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Larger wildflower plantings increase natural enemy density, diversity, and biological control of sentinel prey, without increasing herbivore density

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Abstract. 1. An important means of conserving beneficial insects in resource-limited habitats is to meet their ecological requirements, which may be achieved by providing areas containing flowering plants that bloom throughout the season, but little is known about the importance of wildflower plot size for supporting natural enemies or the biological control they provide.

2. Wildflowers were established in plots of sizes ranging from 1 to 100 m^2, and found that natural enemy density, group richness, and diversity of natural enemy groups increased with plot size.

3. The density of insect herbivores was lower in all flower plots than in the control samples, whereas the diversity of herbivore groups was significantly higher in flower plots.

4. Comparing population growth of sentinel soybean aphids (*Aphis glycines* Matsumura) among plot sizes, aphid colonies were smaller as plot size increased.

5. Providing beneficial insects with flowering resources resulted in significantly more natural enemies and greater pest control than in smaller flower plots or mown grass areas.

6. These results indicate that the density, diversity, and function of natural enemies are sensitive to the size of wildflower plantings, even at relatively small scales. Therefore, larger wildflower plots are more suitable for the conservation of beneficial insects and their provision of natural pest control.

Key words. Beneficial insects, biocontrol, perennial, size.

Introduction

Populations of beneficial insects are at risk of decline, particularly in agroecosystems (Biesmeijer *et al*., 2006; Landis *et al*., 2008) owing to the scarcity of native and flowering plants, insecticide use, and loss or fragmentation of habitat (Landis *et al*., 2000; Goverde *et al*., 2002; Carvell *et al*., 2006). Consequently there has been growing interest in developing approaches to conserve beneficial insects and these strategies often involve integrating floral resource patches into farmland (Bianchi *et al*., 2006; Kremen & Chaplin-Kramer, 2007; Isaacs *et al*., 2008; Letourneau & Bothwell, 2008). For this to be adopted within agricultural systems, support of beneficial insects must be done without increasing herbivore populations (Lavandero *et al*., 2006; Isaacs *et al*., 2009).

Sufficient flower abundance and proper vegetation structure are required to support diverse populations of insects (Zurbrügg & Frank, 2006), and therefore manipulation of structurally resource-poor habitats through the addition of flowering plants and grasses can increase beneficial insect populations in agricultural landscapes (Long *et al*., 1998; Kells *et al*., 2001; Rebek *et al*., 2005). Many beneficial insects, including natural enemies, require access to alternate hosts, overwintering habitats, a constant food supply, and appropriate microclimates in order to survive (Johnson & Triplehorn, 2005; Jonsson *et al*., 2008). These requirements can be fulfilled with a diverse assemblage of flowering plants, which will provide the resources necessary to support populations of predators and parasitoids throughout the season (Landis *et al*., 2000; Ahern & Brewer, 2002; Büchi, 2002; Sanchez *et al*., 2003; Wanner *et al*., 2006).

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Insect population density is expected to be greater in larger habitat patches that have more resources to support populations (Slobodkin, 1980), but few studies have examined this pattern in relation to beneficial insects. While a positive response from insect natural enemies to the size of host patch size has been documented previously (Bach, 1988b; Olson & Andow, 2008), there is little information on the response of natural enemies or herbivorous insects as a function of wildflower patch size. Beneficial insects respond positively to the addition of flowering resources in farmland, but different insect taxa respond to these manipulations in varying ways (Fraser *et al*., 2008; Osborne *et al*., 2008; Tscharntke *et al*., 2008), and may also respond to habitat at different scales. Meyer *et al*. (2007) and Olson and Andow (2008) found that larger grassland habitat areas resulted in greater insect abundance and diversity. In a study by Heard *et al*. (2007), landscape composition influenced bee abundance, but flower patch size had no effect. Conversely, Meyer *et al*. (2007) observed that increasing flowering strip size increased abundance and diversity of pollinators.

Studies measuring the response of insect herbivore abundance to habitat patch size have also resulted in conflicting observations. Raupp and Denno (1979) observed that herbivore density increased with patch size of salt marsh grasses, whereas Grez and Gonzalez (1995) found that herbivore densities do not differ with patch size of cabbage plants. While the patch size of the host crop may be important, insect herbivores may also be able to take advantage of wildflower plantings in the agricultural landscape. Therefore, understanding how generalist herbivores and potential crop pests respond to wildflower habitat patch size will also be important for future implementation of wildflower plantings to conserve beneficial insects in agricultural landscapes.

