Environmental Entomology, 48(6), 2019, 1469–1480
doi: 10.1093/ee/nvz134
Advance Access Publication Date: 8 November 2019
Research

OXFORD

Plant-Insect Interactions

Screening Drought-Tolerant Native Plants for Attractiveness to Arthropod Natural Enemies in the U.S. Great Lakes Region

Daniel R. Gibson,[1,2,4] Logan Rowe,[1,3] Rufus Isaacs,[1] and Douglas A. Landis[1]

[1]Department of Entomology, Michigan State University, Center for Integrated Plant Systems, 578 Wilson Road, East Lansing, MI 48824, [2]Jensen Ecology, 3240 Commercial Avenue, Madison, WI 53714, [3]Michigan Natural Features Inventory, Michigan State University Extension, 525 W. Allegan Street, Lansing, MI 48933, and [4]Corresponding author, e-mail: gibso124@msu.edu

Subject Editor: Christopher Ranger

Received 24 July 2019; Editorial decision 17 October 2019

Abstract

Arthropods provide a variety of critical ecosystem services in agricultural landscapes; however, agricultural intensification can reduce insect abundance and diversity. Designing and managing habitats to enhance beneficial insects requires the identification of effective insectary plants that attract natural enemies and provide floral resources. We tested the attractiveness of 54 plant species with tolerance to dry soils, contrasting perennial forbs and shrubs native to the Great Lakes region to selected non-native species in three common garden experiments in Michigan during 2015–2016. Overall, we found 32 species that attracted significantly more natural enemies than associated controls. Among these, *Achillea millefolium* and *Solidago juncea* were consistently among the most attractive plants at all three sites, followed by *Solidago speciosa, Coreopsis tripteris*, *Solidago nemoralis*, *Pycnanthemum pilosum*, and *Symphyotrichum oolantangiense*. Species which attracted significantly more natural enemies at two sites included: *Asclepias syriaca, Asclepias tuberosa, Monarda fistulosa, Oligoneuron rigidum, Pycnanthemum virginianum, Dasiphora fruticosa, Ratibida pinnata, Asclepias verticillata, Monarda punctata, Echinacea purpurea, Helianthus occidentalis, Silphium integrifolium, Silphium terebinthinaceum, Helianthus strumosus, and Symphyotrichum sericeum.* Two non-native species, *Lotus corniculatus,* and *Centaurea stoebe*, were also attractive at multiple sites but less so than co-blooming native species. Parasitic Hymenoptera were the most abundant natural enemies, followed by predatory Coleoptera and Hemiptera, while Hemiptera (Aphidae, Miridae, and Tingidae) were the most abundant herbivores. Collectively, these plant species can provide floral resources over the entire growing season and should be considered as potential insectary plants in future habitat management efforts.

Key words: beneficial arthropod, biological control-parasitoid & predator, habitat management, natural enemy

Beneficial arthropods provide a variety of ecosystem services in agricultural landscapes and sustaining their populations is crucial for sustainable agricultural systems. Arthropods are valued for providing pollination services, decomposition, and natural pest suppression (Losey and Vaughan 2006, Noriega et al. 2018) and they also form the food base for higher trophic levels (Schowalter et al. 2018, Stanton et al. 2018). However, these services to agriculture are threatened due to a decline in the diversity and abundance of arthropods in these landscapes. Reports of insect biomass declines in agricultural landscapes over recent decades have raised awareness of the problem (Hallmann et al. 2017) and prompted calls for action (Habel et al. 2019). Land-use change, comprised of both habitat loss through conversion to other land uses (e.g., urbanization) and landscape simplification due to agricultural intensification, filters species traits, reducing insect biodiversity (Gámez-Virués et al. 2015) and is considered a leading driver of insect declines globally (Habel et al. 2019). There is an increasing need to design and manage agricultural landscapes to support multiple ecosystem services (Landis 2017, Schulte et al. 2017, Kremen and Merenlender 2018).

Predators and parasitoids (natural enemies) of herbivorous insects provide a key service to agriculture via natural suppression of crop pests, and there is a long history of efforts to conserve their populations in agricultural landscapes (e.g., Thomas et al. 1991, Settle et al. 1996). Conservation biological control seeks to modify cultural or chemical management practices to decrease natural enemy mortality or actively provide resources to enhance their effectiveness (Barbosa 1998). Increasingly, habitat management is used as a specific type of conservation biological control in which the landscape is altered to provide plant-based shelter, prey or other food resources needed by natural enemies (Landis et al. 2000, Gurr et al. 2017). One form of habitat management is the provision of flowering insectary plants that attract natural enemies and provide pollen and nectar resources to enhance their longevity and fecundity (Pickett and Bugg 1998, Parolin et al. 2012, Van Rijn et al. 2013).

Plant species vary greatly in their attractiveness as well as the quality, quantity, and accessibility of floral resources for natural enemies (Patt et al. 1997, Van Rijn et al. 2013). Herbivores may also benefit from intentionally provisioned resource habitats (Zhao et al. 1992, Chaplin-Kramer et al. 2011, Letourneau et al. 2011, Walton and Isaacs 2011, Balzan et al. 2014) requiring efforts to identify species that provide resources to natural enemies but do not favor pests (Baggen et al. 1999, Fiedler and Landis 2007a). Knowledge of where particular crops are produced, the target pests, and how floral resources influence their important enemies is required to successfully implement habitat management (Lavandero et al. 2006). Thus, efforts to enhance natural enemies must be tailored to each new system (Batary et al. 2011).

Procedures for selecting plants for habitat management purposes vary significantly. Many studies simply rely on previous literature to inform the choice of plants to be tested. This has resulted in the repeated use of a small number of primarily annual and frequently non-native plant species in habitat management studies (Fiedler et al. 2008). An alternative approach promoted by Isaacs et al. (2009) is to select species from a region's perennial native flora which have the benefits of being locally adapted, potentially provide more permanent year-round habitat and may help to restore native biodiversity. Screening of potential insectary plants typically occurs in common garden settings (Fiedler and Landis 2007a, Frank et al. 2008, Rodríguez et al. 2018, Lundin et al. 2019), or by contrasting natural enemies attracted to existing plants in the relevant crop settings (James et al. 2014, Retallack et al. 2019).

Prior research by Fiedler and Landis (2007a) examined Michigan native perennial plants adapted for growth on mesic soils for their attractiveness to natural enemies. Overall, they identified 23 species that were highly attractive to natural enemies and as a group provided continuous floral resources over the entire growing season. Moreover, many of these species were also attractive to pollinators (Tuell et al. 2008) making them useful in multipurpose plantings (Collins et al. 2002; Blaauw and Isaacs 2014, 2015; Schulte et al. 2017). However, because much of the fruit and vegetable production in the Great Lakes Region occurs on coarse-textured soils and periods of extended drought are becoming more common in this region (Pryor et al. 2013, Tomasek et al. 2017), we focused our current study on plant species adapted to dry soil conditions. The overall objective of the current study was to compare the relative attractiveness of selected native flowering perennial plants and develop lists of drought-tolerant plants that are highly attractive to natural enemies of crop pests while supporting fewer herbivores. Specifically, we intended to identify 1) which plant species perform better than associated controls at supporting natural enemies while limiting herbivores, and 2) determine the relative attractiveness of flowering plant species to natural enemies and herbivores and site-level variability in attractiveness.

Materials and Methods

Study Sites

We selected three experimental sites representing a latitudinal gradient in west Michigan: Southwest Michigan Research and Extension Center (SWMREC), Berrien County, MI (42° 5′2.19″N, 86°21′12.70″W), Clarksville Research Center (CRC), Ionia County, MI (42°52′14.44″N, 85°15′23.07″W), and Northwest Michigan Horticultural Research Center (NWMHRC), Leelanau County, MI (44°53′2.55″N, 85°40′33.61″W) (see Supp Fig. S1, Supp Table S1 [online only] for additional information). At each site, test plants were established in common gardens planted on 9 June, 2 June, and 16 June 2014 at SWMREC, CRC, and NWMHRC, respectively. At SWMREC and CRC, the plants were established in agricultural fields seeded in early June with a mixture of turf grasses (Earth Carpet Quick-2-Gro, Lacrosse Seed, Lansing, MI) at a rate of 2.44 kg per 100 m^2. This created a uniform matrix in which to embed plots which could be easily managed via periodic mowing. At NWMHRC, we created plots within a previously established grassy area by applying herbicide to individual plots (Roundup Weed & Grass Killer, Monsanto Company, St. Louis, MO). Each common garden was laid out in a randomized complete block design with four replicates. Individual plant species were planted into 1 × 1 m plots arranged in a grid with a spacing of 5 m between plots. Plants were transplanted as seedlings at a density of 3 plants per plot. These plots were mulched with hardwood bark mulch and watered immediately after planting. In each block, two types of control treatments were established to evaluate background levels of plant attractiveness. A 1 × 1 m 'grass control' plot was delineated in the mowed portion of the grassy matrix in each block and a second 'weedy control' consisted of a 1 × 1 m plot that was left unplanted and unmulched allowing natural recruitment of plant species from the seed bank. During the establishment year (2014) the SWMREC and NWMHRC gardens received additional irrigation at a rate of 1 inch per week after factoring in natural rainfall, while CRC was irrigated only once, during the week of initial planting. No irrigation was applied to any site in 2015 or 2016.

