it did achieve the goal of increasing beneficial insects within the landscape. It may be possible that this increase could translate into other ecosystem services, such as biological control of other crop pests.

In the following section, we discuss why the greater abundance of natural enemies in prairie strips did not affect their abundance in the adjacent soybean and the biological control of soybean aphids. We specifically address factors not controlled for in this experiment including: landscape context, the quality of the reconstructed prairie, natural enemies, and bottom-up differences in the form and concentration of plant nutrients and how they may have affected our final results. Despite these limitations, this study does document how prairie strips integrated within row-crop fields can increase field-scale abundance and diversity of the natural enemy community as a whole. It also informs subsequent research on how to measure the full impact of native plants and their attendant insect communities in row crop-dominated landscapes.

Landscape Context. The STRIPS experimental site is embedded within the diverse landscape of the NSNWR (Fig. 1). This location may have reduced our power to detect differences in aphidophagous predator population levels at the catchment scale and their subsequent impact on soybean aphid populations. While agricultural landscapes in Iowa are generally limited in terms of landscape diversity (Brown and Schulte 2011), the Refuge is composed of a cropland, prairie, and forest mosaic. The relatively diverse character of this surrounding landscape may have impacted our ability to detect hypothesized differences among catchments with varying amounts of prairie. Gardiner et al. (2009b) observed within the Midwest-

ern United States that the most accurate model to predict BSI was Simpson's Diversity of the landscape at the level of 1.5 km radius around a soybean field. The BSI values computed by Gardiner et al. (2009b) study range from 0.1 to 1.0, with most above 0.6. Similarly, the mean BSI values for all of our treatments were above 0.6. We suggest that ability to detect differences in natural enemy populations and biological control at the catchment scale may have been overwhelmed by the high overall natural enemy populations resulting from the location of our study within a National Wildlife Refuge.

As noted by Isaacs et al. (2009), improvements in the delivery of insect-derived ecosystem services through conservation efforts may depend upon the landscape in which these efforts are practiced. Landscapes with low to moderate complexity will likely see the greatest improvement in these services when additional habitat for beneficial insects is provided. Woltz et al. (2012) found that when both landscape diversity and field-scale diversity varied, changes in the biological control of the soybean aphid were only correlated with landscape diversity, not field-scale changes. While we do not know what the outcomes of our study would be if conducted in a more simplified landscape dominated by row crops, where the addition of prairie strips may significantly impact landscape diversity measures, we expect the effect of prairie may be more easily detectable. We suggest performing this study across landscapes with variable portions of crop and noncrop habitat, with a focus on landscapes with relatively lower diversity.

We predicted that placement and orientation, or spatial configuration of the buffer strips would impact natural enemies or biological control, but observed no significant difference among treatments with prairie only at the bottom of the slope and those with strips spread throughout a catchment. Components of our experimental design may have limited our capacity to measure the impact of prairie. With some experimental units side by side, insect movement among catchments could have diluted treatment differences. We only tested treatments with small amounts of prairie in three different configurations (three total size and configuration combinations), however, and a higher percentage of prairie or more strips may be needed to translate a change in insect abundance to ecosystem service.

Habitat Quality. Another factor affecting our ability to detect differences relates to the quality of reconstructed prairie established in this study as habitat for natural enemies. While perennial, noncropped habitat can be important for increasing the delivery of ecosystem services within agricultural landscapes (Van Buskirk and Willi 2004, Schulte et al. 2006)—in particular, water quality, water flow, and bird habitat as documented in the STRIPS Project (Zhou et al. 2010, Helmers et al. 2012, MacDonald 2012)—the prairie plant community represented in the experiment does not rank particularly high for the provision of insect-derived ecosystem services. The composition and abundance of plant species cultivated in the prai-

rie strips were not selected on the basis of attractiveness to beneficial insects, but instead to represent a diverse mix of native prairie species in Iowa that contribute to increasing soil and water conservation. Very few of these plant species are documented as attractive to aphidophagus predators and therefore the insect community attracted to these prairies may not be a community optimized for soybean aphid predation.

Additionally, we consider that as the prairie matures and different species establish, beneficial insect dynamics may change. Whether the prairie plants have reached a state of succession that is optimal for beneficial insects is not clear. Within the period of time that this study was conducted, Hirsh et al. (2013) observed changes in prairie plant abundance and diversity with the establishment of prairie at research site. Determining the extant differences in the insect community that occurred between 2009 and 2011 are due to these changes is beyond our experimental design. However, we expect that both plant and insect communities change in response to maturation of the prairie over time.

Natural enemies of specific relevance for soybean aphid biological control is the ability of prairie strips to provide habitat for *H. axyridis*, an aphid predator that, like the aphid, is native to Asia (Koch and Galvan 2008). In Asia, *H. axyridis* is considered an arboreal species and in North America Gardiner et al. (2009a) noted increased abundance of *H. axyridis* and other exotic lady beetles when soybean fields are surrounded by forest. Within this study, exotic lady beetles including *H. axyridis* were found in abundance in both prairie and crop fields in 2009, and only in small numbers in 2011 (Table 2). Our results suggest that exotic lady beetles did not find the prairie any more attractive than the soybean; thus, this form of native habitat may not be optimal for increasing their abundance within an agroecosystem.