To determine how natural enemies respond to wildflower plantings of different sizes, we measured insect density and diversity in wildflower plots of different sizes that remained consistent in plant diversity and species composition. Our hypothesis was that density, richness, and diversity of insect natural enemy groups will increase with the size of wildflower plots, and we predicted that the level of biological control from these insects would increase similarly. To determine whether plot size affected the magnitude of biological control provided by natural enemies, soybean aphid (*Aphis glycines* Matsumura) population growth was measured in the same wildflower plots on sentinel plants. Finally, we also measured the response of herbivorous insects to wildflower plot size to test the hypothesis that the density, richness, and diversity of insect herbivore groups would increase with wildflower plot size.

Methods

Field preparation

A 1-ha grass field was prepared for the experiment in the fall of 2008 at the Trevor Nichols Research Center in Fennville, Michigan. Twenty-five square plots of varying size were mowed and then sprayed with 1% glyphosate herbicide at 206.7 l ha^{-1} (Touchdown®, Syngenta Crop Protection, Inc. Greensboro, NC) twice in the late summer to reduce the growth of weeds. At first vegetative growth in 2009, the same herbicide was applied to all plots 2 weeks before wildflower seedlings were planted. The plots were not tilled in order to prevent the exposure of dormant weed seeds.

The 25 square-shaped plots consisted of a logarithmic series of five size treatments with five replicates each: of 1, 3, 10, 30, and 100 m^2. These plots were arranged in a 5 × 5 grid of 15 × 15 m cells, with the centre of each plot positioned in the centre of a grid cell. Different sized plots were arranged within the grid using a Latin-square design (Fig. 1).

One-year-old plants (Wildtype Native Plant Nursery, Mason, Michigan) of 12 native perennial wildflower species (Table 1) were planted in mid-May 2009. Plants were selected for their known attractiveness to natural enemies and had overlapping bloom periods that spanned May through to October (Fiedler & Landis, 2007). The 12 different species were planted 30–45 cm apart within square groupings of 12 seedlings, with the relative position of each species randomized within every grouping. With this design, to maintain the same relative abundance of species across the experiment, 1 m^2 plots had 1 grouping of 12 seedlings (1 from each species), the 3 m^2 plots had 4 groupings (48 seedlings), 10 m^2 plots had 9 groupings (108 seedlings), 30 m^2 plots had 25 groupings (300 seedlings), and 100 m^2 plots had 64 groupings (768 seedlings). To combat weed growth, a 5 cm depth of wood chips was added to the plots after planting. The grass surrounding the plots was mowed approximately once a month during the summer for the duration of this project, and five locations within the grassy areas and away from the plots served as the negative controls.

Insect sampling

From May to September 2010 each of the 25 wildflower plots were sampled in random order. Once a month on warm,

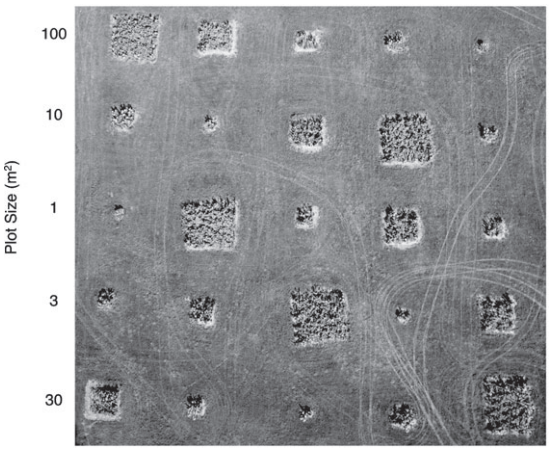

Fig. 1. Aerial image of wildflower plantings in August 2010. Sized plots were arranged using a Latin-square design, and the size (m^2) of the wildflower plantings in the left column are displayed at the side of the photo.

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Table 1. List of native Midwestern annual wildflowers and their bloom periods planted at the Trevor Nichols Research Center in Fennville, Michigan, U.S.A.

