

# Wildflower plantings on fruit farms provide pollen resources and increase nesting by stem nesting bees

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- Abstract**
- 1 Wildflower plantings on farms have been shown to attract foraging wild bees, however, whether these added floral resources increase nesting densities of bees remains largely untested.
  - 2 We placed nest boxes containing natural reeds at 20 fruit farms in Michigan. We then compared nesting densities between farms with and without wildflower plantings and analysed nest provisions to evaluate use of wildflower plantings for brood provisioning.
  - 3 We found significantly greater nesting at farms with wildflower plantings, with only one out of 236 completed nests at a farm without a planting. The majority of nests were completed by *Megachile pugnata*, with a portion of nests completed by *Osmia caerulea*.
  - 4 We found that nesting bees collected pollen from only a subset of the available flowers in the wildflower plantings, with a strong preference for *Centaurea maculosa*, and *Rudbeckia* type pollens. While these species were found growing in the plantings, only *Rudbeckia* type species were seeded in the plantings.
  - 5 This study provides evidence that wildflower plantings (though not only seeded species) are filling a critical resource gap for stem-nesting bees in agricultural landscapes and likely support local populations.

**Keywords** conservation, Megachilidae, population dynamics, *Prunus*, *Vaccinium*.

## Introduction

There is increasing evidence of population decline of wild bee species (Biesmeijer *et al.*, 2006; Bartomeus *et al.*, 2013; Burkle *et al.*, 2013; Powney *et al.*, 2019) and other insects (Hallmann *et al.*, 2017; Lister & Garcia, 2018; Sánchez-Bayo & Wyckhuys, 2019) around the globe. Many of the world's crops, and the majority of insect pollinated plants rely on wild bees as their primary pollinators (Klein *et al.*, 2003a, b; Winfree *et al.*, 2008; Potts *et al.*, 2010). Loss of floral resources has been targeted as a primary cause of wild bee decline, particularly in areas of intensive agriculture (Bennett & Isaacs, 2014; Sánchez-Bayo & Wyckhuys, 2019). Natural areas near agricultural lands increase wild bee diversity and abundance (Kremen *et al.*, 2004), but with rapid agricultural intensification over the past few centuries (Meyer & Turner, 1992), natural areas adjacent to agriculture are becoming increasingly scarce (Landis, 2017). In an effort

to abate wild bee declines, marginal farmlands have emerged as promising targets for habitat enhancements, often with financial support from federal and state/local agencies (Durant & Otto, 2019). Management practices at the farm level can therefore provide a unique opportunity to conserve local wild bee populations.

Establishment of wildflower plantings on marginal farmlands has been shown to increase wild bee diversity and abundance (Carreck & Williams, 2002; Carvell *et al.*, 2007; Garibaldi *et al.*, 2014; Williams *et al.*, 2015; though see Wood *et al.*, 2018) and can enhance pollination of adjacent crops (Carvalho *et al.*, 2012; Blaauw & Isaacs, 2014; Venturini *et al.*, 2017). These plantings are often designed to include a mix of native plant species that provide wild bees with floral resources throughout the summer. This is particularly important in areas of intensive agriculture where monoculture crops often provide only short-term bursts of resources, if they provide any resources at all, and therefore cannot sustain the local bee community throughout the year.

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While there is ample evidence that wildflower plantings in marginal farmlands can attract a diversity of foraging bees, the ability of these enhancements to promote nesting remains largely untested (Requier & Leonhardt, 2020), primarily due to the difficulties in monitoring nesting densities of bees (Carvell *et al.*, 2007). Increased nesting by bees is essential for building populations (Potts *et al.*, 2005). An increase in natural habitat within intensive agricultural landscapes has been shown to increase wild bee nesting (Kim *et al.*, 2006) and it is thought that wildflower plantings can play a similar role. However, the impact of wildflower plantings themselves on nesting of wild bees remains largely untested. If increasing bee population densities is a primary goal for establishing these plantings, then the direct impact on nesting should be measured in order to evaluate the success of this conservation action.

Establishing a link between floral resource availability within the wildflower planting and resource usage by local bees is also important for assessing the suitability of a seed mix to an area. Assessment is most commonly done by monitoring bees visiting the planting (*e.g.* Williams *et al.*, 2015); however, it is not typical to document whether the bees are nectaring at flowers or collecting pollen. Consequently, the link to brood provisioning and population growth is often not established. However, this can be accomplished by identifying the pollen provisions in bee nests that are in close proximity to wildflower plantings.

Stem nesting bees (*e.g.* *Megachile* spp., *Osmia* spp.) are increasingly important managed pollinators, in part due to their willingness to nest in provided substrates (*i.e.* nest boxes) (Maeta & Kitamura, 1964; Krombein, 1967; Bosch & Blas, 1994; Tylianakis *et al.*, 2005; Westphal *et al.*, 2008; Barthélémy, 2012; MacIvor *et al.*, 2014; MacIvor, 2017). They have also been used as indicator species for assessing the impact of habitat management strategies (Klein *et al.*, 2002; Kruess & Tscharntke, 2002; Correia Da Rocha-Filho *et al.*, 2017) and how landscape composition affects local bee communities (Frankie *et al.*, 1998; Steffan-Dewenter, 2002, 2003). Their willingness to use nest boxes make them an optimal group for measuring resource use and nesting densities in association with wildflower plantings, as they will utilize trap nests, allowing for assessment of nesting density and identification of pollen provisions (Killewald *et al.*, 2019).

