Limited phenological and dietary overlap between bee communities in spring flowering crops and herbaceous enhancements

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Abstract. Wild bee populations have undergone declines in recent years across much of the Western world, and these declines have the potential to limit yield in pollination-dependent crops. Highbush blueberry, *Vaccinium corymbosum*, and tart cherry, *Prunus cerasus*, are spring-blooming crops that rely on the movement of pollen by bees and other insects for pollination. Wild bee populations can be increased on farmland by providing floral resources, but whether the addition of these plants translates into increased pollinator density on crop flowers has not been documented in most cropping systems. To determine the importance of providing additional floral resources for wild bee pollinator communities, we selected blueberry fields and tart cherry orchards with and without herbaceous floral enhancements in western Michigan, USA. The bee communities visiting crop flowers, enhancements and control grassy field margins were sampled over a 5-yr period. In addition, the pollen diets of the most abundant wild bee crop pollinators were quantified across Michigan to better understand their foraging niches and to identify potentially important alternative host plants. The presence of floral enhancements did not increase the abundance of wild bees on either blueberry or cherry flowers during bloom. The bee community visiting blueberry was evenly composed of short-season bees that fly only during the spring and long-season bees that fly in both spring and summer. In contrast, the bee community visiting cherry was dominated by short-season spring bees. The majority of pollen collected by the wild bee communities visiting blueberry and cherry was from spring-flowering woody plants, with limited use of the herbaceous enhancements. Enhancements attracted greater abundance and species richness of bees compared to control areas, including twice as many floral specialists. Conserving summer-flying, grassland-associated bees is an appropriate goal for pollinator conservation programs. However, herbaceous enhancements may not provide adequate resources for the wild bees that pollinate spring-flowering crops. This study demonstrates that an examination of the pollen collected by wild bees across their flight periods can identify plant species to help them persist in intensively managed landscapes.

Key words: agroecosystems; Apoidea; bee conservation; biodiversity; farmland; habitat quality; pollen diet; wild bees.

Introduction

Insect pollinators have received a great deal of attention in recent years due to well-documented population declines in some species of managed and wild bees, hoverflies, butterflies and moths across both Europe and the USA (Biesmeijer et al. 2006, Potts et al. 2010). The most pronounced bee declines have occurred in more agriculturally intensified regions, making these declines of particular concern due to the loss of pollination services in agriculture, valued at over US$200 billion to the global economy each year (Gallai et al. 2009). Worldwide, the Western honey bee, *Apis mellifera*, is the most commonly used managed crop pollinator, as beekeepers are able to provide high numbers of bees during crop bloom through the transport of hives to any specified location. Although the honey bee is capable of increasing yield in almost all animal-pollinated crops (Klein et al.

2007), other research has highlighted the importance of wild bees as agricultural pollinators, whether providing the majority of flower visits to crops (Winfree et al. 2008, Garratt et al. 2016), improving the pollination efficacy of honey bees through competitive interactions (Brittain et al. 2013), or more generally increasing fruit set regardless of honey bee abundance (Garibaldi et al. 2013). Abundant wild bee communities may consequently provide insurance against potential honey bee losses (Winfree et al. 2007).

Food availability is the primary limiting factor for wild bee species found in agricultural environments (Roulston and Goodell 2011). One major strategy to increase wild bees is providing food resources (pollen and nectar) through the addition of herbaceous wildflower strips alongside crops (Haaland et al. 2011, though see also Kremen and M'Gonigle 2015). These enhancements can be designed to be multifunctional and to provide resources to many beneficial invertebrates, whereas others are designed with more explicit bee conservation goals in mind. For example, in the United Kingdom, some strips targeted the foraging requirements of rare bumble bee species, which declined following agricultural intensification (Carvell et al. 2007). While their response to these schemes was mixed (Carvell et al. 2007), some studies demonstrate that these wildflower

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enhancements can increase the persistence, fecundity, and population size of more widespread bumble bee species (Wood et al. 2015, Carvell et al. 2017).