Common name	Scientific name	Bloom period (month) M	J	J	A	S	O
Golden Alexanders	*Zizia aurea*	X	X				
Foxglove beard-tongue	*Penstemon digitalis*		X	X			
Sand coreopsis	*Coreopsis lanceolata*		X	X			
Black-eyed Susan	*Rudbeckia hirta*		X	X	X	X	
Butterfly milkweed	*Asclepias tuberose*			X	X		
Spotted beebalm	*Monarda punctata*			X	X		
Boneset	*Eupatorium perfoliatum*		X	X	X		
Blue lobelia	*Lobelia siphilitica*			X	X	X	
Yellow coneflower	*Ratibida pinnata*			X	X	X	
Cup plant	*Silphium perfoliatum*			X	X	X	
Stiff goldenrod	*Solidago rigida*				X	X	X
New England aster	*Aster novae-angliae*				X	X	X

calm, and sunny days between 10.00 and 16.00 hours each plot was sampled four times for 30 s using a modified reversed-flow leaf blower (BG 56 C-E; Stihl, Waiblingen, Germany) with a fine white mesh bag (150 μm; The Cary Company, Addison, Illinois) placed over the intake to capture insects (Fiedler, 2006). Suction sampling can underestimate species richness in cross-habitat comparisons as the efficiency of suction sampling to capture arthropods is higher in shorter vegetation when compared with taller vegetation (Hossain *et al*., 1999; Sanders & Entling, 2011).

Five 30-s negative control samples were also taken in the same manner from the grassy areas. Sampling focused on flowering portions of the plants where available, and the samples were placed in a cooler, returned to the laboratory, and frozen. Insects were later separated from plant matter and identified to major taxonomic groups (Table 2) using standard keys (Borror & White, 1998; Johnson & Triplehorn, 2005). Although it is possible that insect abundance data from the suction-samples underestimated the overall abundance of these arthropods, this approach resulted in collection of insects from a wide variety of taxonomic groups, including parasitoids, predaceous insects, and herbivores.

Biological control and wildflower plot size

Soybean plants, *Glycine max* (L.) Merr., were grown from seed in the greenhouse and transferred into 15.2-cm^2 pots. In 2009 and 2010, 50 soybean plants were grown to the V6-stage and two groups of 25 plants were placed in the wildflower plots for each of two repetitions of the following experiment. This was done only in the wildflower plots and not in the grass control areas. To test the background level of predation among plot sizes before flowers started blooming on 27 July and again 13 August 2009, pairs of soybean plants were infested with a combination of 10 (4 adult, 3 mid-instars, and 3 early instars) apterous soybean aphids and placed near the centre of each of the 25-five wildflower plots for 2 weeks. One control soybean plant in each plot was covered completely, including the pot, with a fine nylon mesh (150-μm hole size; The Cary Company) to exclude all natural enemies from the aphids, and the other soybean plant was left uncovered to allow for predation of aphids (Fox *et al*., 2004; Gardiner *et al*., 2009). Each potted soybean plant was placed into a separate 15.2-cm^2 pot attached to a 45-cm stake and placed near the centre of each plot, providing support and stability to the potted plants. These pots were painted with fluon (Insect-a-slip; Bioquip Products Inc., Rancho Dominguez, California) to keep ground-dwelling arthropods off the potted plants. The number of aphids on each plant was counted after 2 weeks. To test the response of predation to plot size after the flowers had started blooming this experiment was repeated on 30 July and 16 August 2010.

To determine the magnitude of biological control provided in 2009 (before flowering) and in 2010 (after flowering), we calculated the relative aphid suppression in different size plots by expressing the change in aphid numbers on open and caged plants as a proportion of aphid abundance in the absence of predators for each plot. The resulting biocontrol services index (BSI) can vary from 0 to 1, with values increasing as the level of aphid predation increases:

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

where A_c is the number of aphids on the caged plant on day 14, A_o is the number of aphids on the open plant on day 14, p is the plot, and n is the number of replicates for a given plot (Gardiner *et al*., 2009).