In this study, we used nest boxes adjacent to marginal farmland to test the hypotheses that (i) wildflower plantings promote higher nesting densities by local bees, and (ii) local populations of stem nesting bees use the floral resources in the plantings to provision their nests. To test the first hypothesis, we installed nest boxes adjacent to two crops in Michigan, tart cherry and highbush blueberry, with half the farms for each crop having established wildflower plantings, and half without. We then recorded nesting densities by bees, and identified the species nesting at each farm. To test the second hypothesis, we performed floral transects in the wildflower plantings and in unenhanced field margins to compare the floral communities at farms with and without wildflower plantings. We then tested if nesting density is correlated with floral resource abundance and identified the pollen contents of completed bee nests to determine whether the nesting bees were using the flowers available in the wildflower plantings.

## Materials and methods

### Study locations

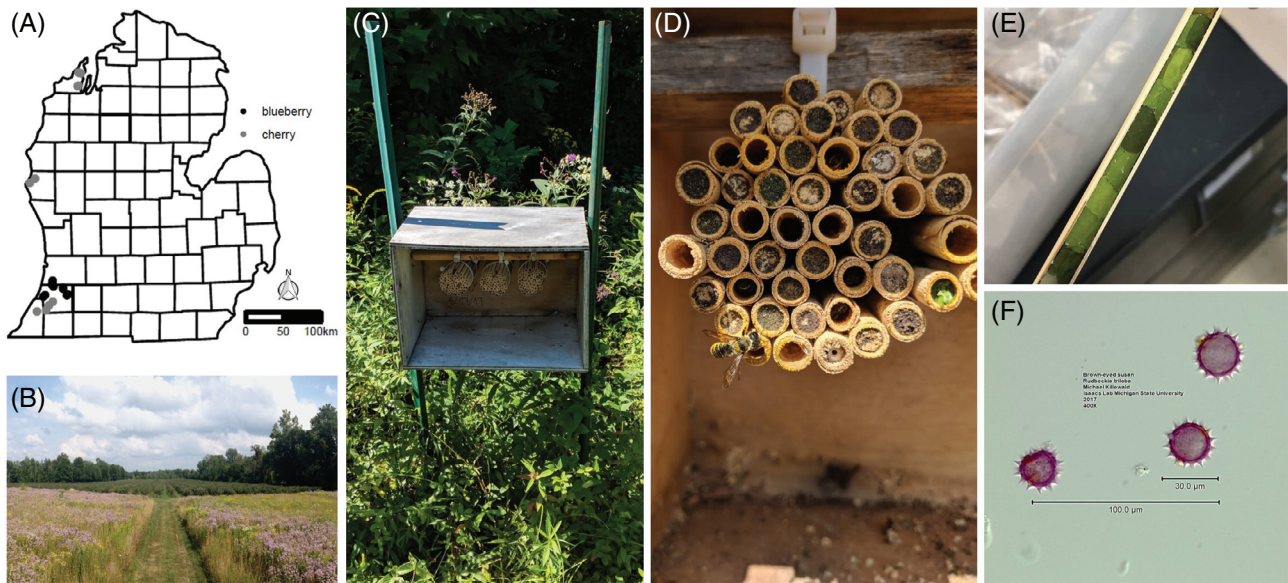
Twenty commercial fruit farms in the western region of Michigan were chosen for this study. These were composed of 10 tart cherry (*Prunus cerasus* L.) orchards and 10 highbush blueberry (*Vaccinium corymbosum* L.) farms within the main production regions of these crops (Fig. 1A). Half of the farms within each focal crop had established wildflower plantings (Fig. 1B) which were seeded in 2011 or 2013 (Table S1). Locations with plantings were paired with a nearby farm without a planting, and paired farms ranged between 1.14 and 12.36 km apart (mean =  $4.55 \pm 1.15$  S.E.). Most paired farms were managed by the same grower, with similar applications of pesticides and weed management strategies (*e.g.* mowing, herbicides, *etc.*) that could affect the suitability of the landscape for bees.

All plantings were seeded with a mix of native forbs and grasses optimized for wild bee conservation (Table S1) and designed to bloom after flowering of the two focal crops. They were located in the field margins adjacent to the crop and bordering a wooded edge. The plantings ranged in size from 0.08 to 1.97 ha (mean =  $0.49 \text{ ha} \pm 0.17$  S.E.). Unenhanced, regularly mowed field margins that were also adjacent to a wooded edge were selected at the paired unenhanced comparison farms (mean =  $0.24 \text{ ha} \pm 0.04$  S.E.).

