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Wild bees and natural enemies prefer similar flower species and respond to similar plant traits

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Abstract

Designing wildflower habitats to support beneficial insects providing pollination and pest control services is important for supporting sustainable crop production. It is often desirable to support both groups of insects, making the selection of resource plants for insect conservation programs more challenging. Moreover, the process of selecting resource plants is complicated by the array of possible options in each region, and the need to provide resources over the entire growing season. Identifying traits shared by resource plants that are attractive to both bees and natural enemies can reduce the need to evaluate new plants in each region, by providing a guide for the types of plants expected to be rewarding to these insects. Using insect visitation data collected from replicated common garden plantings of native wildflower and shrub species from the Great Lakes region of the United States, we found a high degree of correlation between the abundance of bees and natural enemies visiting native plant species. These results were used to identify a set of 15 plant species that can provide resources for these insects throughout the summer. Across all tested species, pollen quantity per flower and the week of bloom were positively correlated with some, but not all, taxonomic groupings of beneficial insects. In contrast, floral area was consistently positively associated with visitation of both natural enemies and wild bees. This trait is easy to document and can allow for efficient local testing of potential resource plants, providing a faster path to implementing insect conservation in working landscapes.

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Introduction

Biodiversity underpins productive agricultural systems globally by providing an array of critical ecosystem services (Bullock, Pywell, Burke, & Walker, 2001; Carvalheiro et al., 2011; Giller, Beare, Lavelle, Izac, & Swift, 1997). Among these services, many are provided by insects including pollination and pest suppression (Lavelle et al., 2006; Losey & Vaughn, 2006; Pascual et al., 2015). Loss of biodiversity has been highlighted as a global challenge to the future of agricultural sustainability (Brussaard et al., 2010; Foley et al., 2005) and is of particular concern in working landscapes where biodiversity loss has been greatest and has the potential to negatively affect food and fiber production (IPBES, 2019). Agricultural landscapes cover a high proportion of the earth's surface

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(Clay, 2004), providing significant opportunity to adapt land management to mitigate biodiversity loss and help food production to meet the growing need to feed human populations (Godfray & Garnett, 2014). Consequently, there has been great interest in understanding how to enhance productivity with conservation of beneficial organisms that support crop production (Bale, van Lenteren, & Bigler, 2008; Blicharska et al., 2019).

Flowering perennial resource plants can support multiple ecosystem services in agricultural landscapes, including pollination, natural pest suppression, carbon sequestration, and water filtration (Albrecht et al., 2020; Sidhu & Joshi, 2016; Wratten, Gillespie, Decourtye, Mader, & Desneux, 2012). Areas with these plants are incorporated on farms so that beneficial insects have access to the pollen and nectar that they need, which provides individuals with protein and carbohydrate macronutrients as well as resins and micronutrients (Tena, Wäckers, Heimpel, Urbaneja, & Pekas, 2016). Diverse agricultural landscapes that provide these resources reliably through the season via habitat complementarity and connectivity can be augmented by adding flowering habitat through seeding or planting of additional resource plants, to provide resources through the summer (Martins, Albert, Lechowicz, & Gonzalez, 2018).

Many countries have developed technical support payment and schemes to increase adoption of resource plantings across farm landscapes (Vaughn & Skinner 2008, Dicks, Vaughan, & Lee-Mader, 2016). In recent years there have been significant advances in our understanding how much land is needed to provide the desired services, where to locate this land, and how it should be arranged in farms so that the ecosystem services can be effectively delivered to crops (Garratt, Senapathi, Coston, Mortimer, & Potts, 2017; Sardinas & Kremen, 2015). Syntheses of studies that evaluated conservation plantings on farms to support beneficial insects indicate that plant species diversity is important for achieving conservation goals (Albrecht et al., 2020; Tscharntke, Klein, Kruess, Steffan-Dewenter, & Thies, 2005). By providing a rich community of plant species, insect conservation plantings on farms can support diverse insect communities, although the majority of responding bee species may be the more common ones that also provide most of the ecosystem services rather than rare species that are of more acute conservation concern (Kleijn et al., 2015). Wildflower plantings may also attract pest insects that use particular flowering species (McCabe, Loeb, & Grab, 2017), requiring an understanding of the pest complex before applying this approach for enhancing crops.

Adding habitat for beneficial insects in working landscapes has generally been achieved through sowing seeds in fallow fields or areas with soils too poor for crops, set-aside areas of farms, or via strips alongside or through crop fields. Using annual plants can provide flexibility and inexpensive seed for this approach (Carreck & Williams, 2002). However, there are some important benefits to using perennial plants that, once established, will provide many years of regrowth and flowering (Isaacs, Tuell, Fiedler, Gardiner, & Landis, 2009). Over the past decade, our research program has evaluated 80 native perennial plant species from the Great Lakes region of the United States for their attraction of bees (Tuell, Fiedler, Landis, & Isaacs, 2008, Rowe *et al.* 2019) and insect natural enemies (Fiedler & Landis, 2007; Gibson, Rowe, Isaacs, & Landis, 2019), identifying the most suitable options for use in insect conservation programs. The earlier studies focused on plants suitable for mesic soils but with increasing periods of summer drought occurring due to climate change, we have more recently evaluated plants able to thrive in drier soils. This is likely to be increasingly important for the persistence of resource plantings, so they are resilient to variable environmental conditions (Upton, Bach, & Hofmockel, 2018).