Analysis

The density, richness, and diversity (Shannon–Wiener Index) of unique taxonomic groups of natural enemies and herbivores (Table 2) were compared among plot sizes using analysis of variance (ANOVA) with data averaged from each month during the growing season (May through to September)

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Table 2. Numbers of unique taxonomic groups collected in the different-sized wildflower plots and the total abundance of natural enemies and insect herbivores observed in those plots from the 4 months of sampling.

	Wildflower plot size (m^2)					
	Control	1	3	10	30	100
Taxonomic group	Number collected					
Natural enemies						
Araneae	60	193	224	225	271	250
Coleoptera						
Coccinellidae	5	11	12	6	11	11
Cantharidae	–	6	15	4	12	22
Dermaptera	–	12	6	1	2	2
Diptera						
Syrphidae	6	34	39	84	102	70
Tachinidae	–	2	5	3	3	1
Dolichopodidae	5	12	15	19	21	26
Asilidae	–	1	–	1	–	1
Hemiptera						
Anthocoridae	4	38	26	45	51	69
Nabidae	29	7	19	11	9	14
Hymenoptera						
Parasitica	319	244	294	378	362	488
Aculeata						
Vespoidea	–	1	1	–	–	–
Formicidae	270	65	78	97	130	152
Neuroptera	4	6	5	20	7	32
Total abundance	702	632	739	894	981	1138
Herbivores						
Coleoptera						
Scarabaeidae	3	14	11	35	37	52
Chrysomelidae	323	35	53	39	44	60
Curculionidae	44	5	24	53	49	3
Hemiptera						
Miridae	363	232	252	320	412	431
Cicadellidae	1472	162	244	280	365	288
Aphidae	303	110	87	89	102	101
Lygaeidae	3	13	17	33	26	35
Tingidae	6	35	4	47	21	24
Cercopidae	29	21	16	25	40	30
Fulgoroidea	38	2	5	4	3	5
Lepidoptera	69	90	49	58	81	70
Total abundance	2654	719	762	983	1180	1099

(JMP, Version 5; SAS Institute Inc., Cary, North Carolina). Insect density and group diversity were further compared among treatments using Student's *t*-test with the alpha level corrected *post hoc* via the Bonferroni method ($\alpha = 0.01$) (Zar, 1999). Each observed taxonomic group of natural enemies were also analysed using ANOVA and Student's *t*-test to determine if specific groups of insects responded positively to wildflower plot size. The biological control experiment was conducted twice over a 2-month timeframe, so the data were pooled and averaged for these months, and the BSI values and aphid abundance were compared among plot sizes using ANOVA. The BSI values and aphid abundance were then compared among plot sizes using Student's *t*-test with the alpha level corrected *post hoc* via the Bonferroni method ($\alpha = 0.01$) (Zar, 1999). To determine the relationship between aphid abundance on open plants and the populations of natural enemies, we calculated the Pearson product-moment correlation of BSI with the natural log transformed ($\log_e + 1$) natural enemy abundance data (Table 2).

Results

Insect natural enemies

The majority of insect natural enemies captured in the wildflower plots included parasitic wasps, spiders, and ants, with other notable collected natural enemies being hoverflies and minute pirate bugs (Table 2). There was an increase in the density (insects per m^2) of insect natural enemies with increasing plot size (Fig. 2a). The density of natural enemies was almost twice as high in the 100-m^2 plots compared with the 1-m^2 plots ($F_{5,144} = 3.39$, $P = 0.0063$). Natural enemy group richness increased significantly across treatments ($F_{5,144} = 4.99$, $P = 0.0003$), with 30- and 100-m^2 plots having significantly more unique natural enemy groups (Table 2) than the 1-m^2 plots or the control (Fig. 2b). The trend of natural enemy group diversity increased across treatments and was significantly higher in all wildflower plots greater than 1 m^2 compared with the grassy control plots (Fig. 2c; $F_{5,144} = 5.09$, $P = 0.0003$), but did not differ significantly among the different wildflower plot sizes.

Both predator and parasitoid insects responded positively to plot size. The density of predaceous insects increased with plot size and differed significantly from the control samples ($F_{5,144} = 3.07$, $P = 0.011$). Parasitoid density also increased significantly with plot size ($F_{5,144} = 3.29$, $P = 0.0076$) with significantly more parasitoids being collected in 100 m^2 compared with the control, 1 m^2, and 3 m^2 samples.