Plant Selection

We selected a total of 54 species of flowering plants for screening using the following criteria: 1) perennial or self-seeding biennial, 2) adapted to growth on dry sandy soils, and 3) commercially available (Table 1). Species were also selected so that in combination they would provide continuous floral resources throughout the growing season (May–October). To assemble the list of candidate plants we consulted with members of the Michigan Native Plant Producers Association and the Michigan Commercial Beekeepers Association. The majority of the plants selected were herbaceous perennial forbs, although one biennial, *Oenothera biennis*, and four flowering shrubs, *Ceanothus americanus*, *Hypericum prolificum*, *Rosa carolina*, and *Rhus copallinum*, were included. All species were native to Michigan, with the exception of *Centaurea stoebe* and *Lotus corniculatus*, which were suggested as potentially important pollinator-supportive plants by the Michigan Commercial Beekeepers Association. Although *C. stoebe* is a noxious weed in Michigan and seeds are prohibited for sale (Michigan Department of Agriculture and Rural Development 2019), it was included for comparison as it is widespread in the state and commercial beekeepers consider it an essential mid-summer nectar source. Fifteen species screened here were also tested by Fiedler and Landis (2007a), allowing comparison with the results of this earlier study. Plant species taxonomy corresponds with the USDA Plants Database (USDA, NRCS 2019).

Native plants were primarily Michigan genotypes obtained from Wildtype Design and Seeds, Mason, MI, and Hidden Savanna Nursery, Kalamazoo, MI. *Pycnanthemum pilosum* was sourced from Prairie Moon Nursery, Winona, MN. Due to limited supply, *P. pilosum* was planted only at SWMREC and NWMHRC. The

Table 1. List of flowering plant species selected for screening to determine attractiveness to insect natural enemies and herbivores

Plant species
Achillea millefolium L. (Asterales: Asteraceae)
Amorpha canescens Pursh (Fabales: Fabaceae)[a]
Asclepias syriaca L. (Gentianales: Asclepiadaceae)
Asclepias tuberosa L. (Gentianales: Asclepiadaceae)[a]
Asclepias verticillata L. (Gentianales: Asclepiadaceae)
Baptisia alba (L.) Vent. var. *macrophylla* (Larisey) Isely (Fabales: Fabaceae)
Campanula rotundifolia L. (Asterales: Campanulaceae)
Ceanothus americanus L. (Rosales: Rhamnaceae)[a,b]
Centaurea stoebe L. ssp. *micranthos* (Gugler) Hayek (Asterales: Asteraceae)[c,d]
Chamerion angustifolium (L.) Holub ssp. *angustifolium* (Myrtales: Onagraceae)
Coreopsis lanceolata L. (Asterales: Asteraceae)[a]
Coreopsis palmata Nutt. (Asterales: Asteraceae)
Coreopsis tripteris L. (Asterales: Asteraceae)
Dalea purpurea Vent. (Fabales: Fabaceae)
Dasiphora fruticosa (L.) Rydb. (Rosales: Rosaceae)[a]
Echinacea purpurea (L.) Moench (Asterales: Asteraceae)
Eryngium yuccifolium Michx. (Apiales: Apiaceae)
Helianthus occidentalis Riddell (Asterales: Asteraceae)
Helianthus strumosus L. (Asterales: Asteraceae)
Heuchera richardsonii R. Br. (Saxifragales: Saxifragaceae)[a]
Hieracium gronovii L. (Asterales: Asteraceae)
Hypericum prolificum L. (Malpighiales: Clusiaceae)[b]
Lespedeza capitata Michx. (Fabales: Fabaceae)
Lespedeza hirta (L.) Hornem. (Fabales: Fabaceae)[a]
Liatris aspera Michx. (Asterales: Asteraceae)[a]
Liatris cylindracea Michx. (Asterales: Asteraceae)
Lotus corniculatus L. (Fabales: Fabaceae)[c,d]
Lupinus perennis L. (Fabales: Fabaceae)
Monarda fistulosa L. (Lamiales: Lamiaceae)
Monarda punctata L. (Lamiales: Lamiaceae)[a]
Oenothera biennis L. (Myrtales: Onagraceae)[a,e]
Oenothera fruticosa L. (Myrtales: Onagraceae)
Oligoneuron rigidum (L.) Small (Asterales: Asteraceae)
Packera obovata (Muhl. ex Willd.) W.A. Weber & Á. Löve (Asterales: Asteraceae)[a]
Penstemon digitalis Nutt. ex Sims (Lamiales: Plantaginaceae)
Penstemon hirsutus (L.) Willd. (Lamiales: Plantaginaceae)[a]
Potentilla arguta Pursh (Rosales: Rosaceae)
Potentilla simplex Michx. (Rosales: Rosaceae)
Pycnanthemum pilosum (Michx.) Pers. var. *pilosum* (Nutt.) Cooper. (Lamiales: Lamiaceae)[c]
Pycnanthemum virginianum (L.) T. Dur. & B.D. Jacks. ex B.L. Rob. & Fernald (Lamiales: Lamiaceae)[c]
Ratibida pinnata (Vent.) Barnhart (Asterales: Asteraceae)[a]
Rhus copallinum L. (Sapindales: Anacardiaceae)[b]
Rosa carolina L. (Rosales: Rosaceae)[b]
Rudbeckia hirta L. (Asterales: Asteraceae)
Silphium integrifolium Michx. (Asterales: Asteraceae)
Silphium terebinthinaceum Jacq. (Asterales: Asteraceae)
Solidago juncea Aiton (Asterales: Asteraceae)
Solidago nemoralis Aiton (Asterales: Asteraceae)
Solidago speciosa Nutt. (Asterales: Asteraceae)[a]
Symphyotrichum oolentangiense (Riddell) G.L. Nesom (Asterales: Asteraceae)
Symphyotrichum sericeum (Vent.) G.L. Nesom (Asterales: Asteraceae)
Tephrosia virginiana (L.) Pers. (Fabales: Fabaceae)
Tradescantia ohiensis Raf. (Commelinales: Commelinaceae)
Verbena stricta Vent. (Lamiales: Verbenaceae)[a]

All species are herbaceous perennials native to Michigan unless otherwise noted. Scientific names are standardized according to the USDA Plants database (https://plants.usda.gov, 1 June 2018).

[a]Species previously tested in Fiedler 2007.

[b]Woody shrub.

[c]Species recommended by the Michigan Commercial Beekeepers Association.

[d]Species not native to Michigan or North America.

[e]Biennial herbaceous species.

non-natives *C. stoebe* and *L. corniculatus* were transplanted from wild-growing local populations. All plots were hand-weeded periodically each season and the grass matrix was mowed regularly to maintain a turf-like background without competing floral resources. Plots at CRC and NWMHRC were re-mulched for weed control in 2016.

Flower Phenology

All plots were monitored weekly from first flowering in mid-May through last flowering in early October 2015 and 2016, and each plant species was sampled during its full bloom period at each site. We defined 'full bloom' as the three consecutive weeks of highest counts of open flowers at a site, and 'peak bloom' as the single week of highest open flower counts at that site.

Arthropod Collection

In 2015 and 2016, we sampled weekly between 0900 and 1400 hours EST on days meeting the following criteria: temperature ≥ 15.5°C, wind speed ≤ 15 km/h, and sunny to partially overcast skies. Arthropods were collected using a modified leaf blower (Model BG 55, Stihl, Norfolk, VA) with the intake reversed and a 3.75 l fine mesh strainer bag (Cary Company, Addison, IL) placed over distal end of the vacuum tube to catch insects as they were suctioned off the plant. We vacuumed flowers and associated foliage in each 1 × 1 m plot until all flowers had been sampled. We then froze the samples and later identified contents to order (Aranae and Opiliones), major taxonomic group (parasitoid wasps), or family (all other insects). Arachnids were identified to class level in 2015, and to order in 2016. Similarly, parasitoid wasps were combined in 2015, and identified to family or superfamily in 2016. Due to time constraints, we enumerated Hemiptera: Auchenorrhyncha and Thysanoptera (except predaceous species in Aeolothripidae and Plaeothripidae) using abundance categories; '0' = 0, '1' = 1–15, '2' = 15 – 50, and '3' = 50+ individuals per sample. We grouped taxa as natural enemies or herbivores based on the broad trophic patterns of each family.