Insect conservation plantings will be more effective and economical if they contain plants that can reliably provide abundantly available resources for multiple types of beneficial insects. However, repeated testing to identify plants that can support different insect groups is time-consuming and costly. Our studies in Michigan, and similar projects in California (Lundin, Ward, & Williams, 2019) and other regions (Nave, Gonçalves, Crespí, Campos, & Torres, 2016) provide research-based recommendations but they are only relevant where those plant species occur naturally and are incomplete for the local flora. Identifying traits of plants that consistently predict insect visitation could significantly reduce the cost of this research and speed the development of plant mixes with a high likelihood of achieving their goal. In previous research, we measured plant traits related to flowering including the timing of peak bloom, floral area, flower height, hue, chroma, and corolla size (Fiedler & Landis, 2007; Tuell et al., 2008), and found that floral area was a primary driver of bee abundance at the sampled plants. A similar approach is needed to examine how traits guide the plants most visited by natural enemies (Hatt, Francis, Xu, Wang, & Osawa, 2020), and to investigate whether this overlaps with the traits predicting wild bee visitation. More recently, trait measurements were expanded to include pollen and nectar measurements (Rowe et al., 2020), finding that while floral area best predicts the abundance of all wild bees, some functional groups of bees also responded to other plant traits including flower height, pollen quantity, and timing of bloom. Our focus has been mainly on traits that are easily measured and therefore accessible to many kinds of land managers although we recognize that other traits, such as plant defense chemistry, will influence insect behavior (Irwin, Adler, & Brody, 2004).

Insect natural enemies are also responsive to specific plant traits, and there is evidence that plant trait diversity affects the richness and diversity of natural enemy communities (Campbell, Biesmeijer, Varma, & Wäckers, 2012). Trait combinations will also interact with the availability of insect prey to affect predator-prey dynamics on individual plant species and in plant communities (Hatt et al., 2017; Moreira, Abdala-Roberts, Rasmann, Castagneyrol, &

Mooney, 2016). Balzan, Bocci, and Moonen (2014) manipulated flower trait diversity in wildflower plantings and increased the abundance of anthocorid predators (but not other natural enemies) and wild bees, demonstrating that diversifying traits in resource plants can support multiple types of ecosystem service providers. By identifying the natural enemies visiting individual plant species, we can use trait metrics from those plants to identify traits that consistently support natural enemies (Hatt et al., 2020). In combination with plant traits that influence bee visitation, these studies can provide practitioners with a set of measurable traits that could aid in the selection of species to include in conservation programs.

In this study, we addressed the hypothesis that native plants have correlated variation in visitation by bees and natural enemies, and that plant traits can be used to predict the most visited plants by both taxa. This was tested by analysis of results from assessing insects visiting 37 native plant species to: 1) Identify multifunctional plants that support a high abundance of both wild bees and natural enemies; 2) Determine whether abundance of wild bees visiting flowering plants is correlated with that of natural enemies; 3) Determine whether plant floral traits predict visitation by both groups of beneficial insects.

Materials and methods

Plant selection and establishment

We selected regionally-native plant species based on ability to provide nectar and pollen resources throughout the growing season, adaptation to course-textured soils with low water holding capacity, and commercial availability in our region (Table 1). Selections were made in consultation with native plant nursery owners with extensive experience in the phenology and soil characteristics suitable for species establishment and persistence. The species tested were primarily perennial forbs, though one biennial (*Oenothera biennis*) and four shrubs (*Ceanothus americanus, Hypericum prolificum, Rosa carolina, and Rhus copallinum*) were also included. Two non-native perennials, *Centaurea stoebe micranthos* and *Lotus corniculatus*, were included at the request of regional beekeepers. When possible, regional genotypes were used when procuring plant stock from nurseries.

In June 2014, we established plants in common garden fields at three agricultural research stations Berrien County (42° 5′2.19″N, 86°21′12.70″W), Ionia County (42° 52′14.44″N, 85°15′23.07″W), and Leelanau County (44° 53′2.55″N, 85°40′33.61″W), Michigan, USA. We used a randomized complete block (RCB) design at each site. Each field was arranged in a grid, with 1 m^2 single-species plots in a turfgrass matrix with 5 m spacing between plots. The 53 plant species were replicated in each of four blocks at each site, for a total of 12 replicates per plant species. Thus, there were 212 plots at each site for a total of 636 plots across the experiment. Based on prior experience and consultation with our native plant suppliers, we installed 3 plants per plot, anticipating that most species would mature to fill the plot by the third year (2016). Plots were mulched after planting and watered weekly during their first summer of growth to facilitate establishment. The plants were weeded and grew during the 2014 and 2015 seasons and in most cases filled the 1 m^2 plots during establishment. The few species in the trials that did not establish were excluded from the data analysis in this study. This study reports arthropod sampling conducted in 2016 when most species were mature and blooming in their normal phenology. During this year plots were maintained by additional mulching and hand weeding to reduce competition and prevent weeds from flowering but received no irrigation. Further details regarding plant selection and study design may be found in Rowe, Gibson, Landis, and Isaacs (2018) and Gibson et al. (2019).

Plant sampling

In late May through early October 2016, we monitored plots weekly and sampled during the bloom period of each species. Each species was sampled for all wild bees and insect natural enemies as well as for plant traits during the period of peak bloom, which was defined as the three consecutive weeks of highest counts of open flowers for each plant species.