Insect herbivores

Plant bugs, leaf hoppers, and aphids were the primary insect herbivores captured in the wildflower plots (Table 2). The density of insect herbivores was lower in all wildflower plots than in the control plots (Fig. 3a; $F_{5,144} = 13.02$, $P < 0.0001$), but did not differ significantly among wildflower plot sizes. Conversely, herbivore group richness (Table 2, Fig. 3b; $F_{5,144} = 2.41$, $P = 0.039$) and diversity (Fig. 3c; $F_{5,144} = 5.94$, $P < 0.0001$) were significantly higher in all wildflower plots compared with the grassy control plots, but neither showed a significant difference among wildflower plot sizes.

Biological control

In 2009, in the absence of blooming wildflowers, aphid populations on open soybean plants after 2 weeks in the field ranged from 15 to 189 aphids per plant and 30 to 203 aphids per plant on caged plants. After wildflower establishment, in 2010 aphid populations on open soybean plants ranged from 7 to 24 aphids per plant and ranged from 54 to 288 aphids per plant on caged plants after 2 weeks in the field. Adult alate

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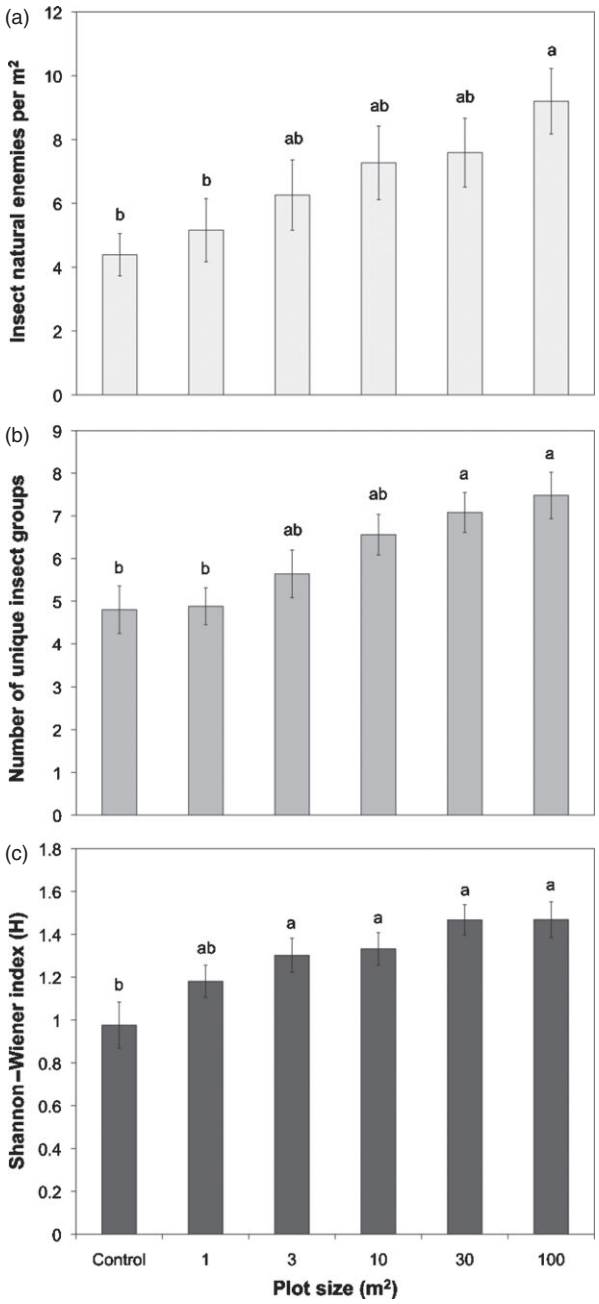

Fig. 2. (a) Density of insect natural enemies (mean ± SE) for the different-sized flower plots. (b) Insect natural enemy group richness (mean ± SE) for the different-sized wildflower plots. (c) Shannon–Wiener diversity index of insect natural enemy groups (mean ± SE) for the different-sized flower plots. Bars within a graph with the same letter are not significantly different (ANOVA, followed by comparisons for each treatment using Student's t with Bonferroni's correction, $\alpha = 0.01$).