Statistical Analysis

Analyses were conducted in R v. 3.2.2 'Fire Safety' (R Core Team 2015). Results from the three different locations were analyzed separately. Means of total natural enemies and total herbivores for each plant species were compared to control means using one-tailed t-tests with Welch's approximation for unequal variances. The relevant control means for each plant species varied with its bloom period and were calculated as the mean of all mowed grass control samples collected during the full bloom period of that species at that site. We selected the mowed grass controls as the relevant comparison because plant recruitment into weedy control plots was highly inconsistent both within and among sites, and because farmers will typically mow grassy areas around crop fields. The field used at SWMREC was previously planted with a cover crop of hairy vetch (*Vicia villosa* Roth), and the seedbank caused this species to dominate the weedy control plots along with nut sedge (*Cyperus* *rotundus* L.). At CRC, the plots were dominated by the turfgrass mixture seeded in the surrounding matrix and had few nectar resources. The dominant weeds at NWMHRC were *Centaurea stoebe* and *Achillea millefolium*.

While plants and natural enemies were sampled in both years; here we primarily focus on 2016 results. Previous research demonstrated that attractiveness to natural enemies is highly influenced by total floral area and relative plant phenology (Fiedler and Landis 2007b), but in 2015, plants were still establishing and were typically not full-sized. In addition, for some species, their bloom period was delayed compared to well-established plants. Focusing on 2016 results allows us to represent natural enemy attractiveness for well-established plants blooming in their normal phenological order and timing. For ease of display in the figures, we only show the top 20 most attractive plant species at each site, regardless of whether they were significantly different from their respective controls. Some plant species not shown also attracted significantly more natural enemies than their associated control. Full data for both years are provided in the supplemental information (Supp Fig. S2–S7 [online only]).

Results

Plant Establishment and Bloom Periods

Most of the plant species selected for testing established well and collectively provided continuous bloom from late May through early October. Of the 54 species tested, a total of 53 plant species bloomed at one or more sites. *Tephrosia virginiana*, (a subshrub) established at all sites but failed to bloom during the first 2 yr. Other species that did not bloom at individual sites included: *Potentilla arguta* and *R. copallinum* at NWMHRC, and *Lupinus perennis* at CRC, so these species were not considered in further analysis.

At all three sites, at least two plant species were in full bloom every week from mid-May to early October (Table 2). The timing of first and full bloom for individual species typically followed a south-to-north pattern. For example, *Penstemon hirsutus* reached full bloom in the last week of May at SWMREC, the first week of June at CRC, and the second week of June at NWMHRC. Although bloom duration was similar for most plant species across sites, there was variation among sites in both the onset of bloom and timing relative to other species. At all sites, the suite of plants selected provided a consistently overlapping supply of floral resources throughout the season.

Natural Enemy Abundance

We collected a total of 20,675 natural enemies in 2015 and 17,154 in 2016 (Table 3). In both years, parasitic Hymenoptera represented the dominant taxa accounting for 41.8 and 33.8% of total captures in 2015 and 2016, respectively. Coleoptera were the next most abundant taxa and were dominated by Cantharidae, which accounted for 21.9 and 20.5% of the total captures in the 2 yr. Hemiptera were nearly as abundant as Coleoptera and were dominated by the Anthocoridae, which accounted for 22.0 and 20.8% of the total captures in the 2 yr. Arachinida accounted for 10.6 to 14.7% of the total captures, while predatory Thysanoptera, Neuroptera, and Diptera comprised less than 2% of the total yearly capture of natural enemies in both years. Sites varied in the overall mean abundance of natural enemies visiting plants, with NWMHRC having the lowest average number of natural enemies per m^2 followed by SWMREC and CRC (Fig. 1A–C). Site-specific totals are available in Supp Table S2 [online only].

In 2016, a total of 32 plant species were significantly more attractive to natural enemies than their associated grass controls at one or more sites (Table 4). Species that were attractive at all three sites include (in order of bloom): *Achillea millefolium*, *L. corniculatus*, *Monarda fistulosa*, *Solidago nemoralis*, *Pycnanthemum virginianum*, *Dasiphora fruticosa*, *Asclepias verticillata*, *Solidago juncea*, *Coreopsis tripteris*, *Helianthus strumosus*, and *Symphyotrichum sericeum*. Species that were attractive at two sites include: *Asclepias syriaca*, *Asclepias tuberosa*, *Ratibida pinnata*, *C. stoebe*, *Monarda punctata*, *Echinacea purpurea*, *P. pilosum*, *Helianthus occidentalis*, *Silphium integrifolium*, *Silphium terebinthinaceum*, *Oligoneuron rigidum*, and *Solidago speciosa*. Finally, those species that were significantly more attractive at only one site included: *Potentilla simplex*, *Rudbeckia hirta*, *Coreopsis palmata*, *Verbena stricta*, *Chamerion angustifolium*, *Eryngium yuccifolium*, *Dalea purpurea*, *H. prolificum*, and *Symphyotrichum oolentangiense*.

Many of the most attractive plant species were broadly similar across sites; however, some notable differences were found (Fig. 1A–C). At NWMHRC the top five most attractive plants in bloom order were; *A. millefolium*, *S. nemoralis*, *P. pilosum*, *S. juncea*, and *O. rigidum* (Fig. 1A), while at CRC; *A. millefolium*, *S. juncea*, *C. tripteris*, *S. oolentangiense*, and *S. speciosa* comprised the top five (Fig. 1B), and at SWMREC; *A. millefolium*, *S. juncea*, *C. tripteris*, *O. rigidum*, and *S. speciosa* (Fig. 1C).

Sites also varied in the number of plant species that were significantly more attractive than their associated grass control and in seasonal patterns of natural enemy taxa they attracted. At NWMHRC, all 20 of the most attractive plant species were significantly more attractive than their respective mown grass controls (Welch's t-test, $\alpha = 0.05$) (Fig. 1A), owing in part to the overall low arthropod abundance in controls at that site. Mean natural enemies per m^2 ranged from 3.8 ± 1.5 SE for *Oenothera fruticosa* and 3.8 ± 0.8 SE for *D. fruticosa* to 34.0 ± 9.1 SE for *O. rigidum*. At this site, early blooming plants attracted primarily Hymenoptera, midseason plants primarily Coleoptera, and late season plants were dominated by Hemiptera (with the notable exception of *O. rigidum*). At CRC, all but one of the 20 most attractive plants were significantly more attractive than the control (Welch's *t*-test, $\alpha = 0.05$) (Fig. 1B). Mean natural enemies per m^2 ranged from 9.0 ± 1.8 SE for *R. hirta* to 103.9 ± 44.4 for *S. speciosa*. Early-season plants again attracted primarily Hymenoptera, with the midseason shift towards Coleoptera occurring earlier than at NWMHRC. Of the 20 plant species most attractive to natural enemies at SWMREC, 14 were significantly more attractive than their associated controls (Welch's *t*-test, $\alpha = 0.05$) (Fig. 1C). Mean natural enemies per m^2 ranged from 6.9 ± 1.8 SE for *C. palmata* to 92.3 ± 29.2 for *O. rigidum*. At this site, Hymenoptera tended to dominate the natural enemy community early on through the middle of the season, while Hemiptera were relatively abundant throughout the season and Coleoptera abundant in the mid-and late season.

Of the two non-native species selected for testing by beekeepers, *L. corniculatus* was consistently among the top 20 plants at each site, attracting primarily Hymenoptera (Fig. 1). In contrast, while *C. stoebe* attracted significantly more natural enemies than its respective control at two sites, it was not among the top 20 most attractive plants at any sites.