We measured multiple floral traits for each species. Maximum floral height was measured as the tallest flower in each plot to the nearest cm. To determine total floral area, we counted the number of flowers in the plot and multiplied by the area of a single flower. In cases where flowers were too numerous and small to count individually, we averaged the number of flowers in 5 inflorescences and then counted the number of inflorescences in the plot. To calculate the average area of a flower, we photographed individual flowers, then processed the images by removing the area of the flower in Photoshop (Adobe, San Jose, CA) and measuring the area of the blank space using ImageJ (imagej.nih.gov/ij) similar to the method used by Fiedler and Landis (2007a). The areas of 5 representative flowers for each species were then averaged.

Chroma of young flowers with intact stamens was analyzed using an S2000 fiber optic spectrometer (PX2 pulsed xenon light source; Ocean Optics, Dunedin, FL), capable of determining floral reflectance in wavelengths 400–700 nm. Chroma values provide an estimate of color intensity, with lower values representing weaker colors and higher values representing vibrant colors.

The quantity of pollen produced in newly opened flowers was sampled by collecting 5, 10, or 20 individual flowers of each species and isolating pollen in the lab using the protocol outlined in Rowe et al., 2020. Prior to pollen collection, exclusion bags were placed over individual flowers or

Table 1. Wildflower species grown in single species plots from 2014−2016 at 3 distinct locations in Michigan, and the values for six traits measured on each plant species. The record number corresponds to the number for each point in Fig. 2. Flower chroma and Pollen per plot were determined using data from subsamples and plot level standard errors are not recorded.

Record number	Family	Scientific name	Season	Floral area (cm^2) ± SE	Flower height (cm)± SE	Flower chroma	Pollen per plot (grains)	Peak bloom (week)± SE
1	Asteraceae	*Achillea millefolium*	Early	1729.40 ± 211.07	63.55 ± 2.53	0.05	1810,874.15	27.00 ± 0.21
2	Asclepiadaceae	*Asclepias syriaca*	Early	643.16 ± 103.07	92.72 ± 1.91	0.15	1797.10	27.06 ± 0.21
3	Asclepiadaceae	*Asclepias tuberosa*	Early	1228.44 ± 170.87	51.90 ± 1.62	0.48	7319.64	27.83 ± 0.17
4	Asteraceae	*Coreopsis lanceolata*	Early	902.02 ± 113.88	58.46 ± 1.56	0.46	717,043.27	25.71 ± 0.22
5	Plantaginaceae	*Penstemon digitalis*	Early	179.55 ± 28.44	69.91 ± 2.04	0.02	14,848.63	26.32 ± 0.21
6	Onagraceae	*Oenothera fruticosa*	Early	287.36 ± 40.07	48.70 ± 2.36	0.30	38,930.43	26.96 ± 0.26
7	Plantaginaceae	*Penstemon hirsutus*	Early	843.98 ± 110.71	44.71 ± 0.95	0.11	132,154.61	25.00 ± 0.21
8	Commelinaceae	*Tradescantia ohiensis*	early	676.65 + 66.85	75.48 ± 2.64	0.27	240,418.68	26.03 ± 0.21
9	Fabaceae	*Baptisia lactea*[1]	early	67.98 ± 13.79	63.33 ± 4.73	0.01	239,906.52	26.08 ± 0.23
10	Asteraceae	*Solidago nemoralis*	middle	1222.37 ± 436.82	94.65 ± 2.87	0.47	1694,667.01	31.38 ± 0.34
11	Lamiaceae	*Monarda fistulosa*	middle	2208.41 ± 292.67	115.79 ± 1.97	0.12	142,244.81	29.67 ± 0.16
12	Lamiaceae	*Pycnanthemum virginianum*	middle	904.49 ± 111.26	78.61 ± 1.14	0.06	116,790.67	30.40 ± 0.18
13	Apiaceae	*Eryngium yuccifolium*	middle	190.36 ± 21.53	100.97 ± 2.36	0.08	153,988.52	32.62 ± 0.16
14	Asclepiadaceae	*Asclepias verticillata*	middle	266.47 ± 42.09	62.94 ± 1.55	0.10	3776.80	31.59 ± 0.35
15	Asteraceae	*Rudbeckia hirta*	middle	2285.13 ± 188.87	61.95 ± 1.78	0.54	677,294.94	28.61 ± 0.17
16	Asteraceae	*Ratibida pinnata*	middle	1020.68 ± 153.17	115.41 ± 2.00	0.42	1036,292.11	31.64 ± 0.19
17	Lamiaceae	*Monarda punctata*	middle	123.78 ± 26.45	46.87 ± 1.90	0.10	76,339.47	32.89 ± 0.36
18	Asteraceae	*Coreopsis palmata*	middle	450.42 ± 74.50	75.34 ± 2.62	0.46	96,234.17	28.96 ± 0.24
19	Asteraceae	*Echinacea purpurea*	middle	704.04 ± 104.83	79.92 ± 3.91	0.25	297,854.25	32.53 ± 0.26
20	Fabaceae	*Dalea purpurea*	middle	105.29 ± 19.33	67.42 ± 2.00	0.31	4141.63	31.59 ± 0.28
21	Clusiaceae	*Hypericum prolificum*	middle	304.94 ± 29.14	81.98 ± 1.96	0.33	1234,133.33	29.42 ± 0.16
22	Campanulaceae	*Campanula rotundifolia*	middle	93.34 ± 19.95	43.47 ± 3.29	0.14	22,697.84	28.72 ± 0.25
23	Asteraceae	*Liatris cylindracea*	middle	55.58 ± 8.67	37.62 ± 2.97	0.29	45,204.48	32.48 ± 0.17
24	Asteraceae	*Hieracium gronovii*	middle	18.86 ± 3.12	53.79 ± 2.32	0.32	9244.80	30.29 ± 0.57
25	Onagraceae	*Chamerion angustifolium*	middle	46.84 ± 9.58	53.64 ± 6.60	0.18	9605.06	31.27 ± 0.60
26	Asteraceae	*Coreopsis tripteris*	late	3565.43 ± 512.14	185.89 ± 5.32	0.41	1996,656.27	35.67 ± 0.32
27	Asteraceae	*Solidago juncea*	late	55.39 ± 8.69	110.35 ± 2.91	0.48	492,745.49	33.39 ± 0.17
28	Asteraceae	*Solidago speciosa*	late	751.12 ± 127.54	116.66 ± 4.59	0.45	719,526.57	39.82 ± 0.22
29	Asteraceae	*Symphyotrichum oolentangiense*	late	424.36 ± 91.95	65.64 ± 4.10	0.12	310,802.69	39.80 ± 0.23
30	Asteraceae	*Symphyotrichum sericeum*	late	524.28 ± 82.30	44.84 ± 2.26	0.27	117,643.63	37.66 ± 0.17
31	Asteraceae	*Helianthus strumosus*	late	1259.83 ± 194.06	111.50 ± 3.87	0.47	778,215.72	36.26 ± 0.25
32	Asteraceae	*Silphium integrifolium*	late	1079.58 ± 115.09	156.08 ± 3.91	0.41	450,613.33	33.67 ± 0.25
33	Asteraceae	*Helianthus occidentalis*	late	780.88 ± 108.71	90.66 ± 3.62	0.50	830,448.30	33.03 ± 0.15
34	Rosaceae	*Dasiphora fruticosa*	late	285.83 ± 43.28	48.06 ± 1.32	0.42	795,023.38	36.03 ± 0.38
35	Asteraceae	*Silphium terebinthinaceum*	late	248.17 ± 34.05	171.34 ± 7.93	0.48	282,121.41	34.41 ± 0.17
36	Asteraceae	*Silphium laciniatum*	late	242.40 ± 0.0	172.00 ± 0.0	0.45	158,940.00	32.00 ± 0.0
37	Asteraceae	*Liatris aspera*	late	216.88 ± 40.51	60.28 ± 3.14	0.26	69,729.15	36.35 ± 0.16