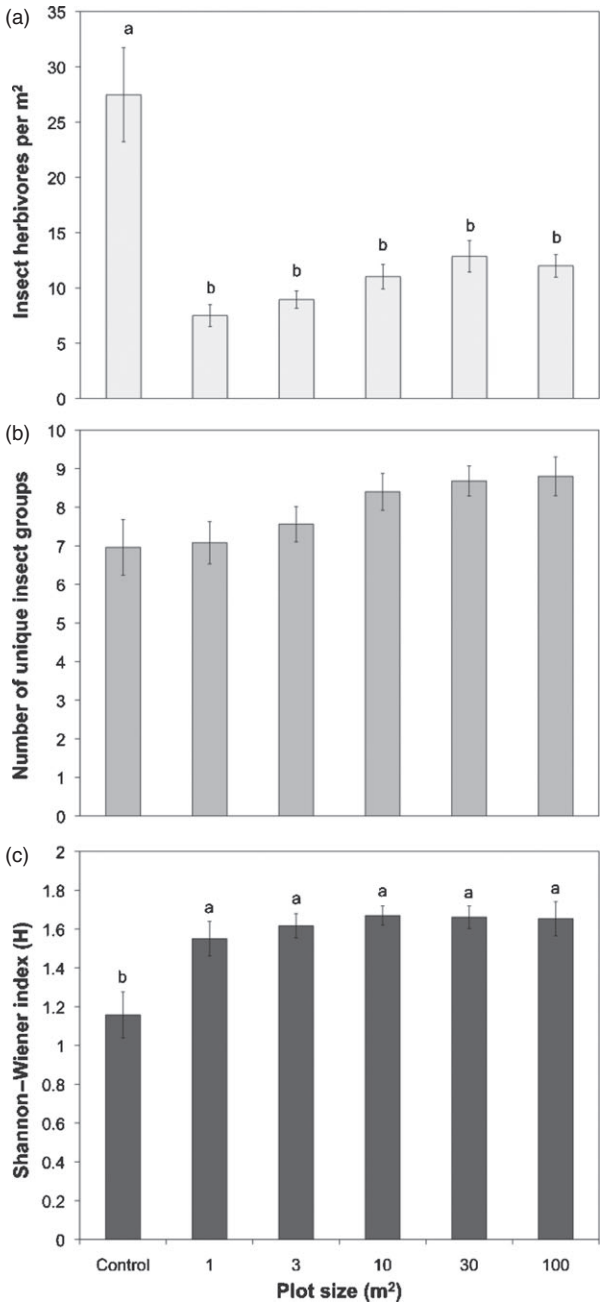

Fig. 3. (a) Density of herbivorous insects (mean ± SE) for the different-sized flower plots. (b) Insect herbivore group richness (mean ± SE) for the different-sized wildflower plots. There was no significant difference amongst treatments. (c) Shannon–Wiener diversity index of insect herbivore groups (mean ± SE) for the different-sized flower plots. Bars within a graph with the same letter are not significantly different (ANOVA, followed by comparisons for each treatment using Student's t with Bonferroni's correction, $\alpha = 0.01$).

soybean aphids were not observed in either year on open or in caged treatments, suggesting no crowding response.

In 2009, aphid abundance on open sentinel soybean plants was lower, but not significantly different than those that were caged ($F_{1,98} = 3.78$, $P = 0.055$). Also, neither aphid abundance ($F_{4,45} = 0.94$, $P = 0.45$), nor the BSI value differed significantly among the wildflower plot sizes in 2009 (Fig. 4a; $F_{4,27} = 0.25$, $P = 0.91$). In 2010 with the presence of flowers,

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the average BSI among all 25 plots was significantly higher than that of 2009 (2010, 0.85 ± 0.036 and 2009, 0.69 ± 0.052; $F_{1,71} = 6.31$, $P = 0.014$). Also, in 2010 after 2 weeks in the wildflower plots, aphid colony sizes were much lower on the exposed soybean plants compared with the control plants with the mesh cages ($F_{4,45} = 57.4$, $P < 0.0001$). There was no significant difference in aphid abundance on caged plants among wildflower plot sizes ($F_{4,45} = 3.65$, $P = 0.832$), and as plot size increased the aphid abundance on open plants decreased. The open plants in the 100-m^2 plots had significantly fewer aphids remaining after 2 weeks than those in the 1-m^2 plots. With increasing plot size there was also an increase in the BSI values. Plots 10 m^2 and larger had significantly greater biological control of soybean aphids than those in the 1-m^2 plots (Fig. 4b; $F_{5,44} = 5.62$, $P = 0.0011$). The BSI values were also positively correlated with the density of predaceous insects ($r = 0.499$, d.f. = 48, $P = 0001$).