Herbivore Abundance

We collected a total of 21,284 herbivores in 2015 and 29,723 in 2016 (Table 5). In both years, Miridae represented the dominant taxa, accounting for 46.1 and 50.4% of total captures in

Table 2. Bloom phenology for all plant species tested for their attractiveness to natural enemies in 2016

	Bloom duration																				
Plant species		May				June				July				Aug.				Sept.			Oct.
Early Season																					
Packera obovata	–	*	*	*	–																
Potentilla simplex	–	*	*	*	–																
Lupinus perennis	–	–	*	*	*																
Penstemon hirsutus		–	–	*	*	*	–														
Heuchera richardsonii			–	*	*	*	–														
Coreopsis lanceolata			–	*	*	*	–	–													
Tradescantia ohiensis			–	–	*	*	*	–													
Baptisia alba var. macrophylla				–	*	*	*	–													
Penstemon digitalis				–	*	*	*	–	–												
Rosa carolina					–	*	*	*	–												
Lotus corniculatus				–	–	*	*	*	–	–	–	–	–								
Oenothera fruticosa					–	*	*	*	–	–											
Achillea millefolium				–	–	*	*	*	–	–											
Asclepias syriaca					–	*	*	*	–	–	–										
Ceanothus americanus					–	–	*	*	*	–											
Asclepias tuberosa						–	–	*	*	–	–										
Potentilla arguta					–	–	*	*	*	–											
Mid Season																					
Rudbeckia hirta					–	–		*	*	*	–	–									
Campanula rotundifolia						–	–	*	*	*	–	–									
Amorpha canescens						–	–	*	*	*	–	–									
Coreopsis palmata							–	*	*	*	–	–									
Hypericum prolificum							–	*	*	*	–	–	–								
Monarda fistulosa								–	*	*	*	–	–	–							
Hieracium gronovii							–	–	*	*	*	–									
Pycnanthemum virginianum							–	–	*	*	*	–	–								
Verbena stricta							–	–	*	*	*	–	–								
Chamerion angustifolium									–	*	*	*	–	–	–						
Centaurea stoebe micranthos								–	–	*	*	*	–	–	–						
Solidago nemoralis									–	*	*	*	–	–	–						
Asclepias verticillata								–	–	*	*	*	–	–	–						
Dalea purpurea									–	*	*	*	–	–							
Ratibida pinnata									–	*	*	*	–	–							
Silphium laciniatum									–	–	*	*	*	–	–						
Echinacea purpurea								–	–	–	*	*	*	–	–						
Liatris cylindracea										–	*	*	*	–							
Pycnanthemum pilosum									–	–	*	*	*	–							
Eryngium yuccifolium										–	*	*	*	–							
Helianthus occidentalis										–	–	*	*	*	–						
Late Season																					
Solidago juncea											–	*	*	*	–						
Silphium integrifolium									–	–	–	*	*	*	–	–					
Silphium terebinthinaceum									–	–	–	*	*	*	–	–	–				
Rhus copallinum												–	*	*	*						
Lespedeza hirta												–	*	*	*	–					
Lespedeza capitata													–	*	*	*	–				
Coreopsis tripteris										–	–	–	–	*	*	*	–	–			
Dasiphora fruticosa										–	–	–	–	–	*	*	*	–			
Helianthus strumosus										–	–	–	–	–	*	*	*	–			
Liatris aspera													–	–	*	*	*	–			
Oenothera biennis												–	–	–	*	*	*	–			
Oligoneuron rigidum													–	–	*	*	*	–	–		
Symphyotrichum sericeum															–	*	*	*	–		
Solidago speciosa																	–	*	*	*	–
Symphyotrichum oolen-tangiense																	–	*	*	*	–

Asterisks indicate the 3 wk of full bloom averaged across replicate plots at three sites in Michigan, and dashes indicate additional weeks in which the plants were blooming. The plants are listed in order of bloom.

Table 3. Overall counts and percent of total captures for natural enemy taxa identified from vacuum collections made at individual plots of flowering plant species during 2015–2016[a]

Taxa	2015		2016	
	Count	Percent	Count	Percent
Arachnida	2,195	10.6%		
Aranae	-	-	2,446	14.3%
Opiliones	-	-	85	0.5%
Hemiptera				
Anthocoridae	4,366	21.1%	3,338	19.5%
Nabidae	158	0.8%	159	0.9%
Reduviidae	33	0.2%	47	0.3%
Geocoridae	-	-	182	1.1%
Thysanoptera				
Aeolothripidae	-	-	324	1.9%
Phlaeothripidae	-	-	51	0.3%
Neuroptera				
Chrysopidae	96	0.5%	139	0.8%
Hemerobiidae	14	0.1%	27	0.2%
Coleoptera				
Cantharidae	4,518	21.9%	3,512	20.5%
Carabidae	23	0.1%	20	0.1%
Coccinellidae	115	0.6%	263	1.5%
Diptera				
Syrphidae	183	0.9%	113	0.7%
Tachinidae	14	0.1%	27	0.2%
Bombyliidae	13	0.1%	2	0.0%
Dolichopodidae	-	-	323	1.9%
Empididae	-	-	23	0.1%
Hymenoptera				
'Parasitica'	8,633	41.8%	-	-
Ichneumonidae	-	-	79	0.5%
Braconidae	-	-	979	5.7%
Chalcidoidea	-	-	4,266	24.9%
Cynipoidea	-	-	470	2.7%
Sphecidoidea	5	0.0%	1	0.0%
Tiphiidae	296	1.4%	270	1.6%
Vespidae	13	0.1%	8	0.0%
Total	20,675	100.0%	17,154	100.0%

Dashes in 2015 indicate taxa that were not counted or were included in higher classification.
[a]This includes insects collected on weedy and mowed grass controls.

2015–2016, respectively. Tingidae were the next most abundant taxa comprising 32.6% of the total herbivores in 2015 and 14.4% in 2016. In 2015, just over 85% of the Tingidae were collected from a single plant species (*S. sericeum*) at a single site (CRC) suggesting a localized outbreak. Seed bugs (Hemiptera: Rhyparochromidae) were not counted in 2015 but represented over 8% of total herbivores in 2016. Lepidoptera consistently contributed 2.2–2.4% of the total herbivores in 2015 and 2016, respectively and Scarabaeidae 2.6% in 2016, while no other taxa exceeded 2% of the total. Sites varied in the overall mean abundance of herbivores visiting plants, with NWMHRC generally having the lowest average number of herbivores per m^2 followed by CRC and SWMREC (Fig. 2A–C). Site-specific totals are available in Supp Table S2 [online only].

Some plant species attracted large numbers of both natural enemies and herbivores, e.g., *S. nemoralis* and *O. rigidum* at NWMHRC, *S. oolentangiense* at CRC, and to a lesser extent *S. speciosa* at SWMREC (Figs. 1 and 2). In contrast, other plants that consistently attracted large numbers of natural enemies tended to attract few herbivores, e.g., *A. millefolium* and *C. tripteris*. Finally, several species of plants that were only modestly attractive to natural enemies attracted large numbers of herbivores, including *L. corniculatus* and *S. sericeum* (2 of 3 locations). The seasonal pattern of attractiveness to herbivores also varied by site. While Miridae generally comprised the bulk of the herbivores collected on plants throughout the season at both NWMHRC and SWMREC, at CRC other Hemiptera were often equally as abundant throughout the season. One of the few plants that consistently supported significant aphid abundance was the exotic legume *L. corniculatus* (Fig. 2A–C).

Discussion

The suite of plants we tested provided consistent and overlapping floral resources that were highly attractive to natural enemy taxa from mid-May through early October. Fifty-three of the 54 species we tested in this study bloomed at one or more sites and were thus available for comparisons of their attractiveness to natural enemies. Of these, *A. millefolium* and *S. juncea* were consistently among the most attractive plants at all three sites, followed by *O. rigidum*, *S. speciosa*, and *C. tripteris* which were among the top five most attractive plants at two sites, and *S. nemoralis*, *P. pilosum*, *S. oolantangiense* at one site each. The two non-native species, *L. corniculatus* and *C. stoebe*, while frequently attractive to natural enemies,