[1] This species is formerly known as *Baptisia alba* var. *macrophylla*.

Table 2. Statistical analysis of the relationship between measured plant traits on native perennial wildflower plant species and the abundance of different beneficial insect groups.

Insect Group	Flower Traits (z-transformed)									
	Floral area (cm^2)		Flower height (cm)		Flower chroma		Pollen quantity		Week of peak bloom	
	$F_{1,31}$	P	$F_{1,31}$	P	$F_{1,31}$	P	$F_{1,31}$	P	$F_{1,31}$	P
Natural Enemies	**16.75**	**<0.001**	1.89	0.179	0.80	0.377	**8.45**	**0.007**	**13.01**	**0.001**
Predators	**16.24**	**<0.001**	**6.03**	**0.020**	0.001	0.973	**5.13**	**0.031**	**28.42**	**<0.001**
Parasitoids	**15.48**	**<0.001**	0.42	0.522	2.51	0.123	**12.11**	**0.002**	0.56	0.459
Wild bees	**31.03**	**<0.001**	**7.26**	**0.011**	0.11	0.748	1.30	0.263	**7.56**	**0.010**

inflorescences to prevent visitation by foraging insects. For each flower, we removed all pollen-bearing stamens, placed material in a 60% ethanol solution, and used a pestle and mortar to carefully dislodge pollen. After isolation, pollen was placed in a known volume of liquid (50 μl of a 60% ethanol solution) and homogenized, then a 5 μl subsample of this mixture was placed on a slide and the individual pollen grains were counted. We then calculated the total number of grains per flower and extrapolated this information to the plot level. This process was done 5 times and then averaged for each species using plant materials from the Ionia County site.

Arthropod sampling

Arthropods were sampled from species in peak bloom which was on the same day as, or occasionally 1−2 days after, plant sampling. Samples were collected between 0900 and 1400 h on days with minimal cloud cover, winds less than 5 m/s, and temperatures above 15.5 °C.

Pollinator sampling consisted of two 2.5 min. observation periods, one in the morning and one in the afternoon, at each plot each week. These two periods were then combined for analysis as a single 5 min. period/plot/week. With 4 replicates per site this totals 20 min of sampling per plant species/week. All wild bees visiting flowers in the plot were collected using a handheld vacuum (model: 2820GA, Bioquip Products Inc., Rancho Domingo, CA). This method caused minimal disturbance to other bees visiting the plant. Honey bee (*Apis mellifera*) visits were recorded, but specimens were not collected (see Rowe et al., 2018 for honey bee abundances). All bee specimens were identified to species, or, in rare instances, to the lowest possible taxonomic level using current keys (Coelho, 2004; Gibbs, Packer, Dumesh, & Danforth, 2013; LaBerge, 1967; LaBerge, 1969; LaBerge, 1971; LaBerge, 1980; LaBerge, 1989; Stephen, 1952; Williams, Thorp, Richardson, & Colla, 2014, www.discoverlife.org) and the assistance of Jason Gibbs.