Discussion

In this study we showed that the density, richness, and diversity of natural enemy groups increase with the native wildflower patch size. The density of predaceous insects in wildflower plots was also positively correlated with BSI as measured using biological control of soybean aphids. In contrast, herbivore density did not increase with planting area, suggesting that wildflower plantings can selectively support beneficial insects, providing support for their application in agricultural settings to help regulate pest populations.

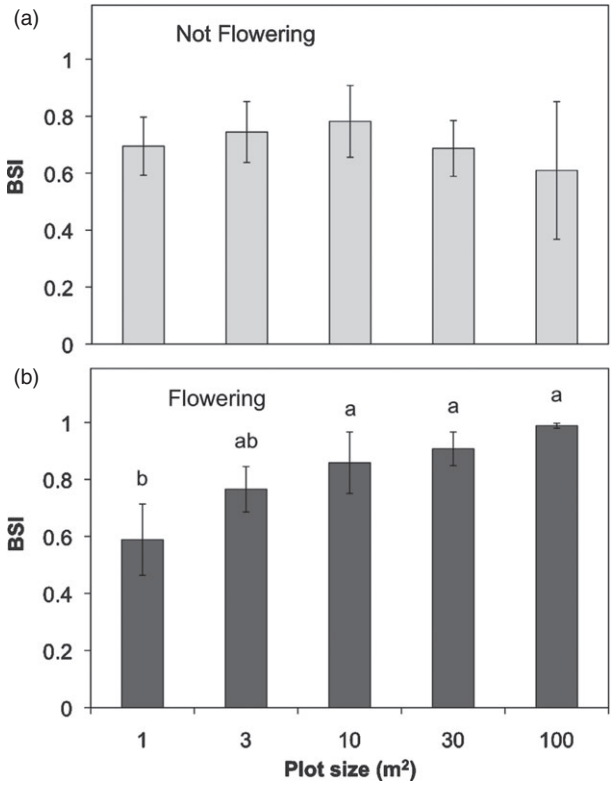

Fig. 4. The biocontrol services index (BSI) values (mean ± SE) for predation of soybean aphid, *Aphis glycines,* colonies placed in wildflower plots that varied in size from 1 to 100 m^2. (a) 2009. There was no significant difference among treatments. (b) 2010. Bars with the same letter are not significantly different (ANOVA, followed by comparisons for each treatment using Student's t with Bonferroni's correction, $\alpha = 0.01$).

The increase in natural enemy density with wildflower plot size supports previous results that natural enemies respond positively to plot sizes in different crops, such as maize and mustard (Olson & Andow, 2008; Bezemer *et al*., 2010). We found that parasitoid wasps (Braconidae and Ichneumonidae), ants (Formicidae), green lacewings (Chrysopidae), and minute pirate bugs (*Orius* spp.) responded positively to wildflower plot size. As these are known to be common insect natural enemies (DeBach & Rosen, 1991), this is a promising result for supporting natural enemies using wildflower plantings because at some point during their life cycles, parasitoid wasps (Winkler *et al*., 2009), ants (Blüthgen & Fiedler, 2004), green lacewing adults and larvae (Silva *et al*., 2007), and minute pirate bugs (Letourneau & Altieri, 1983) depend on and/or are enhanced by pollen and/or nectar from flowering resources.