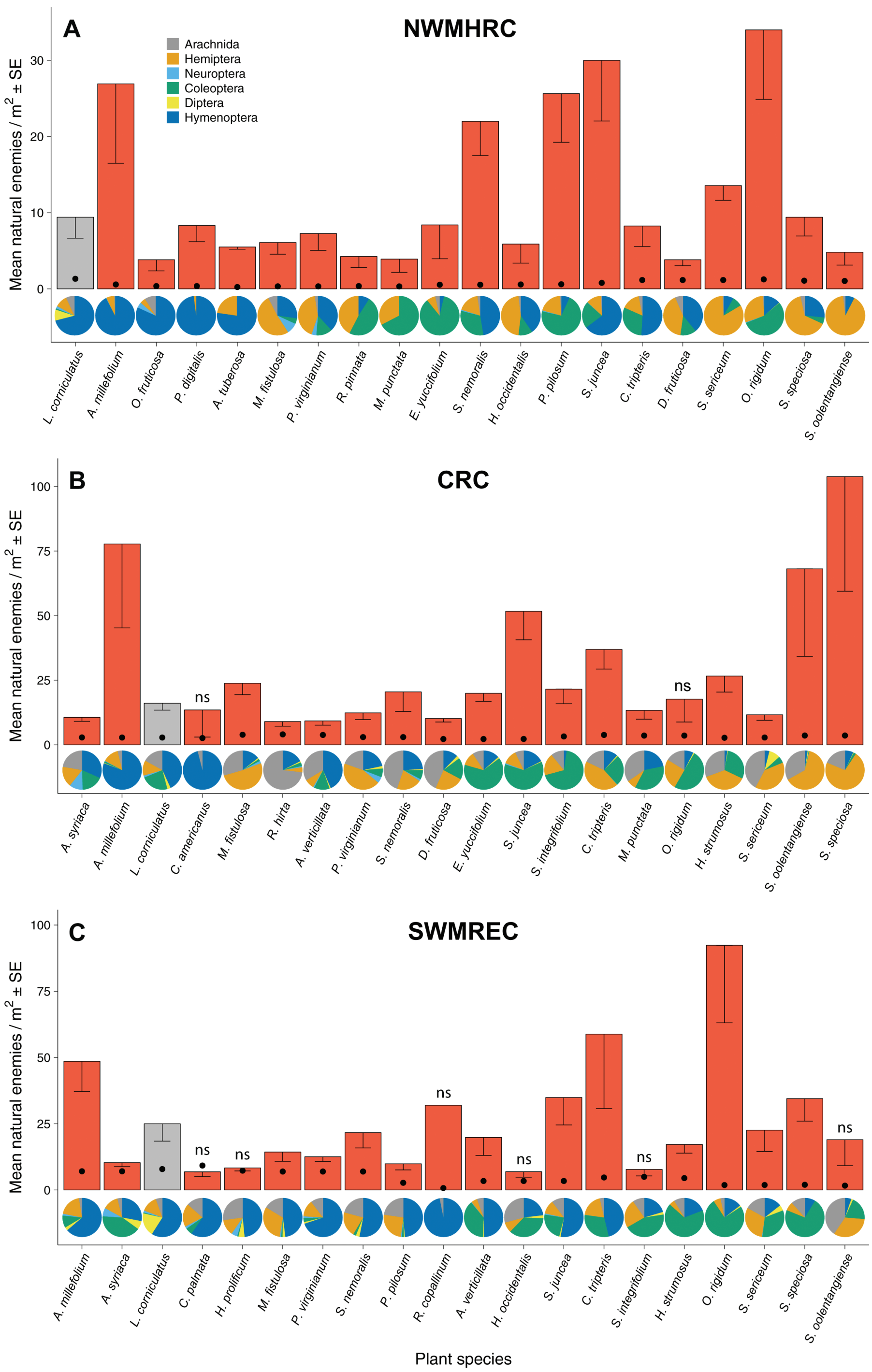

Fig. 1. Mean natural enemy counts and community composition of the 20 most attractive plant species at three research sites; NWMHRC (A), CRC (B), and SWMREC (C) in 2016. Plant species are arranged chronologically by bloom time. Error bars indicate standard error, and black dots indicate the mean natural enemy count of the mowed grass control during peak bloom of each species. Pie charts display the relative natural enemy community composition by taxon. All means are significantly greater than the mowed control unless otherwise noted. Red bars indicate native species, gray bars indicate non-native species.

were often less attractive than native species blooming at the same time (Fig. 1), suggesting that native alternatives to these exotic invasive species are available. While comparable studies are relatively rare, it is notable that research in California also identified *A. millefolium* as a highly attractive plant to natural enemies (Lundin et al. 2019). Similarly, a study in Maryland showed that *M. punctata* was consistently highly attractive to natural enemies (Frank et al. 2008). This suggests that these widely distributed species might have broad applicability across the United States as insectary plants.

Several plants that were only moderately attractive to natural enemies in this experiment also likely have potential value as insectary plants. For example, *D. fruticosa* and *S. terebinthinaceum* are notable for their extended bloom periods which attracted natural enemies for 9 wk from July to September (Table 2). Thus, their utility

Table 4. List of flowering plant species that were significantly more attractive than mowed grass control at one or more sites in 2016

Scientific Name	SWMREC	CRC	NWMHRC
Achillea millefolium	*	*	*
Lotus corniculatus[a]	*	*	*
Monarda fistulosa	*	*	*
Solidago nemoralis	*	*	*
Pycnanthemum virginianum	*	*	*
Dasiphora fruticosa[b]	*	*	*
Asclepias verticillata	*	*	*
Solidago juncea	*	*	*
Coreopsis tripteris	*	*	*
Helianthus strumosus	*	*	*
Symphyotrichum sericeum	*	*	*
Asclepias syriaca		*	*
Asclepias tuberosa[b]		*	*
Ratibida pinnata[b]		*	*
Centaurea stoebe micranthos[a]		*	*
Monarda punctata[b]		*	*
Echinacea purpurea		*	*
Pycnanthemum pilosum	*		*
Helianthus occidentalis		*	*
Silphium integrifolium		*	*
Silphium terebinthinaceum		*	*
Oligoneuron rigidum	*		*
Solidago speciosa		*	*
Potentilla simplex		*	
Rudbeckia hirta		*	
Coreopsis palmata			*
Verbena stricta			*
Chamerion angustifolium			*
Eryngium yuccifolium		*	
Dalea purpurea			*
Hypericum prolificum			*
Symphyotrichum oolentangiense			*

An asterisk indicates a significant difference using a one-tailed Welch's *t*-test, ($\alpha = 0.05$).

[a]Species not native to North America.

[b]Species previously tested in Fiedler 2007.

as insectary plants may be greater when considering their contribution over the entire growing season. Both the shrubs *C. americanus* and *R. copallinum* attracted low numbers of natural enemies but were also not fully mature during this study. These shrubs were less than 1 m tall and had small floral displays unrepresentative of mature plants of these species. Land managers may still wish to consider the potential long-term benefits of including shrubs in insectary planting design, for structural diversity as well as the high densities of flowers possible on these plants (e.g., Mach and Potter 2018).

Our study also documents the potential for plant species to vary in attractiveness when growing under differing soil conditions and floral communities. Our current test list (Table 1) contains 15 plant species that were previously tested by Fiedler and Landis (2007a) at a site with mesic soils and a differing test species list. Of these, five were relatively unattractive to natural enemies in both tests including; *Amorpha canesens*, *C. americanus*, *Lespedeza hirta*, *Liatris aspera*, and *Packera obovata*, while six were moderately to highly attractive in both tests including: *D. fruticosa*, *H. strumosus*, *M. punctata*, *R. pinnata*, *S. speciosa*, and *V. stricta*. One species, *A. tuberosa*, was notably more attractive in the current test, while three species were relatively less attractive than in the prior study, including; *Coreopsis lanceolata* L., *O. biennis*, and *P. hirsutus*. Of these, the most dramatic change being *C. lanceolata,* which was highly attractive in the 2007 study but was not significantly more attractive than its control at any site in the current study. Finally, both studies used mowed turfgrass as the matrix on which to display test plant species and as the habitat sampled for temporally relevant background populations of natural enemies. Natural enemies were consistently present in low abundance in these mowed grass controls suggesting even mowed turf provides some useful resources (potentially foraging or resting habitat). While multiple factors vary between the two studies, these findings suggest that testing candidate plants under a variety of conditions may be necessary to reveal their potential as insectary plants in areas with different environments. It also further supports the typical guidelines for including a diversity of species in plantings designed for insect conservation, to increase the likelihood that there will be a well-established plant community (Sheley and Half 2006).

The types of natural enemies attracted to test plants and their relative effectiveness in controlling targeted pests is ultimately another important factor in plant selection. In both years of the study, parasitic Hymenoptera were the most abundant natural enemy sampled and were dominated by Braconid and Chalcidoid wasps. While braconids are mostly beneficial parasitoids of herbivores, many chalcids are hyperparasitoids and may interfere with effective biological control. Tiphiid wasps, which were identified separately from other parasitoids, parasitize beetle larvae in the superfamily Scarabaeoidea. Two species, *Tiphia popilliavora* Rohwer and *T. vernalis* Rohwer, have been introduced from Asia to control the Japanese beetle (*Popillia japonica* Newman) (King and Holloway 1930, Ramoutar and Legrand 2007). Coleoptera were the next most abundant taxa and dominated by Cantharid beetles. Larvae of cantharid beetles are ground-dwelling predators that consume primarily soft-bodied insects while the adults, which feed on pollen and nectar, are frequently seen at flowers in the late summer (Stugard 1931). The most common coccinellid species collected were *Harmonia axyridis* Pallas and *Coleomegilla maculata* DeG., both known to consume aphids and other small soft-bodied herbivores. Although coccinellids were relatively infrequent in our samples (Table 3) they can have a strong controlling effect (Woltz and Landis 2013) due to their voracious consumption of prey in both the larval and adult stages. Finally, equally as abundant as Cantharids were minute pirate bugs (Hemiptera: Anthocoridae). Anthocorids were present throughout the season and are predators of aphids and other soft-bodied insects and mites, contributing to natural biological control.

The herbivores attracted to our plots represented a mixture of species of agricultural importance as well as miscellaneous herbivores, which are not considered pests. Mirids were the dominant herbivore collected and these can be pests in a variety of cropping systems. In particular, tarnished plant bug (*Lygus lineolaris* Palisot de Beauvois) is a well-known pest of many horticultural crops (Easterbrook 2000) and was often abundant. Aphids were most abundant on the exotic legume *Lotus corniculatus*. While not identified to species, it is possible that these aphids could also be pests in alfalfa and other legume crops. The Pentatomids included a variety of stink bug species, notably the brown marmorated stink bug (*Halyomorpha halys* Stål), which is an agricultural pest (Leskey and Nielsen 2018). Among the other herbivores, the Japanese beetle is probably the most significant pest that can cross over to other crops, including soybeans, grapes, blueberries, and raspberries (Potter and Held 2002). Individual plant species, while attractive to natural enemies, may not be suitable for use in all agricultural systems if they are also attractive to key pests.