### Floral surveys

Once every 2 weeks, floral surveys were conducted at each farm. The first visit was in the week of June 25, 2018, and surveys continued for 10 weeks (five total visits per farm). At each visit, we walked a 50 m transect in front of the nest box, roughly down the middle of the wildflower planting, and parallel to the edge of the crop planting and the wood line. Similar transect samples were taken at unenhanced comparison farms, again directly in front of the nest box. Every 5 m along the transect, a 1 m  $\times$  1 m quadrat was placed on the ground. We then visually estimated the proportional cover (between 0 and 1) of each species of flowering forb within the quadrat. Only the flowering head was considered in the estimate, and flowers that were obviously pre- or post-bloom were not included. Flowering plants were identified to the lowest taxonomic level in the field using Newcomb (1977) and the PI@ntNet app (Joly *et al.*, 2016), usually to species. Any plants that could not be confidently identified in the field were brought back to the lab, pressed, and identified using the keys available in Newcomb (1977).

Analyses and graphs were completed in R version 3.6.2 (R Core Team, 2016) and GraphPad Prism 7 (GraphPad Software, 2017). To compare floral resource availability between wildflower plantings and unenhanced field margins, we compared the proportion of total flowering forbs (all species) within survey quadrats at both field types for each focal crop (separate analyses for blueberry farms and cherry farms). We used GLMMs with beta distributions to account for use of proportional data (function: *glmmTMB*, package: *glmmTMB* (Brooks *et al.*, 2017)). The models included field type (wildflower planting or unenhanced field margin) as the fixed factor and random effects included week as well as quadrat number nested within



**Figure 1** (A) Location of highbush blueberry and tart cherry farms used in this study; (B) wildflower planting at one of our farms (UEP); (C) wooden box containing natural reeds as nesting material; (D) completed nests and a *Megachile pugnata* actively nest provisioning; (E) inside of a *M. pugnata* completed nest. Note the different shades of leaves used to line each cell which each contain a pollen provision ball and a single egg; (F) example of stained pollen (*Rudbeckia triloba*) used for pollen identification. [Colour figure can be viewed at [wileyonlinelibrary.com](http://wileyonlinelibrary.com)].

farm. We checked the models for overdispersion and zero inflation (function: `simulateResiduals`, package: `DHARMa`; simulations = 1000) prior to model selection by comparison of AICc (function: `dredge`, package: `MuMIn`) (Table S3A). *P* values were obtained using the function `Anova` (package: `car`).

To compare the floral communities between field types (wildflower planting or unenhanced field margin) and focal crop we used non-metric multidimensional scaling (NMDS) (function: `metaMDS`, package: `vegan` (Oksanen *et al.*, 2019)). Proportional forb survey data were first grouped by farm and plant species and then summed across all quadrats on all dates. The resulting matrix of data was then multiplied by 10 and rounded to the nearest whole number to simulate count data used in NMDS. NMDS was based on Bray–Curtis dissimilarity calculations, with 1000 iterations, and we used permutational multivariate analysis of variance (PERMANOVA) (function: `adonis`, package: `vegan`) to determine whether the groupings were significantly different in location. A difference in location would indicate that the floral communities were significantly different in composition between field type or focal crop. However, PERMANOVA is sensitive to differences in dispersion among groups, regardless of location. Therefore, we first tested for homogeneity of dispersion using the `betadisper` function (package: `vegan`), which is a multivariate analogue of Levene's test for homogeneity of variances that implements `PERMDISP2` (Anderson, 2004). Homogeneity of dispersion paired with a significant difference according to the PERMANOVA would indicate that the community composition differed between field types or focal crops, while heterogeneity of dispersion would not allow for comparisons of composition using PERMANOVA. Finally, we determined which members of the plant community were significantly contributing to ordination in the NMDS by utilizing the `envfit` function (package: `vegan`, permutations: 999). We then fit vectors on

the NMDS plot according to species contributions (those with  $p < 0.05$  displayed), with the length of the vector corresponding to the strength of the contribution.

#### Nesting density

At each farm, one 45 cm × 30 cm open-faced wooden box was mounted 3 feet off the ground between two metal posts. These were placed along the edge of each wildflower planting or unenhanced field margin, facing the crop and backing up to a wood line (Fig. 1C). Tangle-Trap Sticky Coating (The Scotts Company LLC, Marysville, OH) was sprayed on the posts below the boxes to limit ant activity. A wooden bar running lengthwise 8 cm below the top of the box was used to hang the nesting materials, consisting of 6 mm diameter reeds (*Phragmites* sp.) (Crown Bees, Woodinville, WA). Bundles of 50 reeds each were assembled using zipties and three of these bundles were hung from the crossbar of each nest box. Nest boxes were set up during the week of June 11, 2018 and removed the week of September 4, 2018.