As with the density of insect natural enemies, biological control also increased with wildflower plot size. The relative suppression of soybean aphid populations on open versus caged soybean plants was significantly higher in larger wildflower plots. The BSI values were also positively correlated with the density of predaceous insects, further supporting the role of these insects in natural aphid regulation (Costamagna & Landis, 2007). Calculations for BSI are dependent on growth of aphid populations enclosed in a cage of fine mesh. We designed this portion of the study based on the results of Gardiner *et al*. (2009) and Fox *et al*. (2004), who both gained insights by comparing open and mesh cage populations of aphids. While mesh cages can increase temperature and humidity, which may affect aphid populations (Luck *et al*., 1988), these effects are often either minor (Chambers *et al*., 1983; Fox *et al*., 2004) or insignificant (Brosius *et al*., 2007). In spite of those previous reports, we cannot rule out that cage effects influenced aphid growth or survival, potentially affecting the calculated BSI values.

As wildflower plot size increased, so did the total number of flowers per plot, and it has been shown that this is positively correlated with an increase in the level of biological control, particularly parasitism of pest herbivores (Scheid *et al*., 2011).

Green lacewing larvae and *Orius* spp. are voracious predators of aphids, and their observed increase with wildflower plot size in this study is an additional explanation for the increase in biological control of soybean aphids as planting size increased. From these results, we suggest that providing beneficial insects with larger habitats with densely flowering resources will result in significantly higher densities of natural enemies and subsequently greater pest control within those habitats than provided by small wildflower plots or mown, grass-dominated areas. Hence, larger wildflower plots are more suitable for the conservation of beneficial insects and the natural pest control they provide.

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Wildflower plantings may also provide resources for insect herbivores, with the wildflower plantings supporting a significantly higher diversity (but not abundance) of groups of insect herbivores compared with the control areas. The relative density of insect herbivores increased with wildflower plot size in this study. This result supports the predictions of the resource concentration hypothesis (Root, 1973) and is similar to previous studies in which herbivore density increased with host patch size (Thompson, 1978; Raupp & Denno, 1979). Conversely, other studies have found that herbivore densities do not differ with habitat patch size (Maguire, 1983; Bach, 1988a; Grez & Gonzalez, 1995). These conflicting results may stem from the various sizes and compositions of patches studied, as well as the different organisms observed. Natural enemy retention time is greater in habitats with more abundant prey resources (Vos *et al*., 1998; Seagraves, 2009), but we did not detect a significant increase in herbivore density among plot sizes. The presence of flowers is likely a more important contributing factor. This is supported by our analysis of the 2009 data where there were no wildflowers in the size plots and we found no difference in the density of open aphid colonies across wildflower plot size. Subsequently, in 2010, in the presence of wildflowers, aphid control was observed on open soybean plants and was significantly higher in the larger plantings.

Beneficial insect abundance and diversity are declining in a variety of landscapes as a result of habitat loss and agricultural intensification (Goverde *et al*., 2002; Carvell *et al*., 2006). Hence, the natural ecosystem services these insects provide are also at risk of decline (Kremen *et al*., 2002; Luck *et al*., 2003). In order to support diverse populations of beneficial insect species in agricultural landscapes that may be able to disperse into crop fields for suppression of pests, it is critical to first understand how beneficial insects and their functions respond to the size of habitat comprised of supportive plants. While our study was not designed to determine a specific size of wildflower habitat needed to conserve beneficial insects, we can conclude that natural enemies and their provision of natural control of herbivores are sensitive to the size of wildflower plantings, even at a relatively small scale. The largest wildflower planting tested in this study was comparatively small in terms of the scale of habitat plantings being established on farms for beneficial insect conservation (EU, 2005; NRCS, 2010), so future examination of larger habitat patches would help illuminate the response of natural enemies to broader ranges of habitat patch size.

Conservation of a wide range of beneficial insects is important for providing ecosystem services in agricultural settings (Landis *et al*., 2000; Kleijn & Sutherland, 2003; Bianchi *et al*., 2006). If wildflower plantings are to be used to deliver ecosystem services to crop fields it is essential to determine the optimal plot size and configuration (Brosi *et al*., 2008). Beyond patches of wildflowers, the complexity of the surrounding landscape may also affect local insect diversity in agricultural systems (Tschamtke *et al*., 2002), whereas small-scale habitat manipulation may only attract and concentrate natural enemies that are already present in the surrounding landscape (Gurr *et al*., 1998). Therefore, future studies should address the combined influence of landscape context and habitat planting size on the distribution and dispersal of beneficial insects to and from crop fields in agricultural landscapes.

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