Natural enemies were collected using a modified leaf blower (Model BG 55, Stihl, Norfolk, VA) with the intake reversed and 3.75 l fine mesh bag (Cary Company, Addison, IL) placed over the end of the intake tube. Each plot was vacuumed until all flowers were sampled. Specimens were later identified to order (Aranae and Opiliones), superfamily (some parasitoid wasps), or family. Each taxon was classified as natural enemy or herbivore based on general trophic patterns of the family, with classification following Johnson and Tripelhorn (2005). The mean abundance for each group of insects was calculated by averaging across plant species at each site to generate a single value for pollinators and natural enemies for each plant species over the 3-week peak bloom period. Wild bee and natural enemy voucher specimens were deposited in the Michigan State University A.J. Cook Arthropod Research Collection.

The identity of the bees collected is reported in Table 2 of Rowe et al. (2018) and the natural enemies identified are reported in Table 3 of Gibson et al. (2019). These samples provided values of insect visitation for each species at each site on each sampling date, and the species values were combined for the two main insect groups. As we primarily sampled the flowering portions of the plants, we assume these insects were attracted to floral-associated resources (e.g. pollen, nectar, prey or shelter).

Statistical analyses

To allow us to compare plant species that bloom at similar times, we divided the season into three bloom periods. Species were assigned to a bloom period by averaging the weeks of peak bloom at all sites. The early bloom period includes species whose average week of peak bloom was between May and Mid-July, the middle period between mid-July and mid-August, and late between mid-August and October.

To determine plant trait predictor variables, we calculated the single species plot level mean floral area (cm^2), flower height (cm), flower chroma, the quantity of pollen (estimated # of grains), and the week of peak bloom. Mean values were generated by averaging values across plots within a site, and then across sites. The resulting trait data set had a single value for each measured trait for each plant species. Due to variable establishment and shorter bloom periods for some species, the number of times each plant species was sampled varied by plant species. Most plant species were sampled 7 or

more times, however, one species, *Silphium laciniatum* was only sampled a single time in 2016. Since plant species did not always bloom during the same sampling week at each site, we used data from site-specific peak bloom periods to generate trait values. We were unable to gather plant trait data from 13 plant species due to poor establishment, short bloom periods, or a lack of bloom. The 37 plant species used in the analysis and their trait means are shown in Table 1.

To assess visitation by beneficial insects, we calculated the mean abundance of native bees and natural enemies visiting each plant species during 5 min. collection periods (bees) and vacuum samples (natural enemies). We then converted visitation rates (visits/ sample event) on each plant species to a proportional scale for each bloom period. To do this, we divided the insect visitation rates for each plant species by the total averaged number of wild bees or natural enemies collected during sampling events during each bloom period. This generated a single value for each plant species that represented the proportion of insect visits during sampling events in relation to all insect visits to blooming plants within that bloom period. This method was used in order to standardize values, since not all plant species were sampled the same number of times.

We used Pearson correlation tests to test the relationship between abundance of wild bees (log $x + 1$ transformed) and natural enemies (log $x + 1$ transformed) during each bloom period. Natural enemies were grouped into parasitoid or predator categories in this analysis to facilitate statistical comparison with pollinator visitation. Next, for each insect group (natural enemies, predators, parasitoids, and wild bees), we applied a univariate approach, using linear regression models to test if their abundance was predicted by plant floral area, flower height, flower chroma, pollen availability, and week of peak bloom (R version 3.4.0, R Core Team 2017). We did not include interaction terms between predictors in the models. Prior to analysis, we used log $x + 1$ transformations on the insect data to normalize the visitation data. We used z-transformations on each plant trait variable to standardize plant trait data to the same scale. Variance inflation factors (VIF scores) were used to assess the correlation between plant traits prior to analyses. We did not find any multicollinearity issues with plant traits, as all VIF values were less than 1.79. The effect size (estimated slope) of each predictor variable on our response variables was determined using results from our linear models. All analyses were conducted in R (version 3.4.0, R Core Team 2017).