In countries without subsidies to support pollinator-friendly management, planting wildflower enhancements is more likely to be driven by the financial considerations of the landowner, as creating habitat for pollinators can be expensive (Garbach and Long 2017). Of particular interest is whether such an investment will increase the crop yield to a level sufficient to cover the cost of implementing the enhancement (Blaauw and Isaacs 2014). Wild bee communities that visit crop flowers are usually dominated by a small number of common species, which, on average, represent around 2% of the species present in a study area but provide 80% of the pollination service, and these species are generally more abundant in habitat enhancements compared to unenhanced control areas (Kleijn et al. 2015). Conservation efforts targeting this restricted suite of pollinators would be the most effective way to increase the number of wild bee visits to crop flowers. However, in most systems, it is still unclear if enhancements increase the population size of wild bees, and whether this management translates into higher visitation to crop flowers by wild bees during bloom.

Although bees are observed on enhancement and crop flowers, the importance of different plant groups to maintaining populations of wild bee pollinators is poorly understood at both the individual species and community levels. Wild bee species often have distinct foraging preferences, and many species will only collect pollen from a restricted suite of plants (Westrich 1989, Cane and Sipes 2006). Pollen can be removed from the scopa of bee specimens and identified visually using a microscope. Analysis of pollen loads carried by wild bees is a powerful tool, which can be used to assess species-level pollen preferences and hence foraging niche (Westrich 1989, Cane and Sipes 2006, Müller and Kuhlmann 2008). The different pollen species collected by some wild bee pollinators have been quantified during crop bloom (e.g., Russo and Danforth 2017), but results are dominated by crop pollen, and their use of alternative host plant species outside this bloom period is less well known.

In much of Eastern North America, there is a distinct division in the flowering resources available to bees between the spring, where the flowering plant community is dominated by woody plants, and the summer, where it is comparatively dominated by herbaceous plants (Fye and Medler 1954, Severson and Parry 1981). The wild bee species of this region also follow this phenological pattern and broadly fall into three categories: (1) short-season spring bees, (2) short-season summer bees, and (3) long-season bees that fly in both spring and summer. While variation exists between and within these definitions, they capture the April–June spring and July–September summer seasonality of insects and plants in our study area in Michigan. This seasonality limits the suite of flowering herbaceous plants that can be included in seed mixes for supporting crop-visiting bees, as the majority of these plants flower in the summer rather than when the spring crops bloom. Short-season spring-flying bees like *Andrena* that are important crop visitors (Gibbs et al. 2016, Joshi et al. 2016) are unable to interact with or benefit from sown floral resources. In contrast, long-season bees like bumble bees fly in both the spring and the summer are able

to interact with, and have the potential to benefit from, summer flowering enhancements (Blaauw and Isaacs 2014). There is therefore a potential mismatch between some important crop-visiting bees and herbaceous enhancements.

The current study tested hypotheses related to herbaceous enhancements for wild bees using two contrasting crop systems: highbush blueberry, *Vaccinium corymbosum*, and tart cherry, *Prunus cerasus*. Herbaceous wildflower enhancements were established adjacent to blueberry fields and cherry orchards beginning in 2013–2014 concurrently with extensive surveys of pollinators (2013–2017) in crops, enhancements, and control areas. Blueberry has a relatively long flowering period of several weeks with flowers in a cluster opening sequentially, compared to tart cherry, which can sometimes have a flowering period as short as three days, with most flowers opening concurrently. Previous research in the blueberry system found that wild bees were significantly more abundant on crop flowers three to four years after herbaceous habitat enhancements were established adjacent to blueberry fields (Blaauw and Isaacs 2014), but relatively little is known about enhancing wild bee communities in cherry orchards.

Based on previous results, we hypothesized that the enhancements will increase wild bee abundance on crop flowers in both systems, particularly the abundance of long-season bees. The differential response of bee groups with different phenologies to floral enhancements has not been investigated in detail. Since the majority of the resources provided by herbaceous enhancements are available from July to September, we hypothesized that long-season crop-visiting bees will show a stronger response to enhancements than short-season crop-visiting bees. We also characterized the diets of important short-season crop-visiting wild bees to better understand their ecological niches and to identify potentially more appropriate foraging resources for this group. Based on their April–June flight period, we hypothesized that short-season bees will collect pollen predominantly from woody, spring-flowering plants rather than the summer-blooming plants selected for wildflower plantings.