At the same time as floral surveys were conducted (once every 2 weeks), all reeds with completed nests were collected and replaced with new reeds (Fig. 1D). This included any reeds that had been capped at the end (either by Megachilid bees or Eumenid mason wasps) or were filled with grass (from grass-carrying *Isodontia* wasps). Although only those reeds completed by bees were used for future data analyses. Additionally, ants were occasionally found to be stripping parts of the reeds for nesting materials, at which time all reeds in the nest boxes were removed and replaced, and additional applications of Tangle-Trap were made to the posts to reduce ant visitation.

All completed nests were brought back to the laboratory and the bee nests ( $N = 236$ ) and wasp nests ( $N = 37$ ) were separated.



If we had collected more than one bee nest that day at a farm then one reed per farm, or 10% of collected reeds if there were 20 or more collected, were randomly selected for rearing out. Nests for rearing ( $N = 24$ ) were then put into mesh pollinator exclusion bags which were secured shut with zipties and stored in an unheated barn to overwinter. After the first male bees emerged (June 2019), the rest of the reeds were frozen and then opened to identify adult bees to species using published keys (Arduser, 2009; Sheffield *et al.*, 2011). All other collected bee nests were used for pollen identification ( $N = 212$ ), and therefore placed in the freezer the same day they were collected to halt larval development. Nests used for pollen identification were not used to identify bee species.

We compared the number of completed nests between field types (wildflower planting or unenhanced field margin) and focal crops using a generalized linear mixed effects model (GLMM) (function: `glmer`, package: `lme4` (Bates *et al.*, 2015)), with a Poisson distribution and log link. Field type and Focal crop were included as interacting fixed factors, with farm included as a random effect. We performed model selection (Table S3B) and reporting as above. We also calculated marginal  $R^2$  ( $R^2_m$ ) and conditional  $R^2$  ( $R^2_c$ ) using the R squared function (piecewiseSEM package).  $R^2_m$  describes the proportion of variance explained by the fixed factor(s), whereas the  $R^2_c$  describes the proportion of variance explained by both the fixed and random factors (Nakagawa & Schielzeth, 2013).

We also tested if the number of completed nests collected each week correlated with floral availability (proportion of floral coverage as calculated above). Only floral survey data from the same day/farm that we collected nests were used in this analysis (12 sampling days across eight farms). We first calculated the average floral coverage each sampling day by averaging across quadrats in the transect. We then aligned the bi-weekly average floral coverage data with the bi-weekly nesting data for each unique sampling day/farm and used a GLMM with number of nests as the variable, average floral cover as the fixed factor, and week nested within farm as the random effect. The model had a Poisson distribution with a log link, and we performed model selection (Table S3C) and reporting as above.

#### Pollen identification from nests

Up to 10 nests were randomly chosen from each farm on each collection date and opened (Fig. 1E). Pollen provisions (bee collected pollen found in each cell) were removed and placed in individually labelled tubes. Each pollen provision was then suspended in 70% ethanol, with the amount of ethanol added varying in proportion to the size of the provision, but typically between 0.5 and 1 mL. The sample was then vortexed until the pollen was homogenized (2–3 min), and 20  $\mu$ L of the sample was immediately placed in the middle of a microscope slide, and the ethanol was allowed to evaporate. Pollen grains (Fig. 1F) were then stained with fuchsin gel and the sample was covered with a cover slip. Volumes of pollen species (Folk, 1951) were visually estimated for each sample. We identified the pollen to the lowest taxonomic rank possible using Sawyer (1981) and a reference collection of 254 known pollen species/types collected by bees in Michigan. Reference slides are housed in the Isaacs

Lab at Michigan State University, Department of Entomology and primarily from west Michigan where our project farms were located. Some reference images are also available online: <http://bit.ly/MSUbeepollen>. If the identity of a pollen was uncertain, then it was lumped into a type category. Each pollen type is made up of a group of possible plant species that the pollen could be attributable to (Table 1).

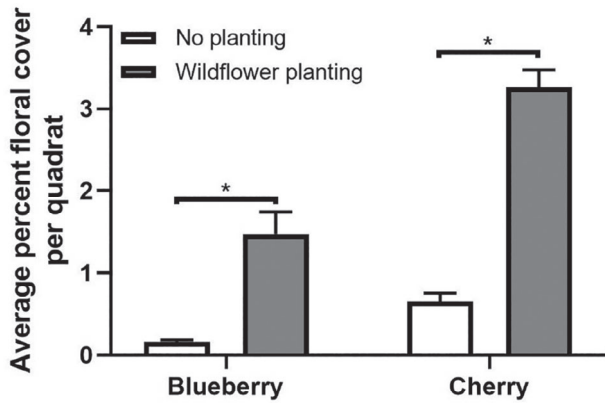
To assess the likelihood that stem nesting bees used floral resources within the wildflower plantings to provision their nests, we again used NMDS based on Bray–Curtis dissimilarity calculations (1000 iterations) to compare the floral community available in the wildflower plantings to the floral community represented in pollen provisions. This was performed on the subset of data where we had both pollen data from collected bee nests and floral survey data from the same day. Data from both focal crops were analysed together due to low sample sizes. In order to make direct comparisons between the community of pollen found in the nests and the floral survey data, we assigned pollen types to the plant data from our floral surveys (Table 2). Pollen type data were then summed by collection date on each farm, multiplied by 10 and rounded to the nearest whole number as done above. Again, we first tested for homogeneity of dispersion between the groups using PERMDISP and used PERMANOVA to determine whether the pollen communities represented in the nests were significantly different in composition to what was available in the wildflower plantings. The pollen types driving ordination of the NMDS plot were also determined using the `envfit` function (package: `vegan`, permutations: 999) and fitted to the plot according to their significant effect ( $p < 0.05$ ) on ordination.