Results

Within each bloom period, we identified plant species which were consistently visited by greater proportions of both wild bees and natural enemies than co-blooming species (Fig. 1). When species were ranked by the proportion of insect visits received during a bloom period, there was high variability in the number of insects visiting the different species. However, there was a general trend, where similar plant species were highly visited by both groups of insects. During the early bloom period, 4 plant species accounted for more than 55% of wild bee visitations. These include *Achillea millefolium* (17.7%), *Asclepias syriaca* (16%), *Coreopsis lanceolata* (11.2%), and *Oenothera fruticosa* (10.8%). *Achillea millefolium* accounted for 61.4% of natural enemy visits per survey during the early bloom period. Within the middle bloom period, *Solidago nemoralis* (wild bees: 23.7% , natural enemies: 20.2%) and *Monarda fistulosa* (wild bees: 8.9%, natural enemies: 13.9%) were the two most visited plant species. Five plant species accounted for more than 55% of wild bee visits per surveys during this period, including *S. nemoralis, M. fistulosa, Rudbeckia hirta* (8%), *Ratibida pinnata* (7.9%), and *Pycnanthemum virginianum* (7.3%). Similarly, for natural enemies, *S. nemoralis, M. fistulosa*, and *P. virginianum* (10.1%), with the addition of *Eryngium yuccifolium* (9.9%), accounted for nearly 55% of insect visits per survey during this period. More variability was found in the late bloom season, with the most visited plant species differing between wild bees and natural enemies. *Coreopsis tripteris* had the highest proportion of wild bees (17% of visits) while *Solidago speciosa* had the highest proportion of natural enemies (22% of visits). However, when assessing plant species accounting for more than 50% of wild bee and natural enemy visits per survey, we found considerable overlap (wild bees: *C. tripteris* = 17%, *Symphyotrichum sericeum* = 11.5%, *Solidago juncea* = 9.8%, *Helianthus occidentalis* = 9.8%, *Silphium integrifolium* = 9.2%; natural enemies: *S. speciosa* = 22.4%, *S. juncea* = 17.7%, *C. tripteris* = 15.8%).

We found a positive relationship between plant species visited by wild bees and natural enemies ($r_{[35]} = 0.67$, $p < 0.001$). The strength of this relationship was greatest during the early ($r_{[7]} = 0.79$, $p = 0.01$) and middle bloom periods ($r_{[14]} = 0.71$, $p = 0.002$), with a similar non-significant trend during the late season bloom period ($r_{[10]} = 0.55$, $p = 0.06$) (Fig. 2). Within the natural enemy community, plant visitation by predators and parasitoids was highly correlated ($r_{35]} = 0.55$, $p < 0.001$). This trend was consistent during each bloom period assessed (early: $r_{[7]} = 0.78$, $p = 0.01$; middle: $r_{[14]} = 0.84$, $p < 0.001$; late: $r_{[10]} = 0.67$ $p = 0.02$).

Floral traits were significant predictors of wild bee and natural enemy abundances on plant species visited (See Table 2 and Fig. 3 for statistical details). The abundance of both insect groups increased with floral area of plant species tested. Wild bees and natural enemies responded in the same directions to the other traits we measured but did so with inconsistent strength. Abundance of both groups increased with flower height. However, this relationship was only significant for wild bees. Similarly, natural enemy abundance increased strongly with pollen quantity, while the increase in wild bees was small and not significant. Finally, flower chroma did not significantly affect abundance of either group, although the direction of the effect was negative for both.