Plant Nutrients. The last variable we consider that may have confounded our findings was the lack of control for plant nutrient levels in our study of soybean aphid predation. As investigated in the sixth hypothesis, nitrogen levels and types of nitrogen varied in different parts of the field. The study suggests that bottom-up factors, such as nutrient availability as influenced by slope position, may also contribute to aphid population dynamics and thus the ability of natural enemies to control them.

Conclusions

We hypothesized that prairie strips within crop fields would increase abundance of aphidophagous predators and biological control services delivered via soybean aphid predation. While an increase in the abundance of aphidophagous predators was observed within prairie strips, our data suggest there was no impact of the amount of prairie in the catchment (0, 10, or 20%) or placement of prairie strips (toe slope or contour strips in field) on either predator abundance in adjacent soybean, total catchment abundance, nor on biological control. Similarly, we did not observe an

impact of proximity to prairie on the biological control of soybean aphid. The impact of prairie on the biological control of soybean aphids may be improved by conserving aphidophagous predators in a more simplified crop landscape or by selecting plants that are more attractive to them buffer strips.

Although increased biodiversity can provide tangible soil, water, and wildlife conservation benefits, during a period of high commodity prices and U.S. Department of Agriculture (USDA) Conservation Reserve Program rental rates that fail to include future price increases, farmers may be less inclined to take land out of production to increase the delivery of ecosystem services (Hellerstein 2010). To provide enough incentive to take land out of crop production, benefits need to be clear and of value to farmers so they may fully consider the benefits:costs of changing practices. Ideally, conservation benefits can be maximized while also maximizing profits from crop production. From the results of this research, we do not expect insect-derived ecosystem services to be a driving factor for adoption of prairie buffer strips. Under our current research design, insect-derived ecosystem services for soybean aphids were not maximized, as no additional pest management services are added by putting prairie into soybean fields. The next step may be to strategically design prairie strips to optimize biological control by incorporating a greater proportion of plants that attract aphidophagous insects. However, the multifunctional, layered benefits of prairie vegetation, such as reductions in sediment and nutrient transport (Zhou et al. 2010, Helmers et al. 2012, Hernandez-Santana et al. 2013) and wildlife habitat (MacDonald 2012, Hirsh et al. 2013) may provide the incentive needed to encourage the establishment of prairie strips within agricultural landscapes.

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Appendix 1: Plant species found in prairie strips in 2011 comprising >1% relative cover and their importance for attracting natural enemies insects or spiders (adapted from Hirsh et al. 2013)

Common name	Species name	Plant type ^a	% cover	Value for natural enemies	Reference
Canadian/Kentucky bluegrass	<i>Poa compressa/pratensis</i>	XPM	22.3	None found	
Tall goldenrod	<i>Solidago canadensis</i>	NPD	10.0	Genus solidago attractive	Fiedler and Landis 2007
Gray-headed coneflower	<i>Ratibida pinnata</i>	NPD	5.8	Attractive	Fiedler and Landis 2007
Queen Anne's lace	<i>Daucus carota</i>	XBD	5.5	Extends life of natural enemies	Walton and Isaacs 2011
Indian grass	<i>Sorghastrum nutans</i>	NPM	4.8	None found	
Wild bergamot	<i>Monarda fistulosa</i>	NPD	3.8	Genus menarda attractive	Fiedler and Landis 2007
Big bluestem	<i>Andropogon gerardii</i>	NPM	3.7	None found	
Smooth brome	<i>Bromus inermis</i>	XPM	3.4	Encyrtidae and Nabidae families more abundant in reseeded brome/alfalfa treatments than three other native and reseeded treatments	O'Neill et al. 2001
Hairy aster	<i>Aster pilosus</i>	NPD	3.1	Genus aster attractive	Fiedler and Landis 2007
Reed canary grass	<i>Phalaris arundinacea</i>	NPM	2.7	None found	
Ox-eye	<i>Heliopsis helianthoides</i>	NPD	2.7	None found	
Yellow nut grass	<i>Cyperus esculentus</i>	NPM	2.4	None found	
Foxtail spp.	<i>Setaria</i> spp.	XAM	1.9	None found	
Little bluestem	<i>Schizachyrium scoparium</i>	NPM	1.9	None found	
Canada wild rye	<i>Elymus canadensis</i>	NPM	1.8	None found	
Hedge false bindweed	<i>Calystegia sepium</i>	NPD	1.7	None found	
Common dandelion	<i>Taraxacum officinale</i>	XPD	1.6	None found	
Spiderwort	<i>Tradescantia ohiensis/bracteata</i>	NPM	1.4	None found	
Side-oats grama	<i>Bouteloua curtipendula</i>	NPM	1.3	None found	
Poison ivy	<i>Toxicodendron radicans</i>	NPD	1.2	None found	
Fox sedge	<i>Carex vulpinoidea</i>	NPM	1.0	None found	
Canada thistle	<i>Cirsium arvense</i>	XPD	1.0	<i>C. septempunctata</i> abundance higher with high density of <i>C. arvense</i> and <i>Elymus repens</i> in barley plots, abundance higher in barley plants exposed to <i>C. arvense</i> volatiles	Ninkovic and Petterson 2003

^a Plant types are represented by: X, non-native; N, native; P, perennial; B, biennial; A, annual; D, dicot; M, monocot.