## Results

### Floral surveys

Blooming flowers represented  $1.4\% \pm 0.3$  S.E., on average, of the surveyed area at wildflower plantings on blueberry farms and  $3.3\% \pm 0.2$  S.E. on cherry farms. This was significantly more floral coverage compared to unenhanced field margins which had  $0.2\% \pm 0.0$  S.E. and  $0.7\% \pm 0.1$  S.E. average floral coverage of the surveyed area, respectively (Blueberry:  $X^2 = 8.9$ ,  $df = 1$ ,  $p < 0.001$ ; Cherry:  $X^2 = 14.1$ ,  $df = 1$ ,  $p < 0.001$ ) (Fig. 2). *Pycnanthemum virginianum*, *Silphium perfoliatum*, and *Ambrosia* sp. were the most abundant flowering plants in the wildflower plantings. The first two were seeded, while the third is a common weed (ragweed). In comparison, *Trifolium arvense*, *Daucus carota*, and *Trifolium repens*, common weeds of disturbed agricultural habitats, were the most abundant species in the comparison unenhanced field margins (Table S2).

Using floral survey data (proportion of flowering forb species per quadrat), we compared the floral communities between focal crops, and we compared the communities in wildflower plantings to those in the unenhanced field margins. The floral communities between focal crops had equal dispersion (PERMDISP:  $F_{1,18} = 0.30$ ,  $p = 0.58$ ) and no significant difference in community composition (PERMANOVA:  $R^2 = 0.05$ ,  $F_{1,18} = 0.87$ ,  $p = 0.56$ ). The floral communities between field types (wildflower plantings and unenhanced field margins) also had equal dispersion (PERMDISP:  $F_{1,18} = 1.10$ ,  $p = 0.29$ ),



**Figure 2** Average percent floral cover in wildflower plantings (grey bars) and unenhanced field margins (open bars). Asterisks denotes a statistically significant difference between treatments ( $p < 0.05$ ).

but were significantly different in composition (PERMANOVA:  $R^2 = 0.22$ ,  $F_{1,18} = 5.00$ ,  $p = 0.001$ ), indicating a difference in the community of flowering plants found at the two field types (Fig. S1). Species that contributed the most to the NMDS ordination of farms with wildflower plantings included *Monarda fistulosa*, *Centaurea maculosa*, *Coreopsis lanceolata*, *Ratibida pinnata*, *Rudbeckia triloba*, *Rudbeckia hirta*, and *Achillea millefolium*, while ordination of the unenhanced field margins were

most affected by the prevalence of *Trifolium pratense* and *Plantago lanceolata* (Fig. S1).

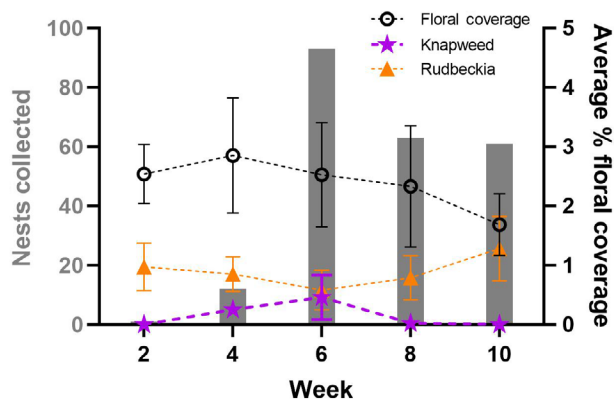
#### Nesting density

Every 2 weeks, we checked nest boxes that each contained 150 reeds. Over the course of 14 weeks, we collected 236 completed bee nests from nine of the 20 farms (Table S4). Presence of a wildflower planting resulted in significantly more completed nests ( $R^2m = 0.32$ ,  $R^2c = 0.62$ ; Field type:  $X^2 = 7.24$ ,  $df = 1$ ,  $p = 0.007$ ) than at farms without, with only one nest completed at a farm without a planting. All other nests (cherry = 29 nests, blueberry = 206 nests) were located at farms with wildflower plantings. There was no significant difference between focal crops (Focal crop:  $X^2 = 0.33$ ,  $df = 1$ ,  $p = 0.57$ ). The majority of nests (203) were found at the blueberry farm with the largest wildflower planting (1.97 ha); therefore, we also ran the model with this farm pairing excluded. Excluding this farm pairing yielded a similar result, though a lower  $R^2$  ( $R^2m = 0.05$ ; Treatment:  $X^2 = 5.7$ ,  $df = 1$ ,  $p = 0.017$ ).