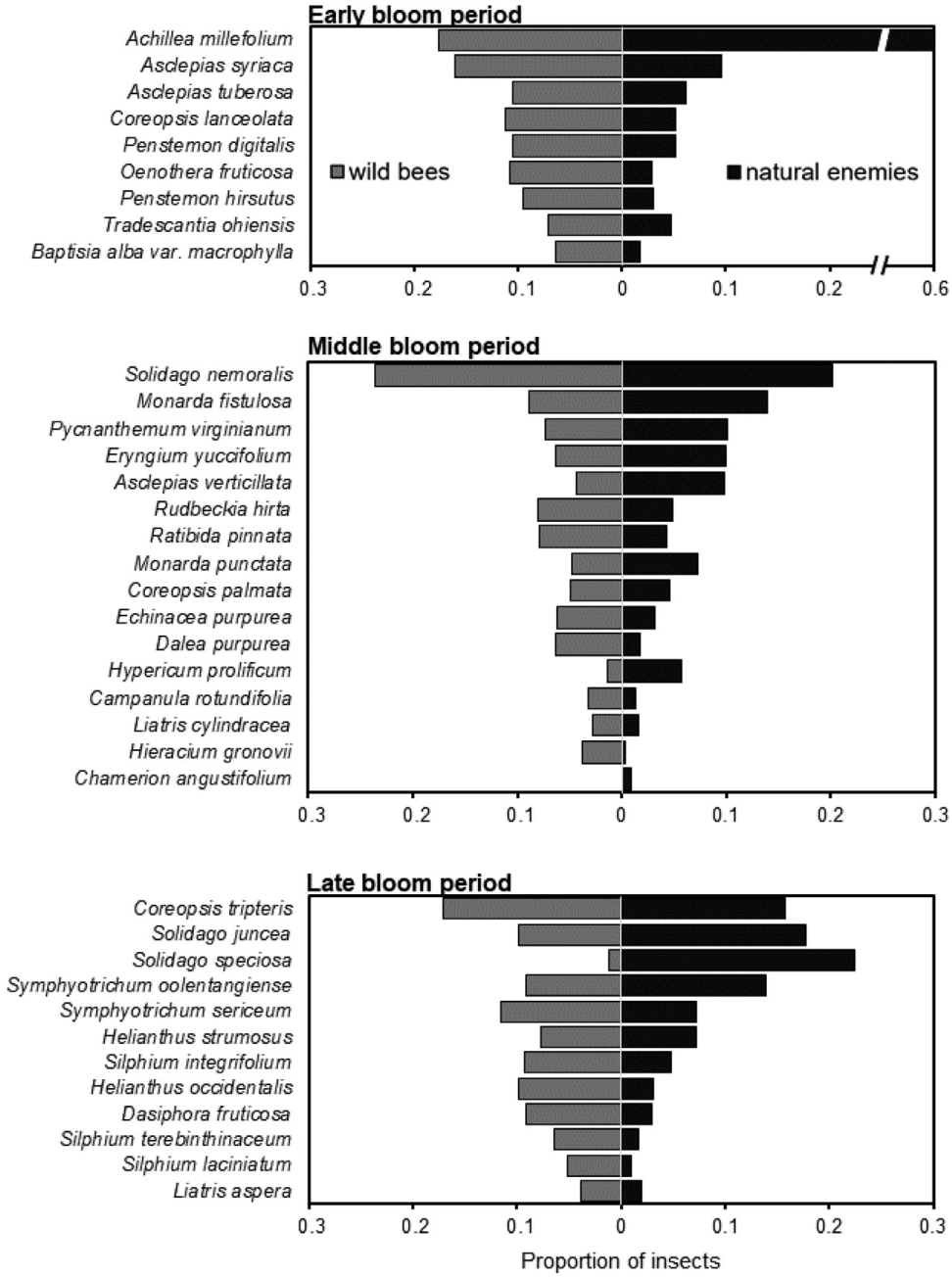


Fig. 1. Proportion of wild bees (gray, left) and natural enemies (black, right) collected during early, middle, and late season that were collected from different native plant species. Note the extended scale for natural enemies in early season. .

Discussion

Many crops benefit from both insect pollination and pest suppression, and selection of resource plants to jointly enhance these services is an important step towards supporting farm biodiversity and the benefits of arthropod-mediated ecosystem services (Albrecht et al., 2020). While there has been increasing interest in documenting the attraction of pollinators *or* natural enemies to resource plants (e.g., Williams *et al.* 2015, Mallinger, Franco, Prischmann-Voldseth, & Prasifka, 2019), fewer identify the plant traits that drive these relationships (Lundin et al., 2019; Rowe et al., 2020). Most of these focus on the relationship with a single floral trait or broad patterns at the habitat level (Conner & Rush, 1996, Potts *et al.* 2003, Mitchell *et al.* 2004, Hatt *et al.*, 2020), rather than exploring across flowering plant species to identify traits that correlate with insect visitation. Here we show that multiple plants species consistently have high visitation by both pollinators and natural enemies, that floral area and bloom timing are the most

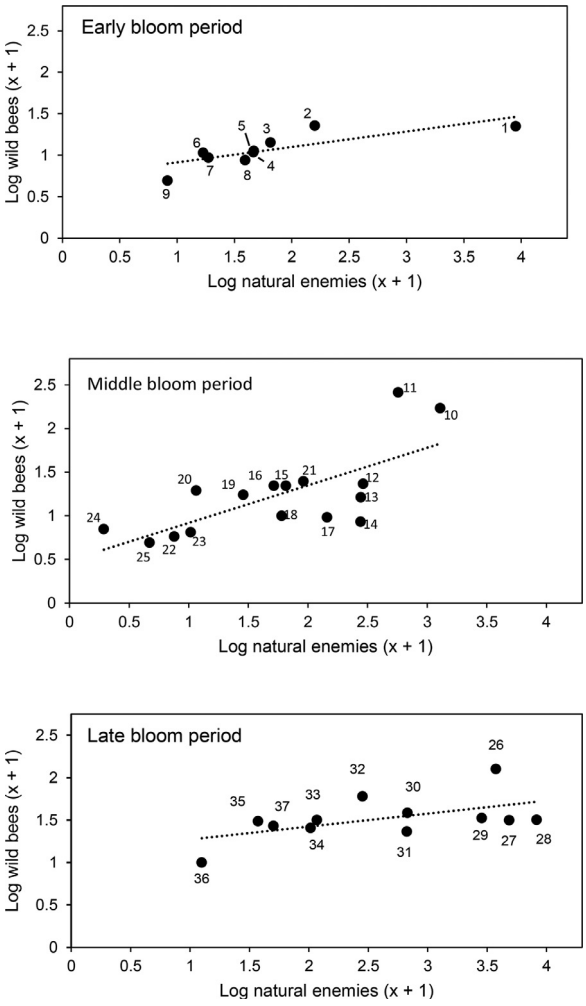


Fig. 2. Linear regression between log transformed ($x + 1$) wild bees and natural enemies visiting 37 blooming plant species in 2016 during the early, middle, and late summer bloom periods. The numbers correspond to plant species listed in Table 1.

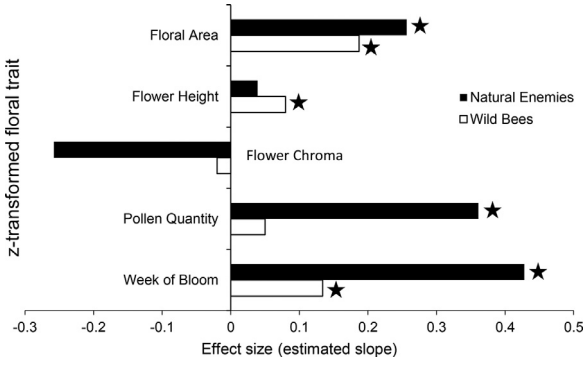


Fig. 3. Effect size (slope estimate) for each z-transformed floral trait influencing visitation by natural enemies and wild bees to native Michigan wildflower species assessed in replicated single species plots.

consistent predictors of these relationships, and that these plants can collectively provide resources across the full growing season.