Insectary plants are typically deployed in agricultural settings to attract and sustain natural enemy communities and provide pest suppression in adjacent crops (Gurr et al. 2017). Though the

Table 5. Overall counts and percent of total captures for herbivore taxa identified from 2015 to 2016 vacuum samples from flowering plants[a]

Taxa	2015		2016	
	Count	Percent	Count	Percent
Orthoptera	552	2.6%	346	1.16%
Hemiptera				
Aphidae	2,697	12.7%	3,652	12.29%
Auchenorrhyncha	**	**	**	n/a
Miridae	9,815	46.1%	14,987	50.42%
Pentatomidae	165	0.8%	454	1.53%
Tingidae[b]	6,949	32.6%	4,271	14.37%
Rhyparochromidae	-	-	2384	8.02%
Thysanoptera	-	-	**	n/a
Coleoptera				
Cerambicidae	36	0.2%	20	0.07%
Chrysomelidae	225	1.1%	469	1.58%
Curculionidae	211	1.0%	394	1.33%
Elateridae	6	0.0%	32	0.11%
Scarabaeidae	169	0.8%	757	2.55%
Popillia japonica	133	0.6%	556	1.87%
Cetonia aurata	-	-	124	0.42%
Nitidulidae	-	-	574	1.93%
Stelidota geminata	-	-	0	0.00%
Lepidoptera	459	2.2%	703	2.37%
Total	21,284	100%	29,723	100.00%

Dashes in 2015 indicate taxa that were not counted or were included in higher classification.
[a]This includes insects collected on weedy and mowed grass controls.
[b]Of the 2015 total, 6,930 were collected at CRC and 5,907 on *Symphyotrichum sericeum*.

magnitude of those effects was not a focus of this study, other experiments using some of the same plant species in the same region have demonstrated that plots attracting a greater density of predaceous natural enemies also have greater levels of biological control of sentinel soybean aphids (Blaauw and Isaacs 2012). Wildflower plantings established at commercial farms and seeded with a community of plant species selected from the earlier screening research of Fiedler and Landis (2007b) were also found to increase natural enemies in adjacent crop fields, with an associated increase in predation of sentinel caterpillar eggs (Blaauw and Isaacs 2015). Wildflower strips to enhance insect conservation have been widely studied in Europe (Haaland et al. 2011). Successful suppression of crop pests has been demonstrated suggesting that when carefully implemented the use of resource providing plants can support increased biological control in some settings (Tschumi et al. 2015, 2016; Pollier et al. 2019).

While this study is one of the largest screenings of insectary plants ever conducted, there are limitations that should be acknowledged. The sampling methodology we used likely underestimates the abundance of certain taxa. Collecting during the middle of the day undoubtedly resulted in an underrepresentation of crepuscular and nocturnal taxa, such as adult Chrysopidae, which are less likely to be found at flowers during the day. The vacuum collection method is effective and does little physical damage to the plant (in contrast to sweep netting), but it tends to bias the sample toward less mobile insects and against agile fliers that are easily disturbed (e.g., large dipterans and hymenopterans, lepidopteran adults). Sampling efficiency also depends on the growth form of the sampled plant. Short, compact species (e.g., *A. verticillata*) can be sampled quickly, providing less time for agile flying insects to escape. Conversely, sampling very large, tall species such as *C. tripteris* requires more time and moves other stems before they are vacuumed, making it difficult to capture easily disturbed insects. The structure of the plant also affected how much foliage was sampled in addition to the flowers. For example, sampling the ground-hugging species *L. corniculatus* and *P. simplex* requires vacuuming the majority of the foliage as well. Acknowledging the potential limitations, vacuum sampling is an effective method to sample floral visitors that has been used previously in studies of insectary plants (Fiedler and Landis 2007a, Bennett and Gratton 2013, Lundin et al. 2019). Finally, while we measured attractiveness of insect taxa to flowers, we did not quantify utilization of nectar or pollen resources. Additional experiments at finer scales of diversity and observation as well as analyses of pollen and nectar supply and quality can refine our understanding of the use and nutritional value of plant species for attracting beneficial insects.

We anticipate that these results can be used to inform seed mix guidelines for insectary plantings across the Great Lakes region and even more broadly. For example, based on a prior study (Fiedler and Landis 2007a), Gill et al. (2014) selected subsets of attractive plants and tested them in Iowa. They found that plots established from plants previously selected for their attractiveness were significantly better than existing conservation habitats and attracted more natural enemies than treatments containing single species or prairie restoration mixtures. The next step for improving habitat management with these native plants will be to establish mixed plantings in different regional agroecosystem contexts. Plantings established adjacent to different crops and using the plant species highlighted in this study will enable functional studies of biological control of key pests (and the potential for enhancing herbivores) by measuring variables such as pest populations, parasitism rates, crop damage, and yield. Furthermore, plant community composition may also be tailored to specific crops by identifying which flowering plant species are most beneficial in the context of a specific set of pests and natural enemies. The biology of important pest-enemy relationships may also inform management of the insectary habitat, such as mowing the habitat at

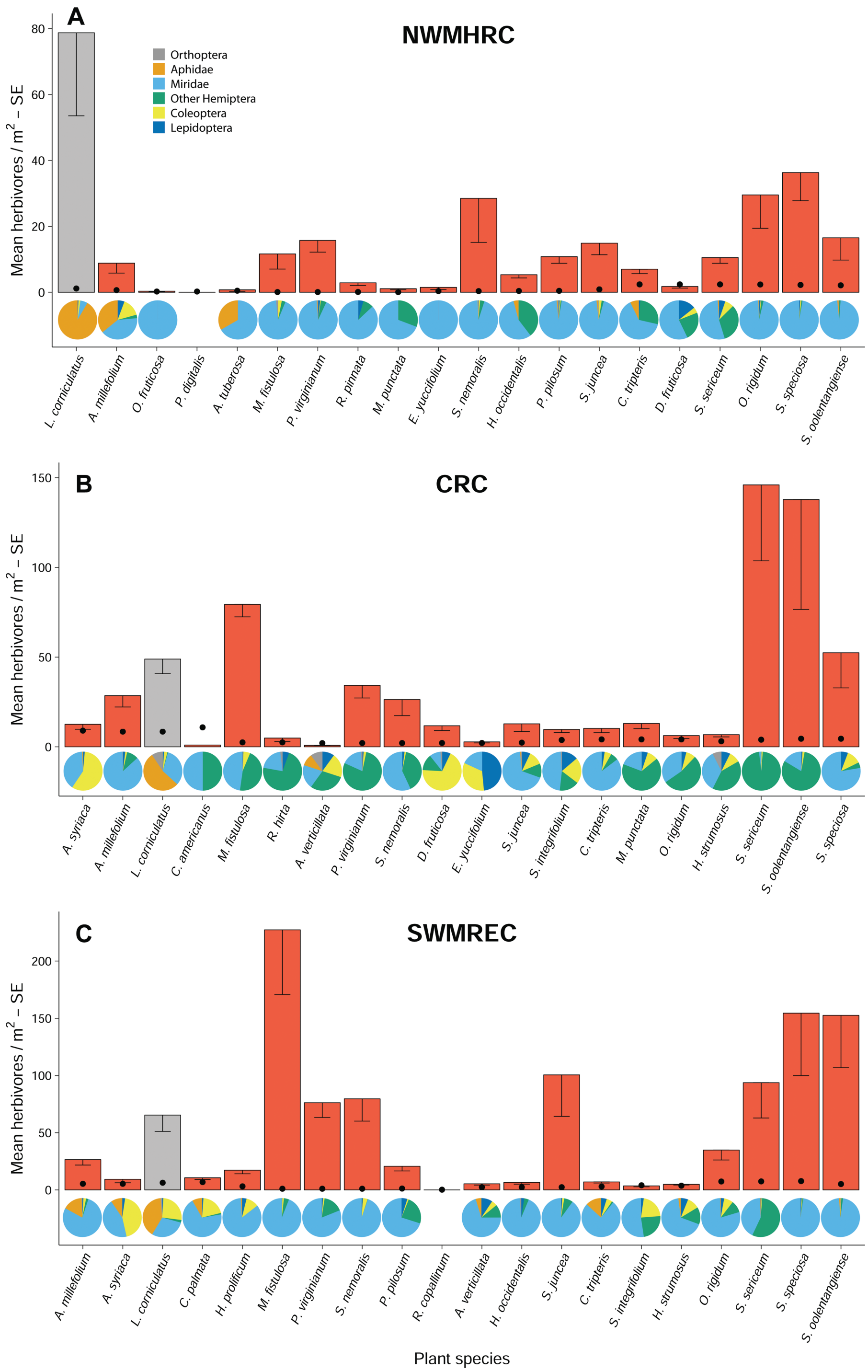

Fig. 2. Mean herbivore counts and community composition of the 20 plant species most attractive to herbivores at three research sites; NWMHRC (A), CRC (B), and SWMREC (C) in 2016. Plant species are arranged chronologically by bloom time. Error bars indicate standard error, and black dots indicate the mean herbivore count of the mowed grass control during peak bloom of each species. Pie charts display the relative herbivore community composition by taxon. Red bars indicate native species, gray bars indicate non-native species.

a strategic time to force natural enemies to forage within the crop fields.