We reared out a subset of the nests from the three farms where we collected more than one nest (UEP (blueberry), BL2 (cherry), and RW2 (cherry)) to identify occupants (Tables 1 and S4). Of the 24 nests reared out, all but two were completed by *Megachile pugnata* (Say, 1837). The other two nests were completed by *Osmia caerulea* (Linnaeus, 1758) and both were from the same cherry farm (BL2), collected on different days.

**Table 1** Average percent of each pollen type identified from nest provisions. *Megachile pugnata* were identified as nest occupants at UEP, BL2, and RW2, and *Osmia caerulea* were identified as nest occupants at BL2. At farms where only one nest was collected, the nesting species was not identified. Four of the farms were adjacent to blueberry fields, and four were adjacent to cherry orchards. The number of nests used for pollen identification are indicated by the n values. Plant species that were seeded in the wildflower plantings are bolded. Nests were collected between 26 June and 4 September 2018.

		Blueberry farms				Cherry farms			
		FSL	GHP	LDH	UEP	BL2	CB2	RW2	SW2
		n = 1 (%)	n = 1 (%)	n = 1 (%)	n = 41 (%)	n = 14 (%)	n = 1 (%)	n = 2 (%)	n = 1 (%)
Found in wildflower planting	<i>Centaurea maculosa</i> type	66.7		85.0	57.5	8.3		68.0	41.7
	<i>Cirsium</i> type				1.1	0.7		2.0	
	<i>Solanum</i> sp.		77.7			1.7			
	<b><i>Rudbeckia</i> type</b>			1.7	23.7	36.4	5.7	25.0	58.3
	<b><i>Symphoricarpos</i> type</b>				1.2		33.6		
	<i>Taraxacum</i> type			3.3	5.7	0.7	60.7		
	<i>Trifolium pratense</i>	33.3				18.8			
	<i>Trifolium repens</i> type		11.7			7.4			
	<i>Vicia</i> sp.					0.8			
	<i>Cichorium intybus</i> type				1.3				
Not found in wildflower planting	<i>Fagopyrum</i> sp.					2.5			
	<i>Helianthus</i> sp.			10.0	9.4	1.1		5.0	
	<i>Melilotus</i> sp.		1.7						
	<i>Prunus</i> type		4.0			0.3			
	<i>Rhamnus</i> / <i>Frangula</i> type					0.3			
	<i>Rhus</i> sp.					15.8			
	<i>Rubus</i> type					4.4			
	Unknown type 1					0.6			
	Unknown type 2		5.0						
	Unknown type 3					0			



**Figure 3** Relationship between nesting density and floral abundance in the wildflower plantings across the 10 weeks of sampling. Bars represent the number of nests collected in each week of sampling (across all farms). Black circles represent the overall average percent floral coverage in wildflower plantings in corresponding farms to where the nests were collected each week. Purple stars represent just the average floral cover of *Centaurea maculosa* (spotted knapweed), and orange triangles represent the average floral cover of *Rudbeckia* type pollens (*R. hirta*, *R. triloba*, *Echinacea purpurea*, or *Coreopsis lanceolata*). [Colour figure can be viewed at [wileyonlinelibrary.com](http://wileyonlinelibrary.com)].

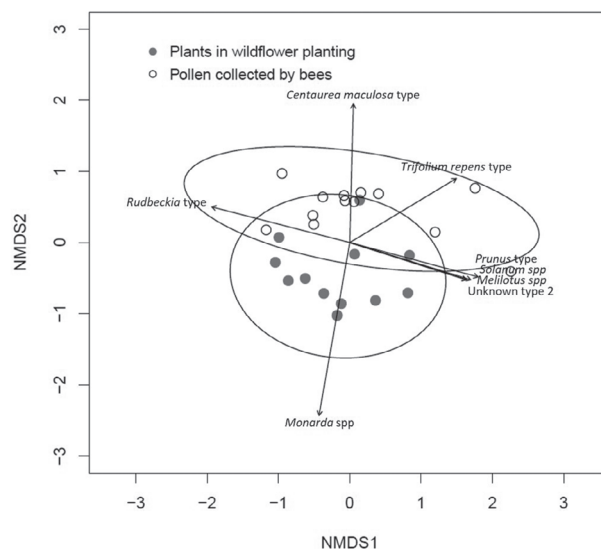
The greatest number of completed nests was collected in Week 5 (July 24–31). Overall floral abundance was relatively consistent over time but peaked in Week 3 (July 9–17) (Fig. 3). There was no significant correlation between average floral cover and nesting density ( $R^2_m = 0.03$ ,  $R^2_c = 0.94$ ;  $X^2 = 1.12$ ,  $df = 1$ ,  $p = 0.29$ ).