Materials and Methods

Study region and experimental design

The study was conducted in Michigan, a major production region for highbush blueberry and tart cherry. Ten blueberry fields and ten cherry orchards were identified along the western edge of Michigan's Lower Peninsula, the most important area for fruit production in the state. Blueberry fields were located in Van Buren, Allegan, and Ottawa counties, and cherry orchards were located in Berrien, Van Buren, Oceana, and Leelanau counties (Fig. 1). All blueberry sampling was conducted on the variety Bluecrop, which comprises 26% of all blueberries grown in the state. All cherry sampling was conducted on the variety Montmorency, which comprises 98% of all tart cherries in the state. Fields and orchards were all adjacent to a seminatural habitat, in most cases woodland or wooded border. Crop plantings had sufficient area of the same cultivar to sample up to 100 m into the field from the seminatural edge with additional crop plants extending beyond that distance. Four transects each 40 m in length were laid out in each field
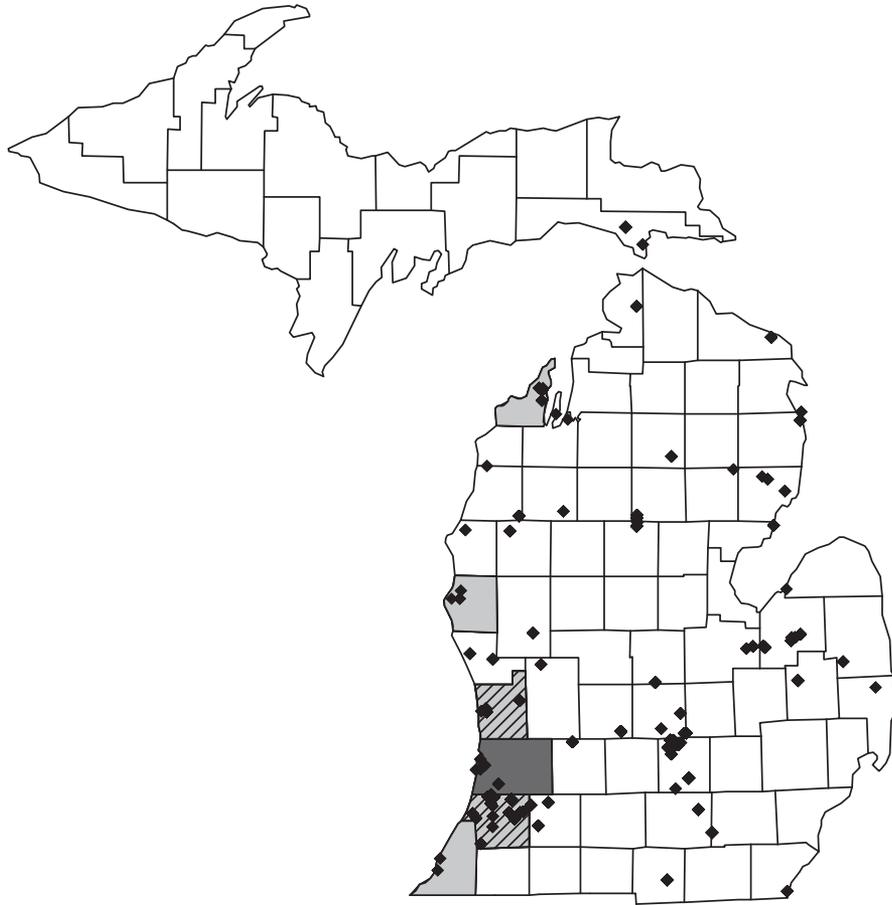
Fig. 1. Map of Michigan, USA, showing the sampling locations for the 471 bee specimens from 31 species collected between 2013 and 2017 that were used for pollen load analysis (black dots). Counties with surveyed blueberry fields only are highlighted in dark gray, counties with surveyed cherry orchards only are highlighted in light gray, and counties with surveyed blueberry fields and cherry orchards are marked with black hashes.

running parallel to the border, at distances of 0, 25, 50, and 100 m from the field edge or wildflower planting. At one blueberry field, a change in cultivar occurred between the 50- and 100-m distances, so a replacement transect was set up at approximately 75 m.