Beyond providing resources for natural enemies, insectary plants can also be used to support other ecosystem services to agriculture as well as biodiversity for its own sake. For example, the plants screened here were simultaneously evaluated for their attractiveness to pollinators and many species ranked highly for natural enemies also attracted a wide diversity of managed and wild bees (Rowe et al. 2018). Carefully selected insectary plants deployed in association with pollination-dependent crops can increase yields and pay for the habitat installation and maintenance in as little as 4 yr (Blaauw and Isaacs 2014). Moreover, insectary plantings can enhance activity of biological control agents in adjacent fields (Morandin et al. 2014) and also contribute to overall biological diversity (Ponisio et al. 2016, Schulte et al. 2016) and functional trait diversity which is critical to overall resiliency of agricultural systems (Liebman and Schulte 2015, Wood et al. 2015).

By increasing the number of insectary plant species tested in our region and by focusing on plant species adapted to dry soils, the results of this study expand the palette of resource plants that can be considered for conserving natural enemies and pollinators (Rowe et al. 2018). The ability of these plants to perform in dry soils is advantageous for many settings in fruit and vegetable farms and it may become increasingly important if the frequency of summer drought increases as anticipated in many future climate models (Pryor et al. 2013, Tomasek et al. 2017). By supporting ecosystem services in a variety of cropping systems and environmental conditions, insectary plants are poised to become an important tool in increasing the resilience of agricultural landscapes.

Supplementary Data

Supplementary data are available at *Environmental Entomology* online.

Acknowledgments

Bill Schneider of Wildtype Nursery and Chad Hughson of Hidden Savanna Nursery provided valuable plant selection advice and much of the plant material used in this study. We also thank the Michigan Commercial Beekeepers Association for their guidance on plant selection. Farm managers Dave Francis (SWMREC), Jerry Skeltis and Dan Platte (CRC), and Bill Klein (NWMHRC) and their staff assisted in maintenance of the research plantings. Christie Bahlai was of great help in statistical analysis. Thanks to Julia Perrone, Nathaniel Walton, Marguerite Bolt, Katie Manning, Michael Killewald, Gabe King, Lindsey Hawkins, Jessica Kalin, Erin Forster, and Marissa Tucker. Funding was provided by the United States Department of Agriculture Sustainable Agriculture Research and Education Program (USDA-SARE) (NCR13-075), Michigan State University Project GREEEN (GR14-011), and Michigan State University AgBioResearch. D.R.G. also acknowledges degree completion fellowship support from Michigan State University College of Agriculture and Natural Resources. Voucher specimens have been deposited in the A.J. Cook Arthropod Research Collection at Michigan State University. Further information on these resource plants can be found at www.nativeplants.msu.edu.

References Cited

Baggen, L. R., G. M. Gurr, and A. Meats. 1999. Flowers in tri-trophic systems: mechanisms allowing selective exploitation by insect natural enemies for conservation biological control. Entomol. Exp. Appl. 91: 155–161.

Balzan, M. V., G. Bocci, and A. C. Moonen. 2014. Augmenting flower trait diversity in wildflower strips to optimise the conservation of arthropod functional groups for multiple agroecosystem services. J. Insect Conserv. 18: 713–728.

Barbosa, P. 1998. Conservation biological control. Academic Press, San Diego, CA.

Batary, P., A. Baldi, D. Kleijn, and T. Tscharntke. 2011. Landscape-moderated biodiversity effects of agri-environmental management: a meta-analysis. Proc. R. Soc. B Biol. Sci. 278: 1894–1902.

Bennett, A. B., and C. Gratton. 2013. Floral diversity increases beneficial arthropod richness and decreases variability in arthropod community composition. Ecol. Appl. 23: 86–95.

Blaauw, B. R., and R. Isaacs. 2012. Larger wildflower plantings increase natural enemy density, diversity, and biological control of sentinel prey, without increasing herbivore density. Ecol. Entomol. 37: 386–394.

Blaauw, B. R., and R. Isaacs. 2014. Flower plantings increase wild bee abundance and the pollination services provided to a pollination-dependent crop. J. Appl. Ecol. 51: 890–898.

Blaauw, B. R., and R. Isaacs. 2015. Wildflower plantings enhance the abundance of natural enemies in adjacent blueberry fields. Biol. Control 91: 94–103.

Chaplin-Kramer, R., M. E. O'Rourke, E. J. Blitzer, and C. Kremen. 2011. A meta-analysis of crop pest and natural enemy response to landscape complexity. Ecol. Lett. 14: 922–932.

Collins, K. L., N. D. Boatman, A. Wilcox, J. M. Holland, and K. Chaney. 2002. The influence of beetle banks on aphid population predation in winter wheat. Agric. Ecosyst. Environ. 93: 337–350.

Easterbrook, M. A. 2000. Relationships between the occurrence of misshapen fruit on late-season strawberry in the United Kingdom and infestation by insects, particularly the European tarnished plant bug, *Lygus rugulipennis*. Entomol. Exp. Appl. 96: 59–67.

Fiedler, A. K., and D. Landis. 2007a. Attractiveness of Michigan native plants to arthropod natural enemies and herbivores. Environ. Entomol. 36: 751–765.

Fiedler, A. K., and D. Landis. 2007b. Plant characteristics associated with natural enemy abundance at Michigan native plants. Environ. Entomol. 36: 878–886.

Fiedler, A. K., D. Landis, and S. D. Wratten. 2008. Maximizing ecosystem services from conservation biological control: the role of habitat management. Biol. Control 45: 254–271.

Frank, S. D., P. M. Shrewsbury, and O. Esiekpe. 2008. Spatial and temporal variation in natural enemy assemblages on Maryland native plant species. Environ. Entomol. 37: 478–486.

Gámez-Virués, S., D. J. Perović, M. M. Gossner, C. Börschig, N. Blüthgen, H. De Jong, N. K. Simons, A. M. Klein, J. Krauss, G. Maier, *et al*. 2015. Landscape simplification filters species traits and drives biotic homogenization. Nat. Commun. 6: 8568.

Gill, K. A., R. Cox, and M. E. O'Neal. 2014. Quality over quantity: buffer strips can be improved with select native plant species. Environ. Entomol. 43: 298–311.

Gurr, G. M., S. D. Wratten, D. A. Landis, and M. You. 2017. Habitat management to suppress pest populations: progress and prospects. Annu. Rev. Entomol. 62: 91–109.

Haaland, C., R. E. Naisbit, and L.-F. Bersier. 2011. Sown wildflower strips for insect conservation: a review. Insect Conserv. Divers. 40: 60–80.

Habel, J. C., M. J. Samways, and T. Schmitt. 2019. Mitigating the precipitous decline of terrestrial European insects: requirements for a new strategy. Biodivers. Conserv. 28: 1343–1360.

Hallmann, C. A., M. Sorg, E. Jongejans, H. Siepel, N. Hofland, H. Schwan, W. Stenmans, A. Müller, H. Sumser, T. Hörren, *et al*. 2017. More than 75 percent decline over 27 years in total flying insect biomass in protected areas. PLoS One 12: e0185809.

Isaacs, R., J. K. Tuell, A. K. Fiedler, M. M. Gardiner, and D. Landis. 2009. Maximizing arthropod-mediated ecosystem services in agricultural landscapes: the role of native plants. Front. Ecol. Environ. 7: 196–203.

James, D. G., L. Seymour, G. Lauby, and K. D. Buckley. 2014. Beneficial insects attracted to native flowering buckwheats (*Eriogonum michx*) in central Washington. Environ. Entomol. 43: 942–948.

King, J. L., and J. K. Holloway. 1930. The establishment and colonization of *Tiphia popilllavora*, a parasite of the Japanese beetle. J. Econ. Entomol. 23: 266–274.

Kremen, C., and A. M. Merenlender. 2018. Landscapes that work for biodiversity and people. Science. 362: eaau6020.

Landis, D. A. 2017. Designing agricultural landscapes for biodiversity-based ecosystem services. Basic Appl. Ecol. 18: 1–12.