We found strong overlap between natural enemies and wild bees in preferred floral resources through the summer. These patterns were strongest in the early and middle parts of the season, and non-significant during the latest bloom period. During this time, *S. speciosa* accounted for more than 22% of natural enemy visits and 1% of wild bee visits during 5-min sampling periods. This species was visited by high numbers of honey bees, which may have limited wild bee access to pollen and nectar resources due to competitive interactions (Paini, 2004). Similarly, during the early season *A. millefolium* accounted for 61% of natural enemy visits during sampling periods, while the remaining 8 plant species had low visitation levels. This plant species was visited primarily by wasps in the superfamily Chalcidoidea, which accounted for over 70% of natural enemies found on this species. This overlap in response between two different insect groups suggests similar traits are guiding visits by both groups of insects, perhaps through a combination of the initial visual cues for longer-range attraction and the rewards provided by flowers after arrival.

Despite an overall correlation between the number of wild bees and natural enemies visiting these plants, there were clear differences in the responses by these insect groups. For wild bees, the strength of the correlation declined through the season, while natural enemies tended to have a much stronger preference for a subset of the available plant species within each bloom period. These relationships may, in part, be driven by the life histories of wild bees and natural enemies, and variation within these groups is also expected because of this. While bees rely on pollen and nectar from flowers (Michener, 2000; Vaudo et al., 2020), these resources are thought to be a secondary resource for natural enemies when prey are not abundant or available (Lu et al., 2014). We did not assess herbivore abundance in this study, but Lundin et al. (2019) found that predator and parasitic wasp abundance were correlated with herbivore abundance in a set of wildflower species in California, USA. Therefore, natural enemies may be visiting plant species with either high abundances of prey or utilizing plant species with traits signifying high levels of pollen and nectar resources when prey are not available. This idea is strengthened by studies demonstrating that plants with high floral area tend to retain more nutritional resources for flower visitors (Potts *et al.* 2003, Hicks et al., 2016, Rowe et al., 2020).

To support a diversity of beneficial insects, Hatt et al. (2020) have recently argued for developing resource plantings for beneficial insects that provide tailored functional plant diversity, suggesting that by combining a range of plant traits that focal insects respond to in multiple flower species, improved insect community abundance and diversity will be achieved. The identification of plant traits associated with higher visitation by wild bees and natural enemies helps break down the geographic barrier generally

applied to selecting plant species to support beneficial insects. In this study, we found that floral area and the week of peak bloom are the primary traits associated with increased abundance of wild bees and natural enemies. Plant species with greater floral area tended to recruit higher abundances of these insects, supporting the previous studies by Fiedler and Landis (2007), Tuell et al. (2008), and Rowe et al. (2018). While most studies target specific taxa of beneficial insects, we provide evidence that functionally distinct beneficial insects can respond similarly to shared plant species and their traits. Further investigations could also explore how insect traits determine the outcome of these interactions as has been done for crop-pollinator interactions (Garibaldi et al., 2015). Our results suggest it is important to maintain flowering plants with high levels of floral area throughout the flight periods of beneficial insects to support entire communities. Floral area may signal the quality of quantity of pollen and nectar available at the individual flower level (Lunau, 2000), and can be a clear visual signal for foraging bees and natural enemies as they make choices about where to forage and where the greatest overall reward will be found. Since insects can only select plant species blooming during their flight period, we interpret the relationship between visitation abundance and week of peak bloom as a product of higher insect abundance later in the growing season. In general, plant traits had a greater effect on visitation by natural enemies, particularly in relation to pollen quantity and the week of peak bloom, than visitation by bees. Both wild bees and natural enemies tended to respond negatively (although not significantly) to increasing flower chroma, where flowers of increasing intensity tended to be less visited.

While generally providing clear results, we acknowledge several caveats regarding this study. First, while individual plots were separated by 5 m (the maximum distanced allowed by our overall field size) the potential for interplot interference still exists. A highly attractive neighboring species could influence visitation to adjacent plots either positively or negatively, but our RCB design would have controlled for this. Future studies should also consider interplot distances in project design. Additionally, since our investigations were focused on easy-to measure traits, we did not assess other factors such as UV-reflective patterns of the sampled flowers or plant chemical profiles that could also influence visitation. Finally, an experimental design using consistent rather than naturally occurring insect communities could be a complementary approach to explore how plant traits affect visitation by selected species of pollinators and natural enemies. This could also be used to understand more about how insect traits influence their capacity to access the plant rewards that may influence their visitation.

The results of this study can inform plant selection for habitat programs that aim to support wild bees, natural enemies, or combinations of these beneficial insects. To maximize the ecosystem services provided by pollinators and natural enemies in other geographic regions, plants can be selected to maximize the traits associated with high abundances of beneficial insects. We envision that this improved selection of plants supportive of beneficial insects can be used in two ways. First, for research to select locally optimal plants in which careful comparisons are run to support designing locally relevant plant mixes, and secondly to move directly to seed mix design taking plant traits into account. Developing a deeper understanding of traits that shape the likelihood of plants being attractive to beneficial insects may help reduce the situations where wildflower plantings do not deliver the expected ecosystem services (Albrecht et al., 2020; Lowe et al., 2020, Nicholson *et al.* 2020). Integrating this knowledge into existing tools to select plants for integration into farmland (M'Gonigle *et al.* 2017) can also facilitate plant selection and increase the effectiveness of on-farm habitat conservation programs to support beneficial insects.

Declaration of Competing Interest

None

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