#### Floral resource use by stem nesting bees

We compared the floral community represented in the pollen provisions of nests to the plants found in the floral surveys on the same day/farm that nests were collected. All nests used for these analyses were from farms with wildflower plantings, as unfortunately the one nest collected at an unenhanced farm had deformed pollen in the nest that we were unable to identify. We found that the resources used by bees for provisioning nests at sites with wildflower plantings came from a subset of the plants available in the wildflower plantings (Table 2, Fig. 4).

The most common pollen types found in the nests were *C. maculosa* and *Rudbeckia* type pollens, which were present in pollen provisions collected from six of the eight farms with nesting (Table 2, Fig. S2). Both plant groups were growing in the wildflower plantings, and not in the unenhanced field margins, although only the *Rudbeckia* type group (*R. hirta*, *R. triloba*, *Echinacea purpurea*, or *C. lanceolata*) were seeded in the plantings. The majority of the pollen identified in nests came from the invasive weed *C. maculosa* (spotted knapweed), which is also commonly found in unmanaged open areas in the region.

Due to the preference for *C. maculosa* and *Rudbeckia*-type pollen (*R. hirta*, *R. triloba*, *E. purpurea*, or *C. lanceolata*), we also looked at the correlation between these species' abundances in the wildflower plantings and bee nesting density. Floral abundance of *Rudbeckia*-type plants peaked in Week 9, while nesting density peaked in Week 5. Floral abundance of *C.*



**Figure 4** Non-metric multidimensional scaling (based on Bray–Curtis dissimilarity distances) comparing the community of floral resources found in wildflower plantings to the pollen types collected by stem nesting bees. Plants identified in wildflower plantings were assigned a corresponding pollen type before analysis to make comparisons between floral survey data and pollen identification. Grey data points represent the plant community surveyed on an individual farm on a day when bee nests were collected there. White data points represent the community of pollen types identified in nests on the same day/farms. Ellipses represent the 95% confidence interval around each group. Arrows indicate the most significant plant species ( $p < 0.01$ ) driving the ordination of points. The arrow length corresponds to the strength of the correlation between the species and the ordination.

*maculosa* peaked in Week 5, at the same time as nesting density (Fig. 3). However, the abundances of these flowers (either analysed separately or together, Table S3) were not significantly correlated with nesting density (*C. maculosa*:  $R^2_m = 0.03$ ,  $R^2_c = 0.96$ ;  $X^2 = 1.30$ ,  $df = 1$ ,  $p = 0.26$ ; *Rudbeckia*-type:  $R^2_m = 0.03$ ,  $R^2_c = 0.93$ ;  $X^2 = 0.79$ ,  $df = 1$ ,  $p = 0.37$ ; Combined:  $R^2_m < 0.01$ ,  $R^2_c = 0.94$ ;  $X^2 = 0.02$ ,  $df = 1$ ,  $p = 0.88$ ).

The community of pollen found in nests and the plant community in the wildflower plantings on the same days that nests were collected (and after pollen type assignment) were equally dispersed ( $F_{1,24} = 0.01$ ,  $p = 0.92$ ) and significantly different in composition (PERMANOVA:  $R^2 = 0.16$ ,  $F_{1,24} = 4.7$ ,  $p = 0.001$ ) (Fig. 4). Ordination of the pollen provisions were significantly influenced by bee preference for *C. maculosa* type pollen and *Trifolium repens* type pollens, while they did not collect *Monarda* spp. pollen, despite it being widely available in the wildflower plantings (Fig. 4, Table S2). Collection of *Rudbeckia* type, *Prunus* type, *Solanum* spp., *Melilotus* spp. and unidentifiable pollens also significantly contributed to the ordination of the NMDS (Fig. 4).

#### Discussion

Investing in wildflower enhancements on farms can provide valuable resources for wild bees (Williams *et al.*, 2015; Burkle *et al.*, 2020). Our data provide evidence that installation of

wildflower plantings on cherry and blueberry farms in west Michigan significantly increased the diversity of floral resources available to bees in field margins and significantly increased nesting by stem-nesting bees. This suggests that wildflower plantings on farms can promote the stability and/or growth of wild bee populations (Potts *et al.*, 2005).

However, while we found significantly greater nesting densities at farms with wildflower plantings, the majority of nests were from one farm (UEP), which makes it worthy of closer review. This farm had by far the largest wildflower planting (Fig. 1B), four times the average size of wildflower plantings in this study. The resource availability on this farm may therefore support a much larger population of stem-nesting bees than at other farms with smaller wildflower plantings. The larger population at this farm may also have increased competition for nesting resources, making our provided nest boxes more attractive. This population may therefore benefit most from additional nesting resources to increase population size. Conversely, low-density nesting at the farms with smaller wildflower plantings suggests that these populations may still be limited by floral resources and not nesting resources, and that additional floral resources would promote population growth. However, fully understanding the interaction of floral and nesting requirements of these populations would require a multi-year study that varies availability of either floral or nesting resources (Dainese *et al.*, 2018).