Landis, D. A., S. D. Wratten, and G. M. Gurr. 2000. Habitat management to conserve natural enemies of arthropod pests. Annu. Rev. Entomol. 45: 175–201.

Lavandero, B., S. D. Wratten, R. K. Didham, and G. M. Gurr. 2006. Increasing floral diversity for selective enhancement of biological control agents: a double-edged sward? Basic Appl. Ecol. 7: 236–243.

Leskey, T. C., and A. L. Nielsen. 2018. Impact of the invasive brown marmorated stink bug in North America and Europe: history, biology, ecology, and management. Annu. Rev. Entomol. 63: 599–618.

Letourneau, D. K., I. Armbrecht, B. S. Rivera, and A. Others. **2011**. Does plant diversity benefit agroecosystems? A synthetic review. Ecol. Appl. 21: 9–21.

Liebman, M., and L. A. Schulte. 2015. Enhancing agroecosystem performance and resilience through increased diversification of landscapes and cropping systems. Elem. Sci. Anthr. 3: 000041.

Losey, J. E., and M. Vaughan. 2006. The economic value of ecological services provided by insects. Bioscience. 56: 311.

Lundin, O., K. L. Ward, and N. M. Williams. 2019. Identifying native plants for coordinated habitat management of arthropod pollinators, herbivores and natural enemies. J. Appl. Ecol. 56: 665–676.

Mach, B. M., and D. A. Potter. 2018. Quantifying bee assemblages and attractiveness of flowering woody landscape plants for urban pollinator conservation. PLoS One 13: e0208428.

Michigan Department of Agriculture and Rural Development. 2019. Michigan prohibited and restricted weeds. Available from https://www.michigan.gov/documents/mdard/Michigan_Prohibited_and_Restricted_Weeds_641413_7.pdf

Morandin, L. A., R. F. Long, and C. Kremen. 2014. Hedgerows enhance beneficial insects on adjacent tomato fields in an intensive agricultural landscape. Agric. Ecosyst. Environ. 189: 164–170.

Noriega, J. A., J. Hortal, F. M. Azcárate, M. P. Berg, N. Bonada, M. J. I. Briones, I. Del Toro, D. Goulson, S. Ibanez, D. A. Landis, *et al*. 2018. Research trends in ecosystem services provided by insects. Basic Appl. Ecol. 26: 8–23.

Parolin, P., C. Bresch, N. Desneux, R. Brun, A. Bout, R. Boll, and C. Poncet. 2012. Secondary plants used in biological control: a review. Int. J. Pest Manag. 58: 91–100.

Patt, J. M., G. C. Hamilton, and J. H. Lashomb. 1997. Foraging success of parasitoid wasps on flowers: interplay of insect morphology, floral architecture and searching behavior. Entomol. Exp. Appl. 83: 21–30.

Pickett, C. H., and R. L. Bugg. 1998. Enhancing biological control: habitat management to promote natural enemies of agricultural Pests. University of California, Berkeley, CA.

Pollier, A., Y. Tricault, M. Plantegenest, and A. Bischoff. 2019. Sowing of margin strips rich in floral resources improves herbivore control in adjacent crop fields. Agric. For. Entomol. 21: 119–129.

Ponisio, L. C., L. K. M'Gonigle, and C. Kremen. 2016. On-farm habitat restoration counters biotic homogenization in intensively managed agriculture. Glob. Chang. Biol. 22: 704–715.

Potter, D. A., and D. W. Held. 2002. Biology and management of the Japanese beetle. Annu. Rev. Entomol. 47: 175–205.

Pryor, S., R. Barthelmie, and J. Schoof. 2013. High-resolution projections of climate-related risks for the Midwestern USA. Clim. Res. 56: 61–79.

Ramoutar, D., and A. Legrand. 2007. Survey of *Tiphia vernalis* (Hymenoptera: Tiphiidae), a parasitoid wasp of *Popillia japonica* (Coleoptera: Scarabaeidae), in Connecticut. Florida Entomol. 90: 780–782.

R Core Team. 2015. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. Available from https://www.R-project.org/.

Retallack, M. J., L. J. Thomson, and M. A. Keller. 2019. Predatory arthropods associated with potential native insectary plants for Australian vineyards. Aust. J. Grape Wine Res. 25: 233–242.

Rodríguez, E., M. González, D. Paredes, M. Campos, and E. Benítez. 2018. Selecting native perennial plants for ecological intensification in Mediterranean greenhouse horticulture. Bull. Entomol. Res. 108: 694–704.

Rowe, L., D. Gibson, D. Landis, J. Gibbs, and R. Isaacs. 2018. A comparison of drought-tolerant prairie plants to support managed and wild bees in conservation programs. Environ. Entomol. 47: 1128–1142.

Schowalter, T. D., J. A. Noriega, and T. Tscharntke. 2018. Insect effects on ecosystem services—introduction. Basic Appl. Ecol. 26: 1–7.

Schulte, L. A., A. L. MacDonald, J. B. Niemi, and M. J. Helmers. 2016. Prairie strips as a mechanism to promote land sharing by birds in industrial agricultural landscapes. Agric. Ecosyst. Environ. 220: 55–63.

Schulte, L. A., J. Niemi, M. J. Helmers, M. Liebman, J. G. Arbuckle, D. E. James, R. K. Kolka, M. E. O'Neal, M. D. Tomer, J. C. Tyndall, *et al*. 2017. Prairie strips improve biodiversity and the delivery of multiple ecosystem services from corn-soybean croplands. Proc. Natl. Acad. Sci. USA 114: 11247–11252.

Settle, W. H., H. H. Ariawan, E. T. Astuti, W. Cahyana, A. L. Hakim, D. Hindayana, and A. S. Lestari. 1996. Managing tropical rice pests through conservation of generalist natural enemies and alternative prey. Ecology 77: 1975–1988.

Sheley, R. L., and M. L. Half. 2006. Enhancing native forb establishment and persistence using a rich seed mixture. Restor. Ecol. 14: 627–635.

Stanton, R. L., C. A. Morrissey, and R. G. Clark. 2018. Analysis of trends and agricultural drivers of farmland bird declines in North America: a review. Agric. Ecosyst. Environ. 254: 244–254.

Stugard, B. 1931. Biological notes on *Chauliognathus pennsylvanicus* DeGeer (Coleoptera: Cantharidae). M.S. Thesis, University of Kansas, Lawrence, KS.

Thomas, M. B., S. D. Wratten, and N. W. Sotherton. 1991. Creation of 'island' habitats in farmland to manipulate populations of beneficial arthropods: predator densities and species composition. J. Appl. Ecol. 28: 906–917.

Tomasek, B. J., M. M. Williams, and A. S. Davis. 2017. Changes in field workability and drought risk from projected climate change drive spatially variable risks in Illinois cropping systems. PLoS One 12: e0172301.

Tschumi, M., M. Albrecht, M. H. Entling, and K. Jacot. 2015. High effectiveness of tailored flower strips in reducing pests and crop plant damage. Proc. R. Soc. B. 282: 20151369.

Tschumi, M., M. Albrecht, J. Collatz, V. Dubsky, M. H. Entling, A. J. Najar-Rodriguez, K. Jacot, and D. Kleijn. 2016. Tailored flower strips promote natural enemy biodiversity and pest control in potato crops. J. Appl. Ecol. 53: 1169–1176.

Tuell, J. K., A. K. Fiedler, D. Landis, and R. Isaacs. 2008. Visitation by wild and managed bees (Hymenoptera: Apoidea) to eastern U.S. native plants for use in conservation programs. Environ. Entomol. 37: 707–718.

USDA, NRCS. 2019. The PLANTS database. National Plant Data Team, Greensboro, NC. Available from http://plants.usda.gov

Van Rijn, P. C. J., J. Kooijman, and F. L. Wäckers. 2013. The contribution of floral resources and honeydew to the performance of predatory hoverflies (Diptera: Syrphidae). Biol. Control 67: 32–38.

Walton, N. J., and R. Isaacs. 2011. Influence of native flowering plant strips on natural enemies and herbivores in adjacent blueberry fields. Environ. Entomol. 40: 697–705.

Woltz, J. M., and D. A. Landis. 2013. Coccinellid immigration to infested host patches influences suppression of *Aphis glycines* in soybean. Biol. Control 64: 330–337.

Wood, S. A., D. S. Karp, F. DeClerck, C. Kremen, S. Naeem, and C. A. Palm. 2015. Functional traits in agriculture: agrobiodiversity and ecosystem services. Trends Ecol. Evol. 30: 531–539.

Zhao, J. Z., G. S. Ayers, E. J. Grafius, and F. W. Stehr. 1992. Effects of neighboring nectar-producing plants on populations of pest Lepidoptera and their parasitoids in broccoli plantings. Gt. Lakes Entomol. 25: 253–258.