Through identification of pollen in nests, we were able to critically evaluate if resource availability was linked with resource usage by nesting bees. We found that bees use flowers growing in the wildflower plantings; however, this included volunteer species that were not originally seeded. The most dominant pollen types identified in nest provisions were from flowers available in the wildflower plantings, *C. maculosa* and *Rudbeckia* type; however, while *Rudbeckia* type pollen likely came from *R. hirta*, *R. triloba*, *E. purpurea*, or *C. lanceolata*, all of which were seeded in the wildflower plantings, the most abundant pollen was from the unseeded and invasive weedy species, *C. maculosa*. While this species was not documented in unenhanced field margins, it is known to be widespread in unmanaged open areas across Michigan (Sheley *et al.*, 1998; Emery & Gross, 2005); therefore, pollen collected from this species cannot definitively be attributed to the plantings themselves. It is also widely considered an invasive species by land managers and ecologists, though it is highly prized by beekeepers for its benefits for honey production (Jacobs, 2012). At the site with the highest nesting densities, there are unmanaged open areas in close proximity to the wildflower planting that have become near monocultures of *C. maculosa*. This farm is often used by local beekeepers as a honey yard because of the abundance of flowers, both from the large wildflower planting and unmanaged open areas with abundant *C. maculosa*. This further supports the idea that an overabundance of resources at this farm, be it from the wildflower planting and/or unmanaged open areas with *C. maculosa*, may have been driving the particularly high nesting densities we observed there.

Nesting bees used a relatively small proportion of the flowers that were available in the plantings for provisioning nests, and the community of pollen represented in nests was significantly different from that available in the plantings. This indicates that the pollen preferences of nesting bees did not align perfectly with the composition of the wildflower plantings; though the

plantings were not designed with only stem-nesting bees in mind, but instead were designed to support a wide community of bees including bumble bees that use the abundant *M. fistulosa*. Nonetheless, while these wildflower plantings were not specifically designed for stem-nesting bees, they appear to provide enough resources to promote higher nesting densities, as bee nesting was almost exclusively at farms with plantings.

Misalignment of pollen preferences of nesting bees was also reflected in the lack of correlation between nesting density and resource availability. This finding was contrary to other studies which have found that stem-nesting bees have greater reproductive output in correlation with nearby floral resource availability (Dainese *et al.*, 2018). It is possible that the predominant nesting species in our study (*M. pugnata*) is more affected by fluctuations in resources not represented in the wildflower plantings. *M. pugnata* has previously been shown to collect predominantly Asteraceae pollen (Tepedino & Frohlich, 1982), and our results support this finding with nesting bees showing a strong preference for Asteraceae pollens (*Rudbeckia* type and *C. maculosa* type). However, these plants made up a relatively small proportion of the surveyed area in wildflower plantings; therefore, our floral surveys may not have allowed for a detection in correlation of nesting density and resource availability, even if small fluctuations in resource abundances were biologically meaningful to bees.

This study adds to an ongoing assessment of wildflower plantings for supporting wild bee conservation in agroecosystems (Nicholls & Altieri, 2013; Morrison *et al.*, 2017; Wood *et al.*, 2018). The increase in nesting density observed at farms with wildflower plantings suggests that these plantings provide a critical resource that is not being fulfilled at unenhanced farms. Additionally, by connecting floral surveys with bee-collected pollen, we provide evidence that wildflower plantings support the pollen needs of stem nesting bees, though are not optimal in floral composition for all species' needs. Seed mixes for future plantings could be optimized using similar methods to link pollen preferences with resource availability, if supporting specific bee groups is the goal.

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## Authors contribution

KKG conceived of the study idea and designed and led data collection, and was responsible for data analyses, and manuscript authorship. JAP organized data collection at cherry farms and assisted with manuscript writing. AP organized data collection at blueberry farms. MK and JZ completed pollen identification.



JW and RI advised on project design implementation and assisted with manuscript writing. Project funding was awarded to JKW and RI (U.S. Department of Agriculture National Institute of Food and Agriculture through awards 2012-51181-20105 and 2017-68004-26323).

## Conflict of interest

The authors declare that they have no conflict of interest.

## Data availability statement

The data that support the findings will be available in DataDryad at the publication of this manuscript.

## Supporting information

Additional supporting information may be found online in the Supporting Information section at the end of the article.

**Figure S1** Non-metric multidimensional scaling to compare the community of plants found in wildflower plantings to the unenhanced field margins. Ellipses represent the 95% confidence interval around each group. Arrows indicate the most significant species ( $p < 0.01$ ) driving the ordination of points. The arrow length corresponds to the strength of the correlation between the species and the ordination.

**Figure S2** Pollen types identified from provisions in bee nests. *Megachile pugnata* were identified as nesting at UEP, BL2, and RW2, and *Osmia caerulea* were identified as nesting at BL2. At farms where only one nest was collected, the nesting species was not identified. Four of the farms were adjacent to blueberry fields, and four were adjacent to cherry orchards. The number of nests used for pollen identification are noted above the bars. Nests were collected between 26 June and 4 September 2018.

**Table S1** Supporting information

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