At five of the blueberry and five of the cherry sites, an area of land adjacent to the crop field was prepared for seeding in 2013, and seeded with a mix of native wildflowers in the fall of 2013 or spring of 2014. The seed mix is provided in Appendix S1. The sites were maintained during their establishment phase in 2014 and 2015 using mowing and spot herbicide applications to control problem weeds or invasive plants. For both crops, the control sites had a typically grassy field margin without any floral enhancement.

Pollinator surveys and specimen collection

Bee observations were conducted during crop bloom. As blueberry fields flower for longer than cherry, each blueberry field was visited three times during bloom in each year, with each cherry orchard visited just once. In suitable weather conditions (>15°C, low wind speeds, at least partial sun, no precipitation), each transect was visually surveyed, with all bees visiting crop flowers counted and identified to group (honey bees, bumble bees, and other wild bees).

Blueberry transects were walked for 10 min and cherry transects for 30 min so that total survey effort was equivalent. In addition to these visual observations, collections were made from the same transects to allow for species-level identification of wild bees (Winfree et al. 2008). Following the observations, each transect was walked for the same length of time, with all wild bee species visiting crop flowers netted and killed. Specimens were identified to species by J. Gibbs and T. J. Wood using published keys as well as reference to voucher material in the A. J. Cook Arthropod Research Collection, Michigan State University, East Lansing, Michigan, USA. Collected species were classified as long or short season based on their flight phenology (see Appendix S2). Blueberry field sites were visited at different times of day between rounds to minimize temporal biases. All cherry sites were surveyed between 2013 and 2017, with the exception of one site that was not sampled in 2016 because the grower removed the orchard without warning. The 2017 transect was switched to a different orchard at the same site.

Pollen diet analysis

Based on their abundance during specimen collection, the wild bee species representing 90% of the visits to blueberry and cherry were selected for dietary analysis. Specimens of

these species were collected between 2013–2017 from a range of different habitats and locations across the Lower Peninsula of Michigan (Fig. 1) and were taken from the Isaacs lab collection and the personal collections of T. J. Wood and J. Gibbs. Large geographic and temporal ranges were selected to ensure that this dietary analysis would be more representative of the range and relative importance of species of pollen collected by these wild bees than those collected only in blueberry fields and cherry orchards. In this way, we aimed to build up a more representative picture of the true foraging niche of each bee species (Cane and Sipes 2006, Müller and Kuhlmann 2008), rather than the foraging choices observed solely within contemporary agricultural systems. A minimum of 10 pollen loads were analyzed per species, with the exception of *Andrena carolina* ($n = 3$), *A. w-scripta* ($n = 9$), and *Osmia bucephala* ($n = 8$). *Andrena carolina* is a well-known oligolege of *Vaccinium* (LaBerge 1980) and so it was not considered necessary to analyze additional samples. Insufficient specimens with pollen loads collected between 2013 and 2017 could be sourced for the other two species.

The scopal pollen load was analysed using light microscopy following the method detailed in Wood et al. (2016). The size of pollen loads on individual bees was estimated, ranging from a full load to a one-eighth load. Pollen grains were removed from the scopae and transferred to a drop of water on a microscope slide, which was gently heated to allow evaporation. Molten glycerine jelly stained with fuchsin was then added and the slide was sealed with a coverslip. The percentage of the load composed of different plant species was estimated along three randomly selected lines across the cover slip at a magnification of 400. The percentage of the load by volume was estimated by the relative area of the slide occupied by each plant species, rather than the absolute number of grains. Species representing <1% of the load were excluded from further analysis as their presence may have arisen from contamination. The percentage of pollen collected was corrected according to the overall size of each load to give a final weighting. Pollen loads were identified to the lowest taxonomic level possible using a reference collection assembled during the project, in most cases to genus (see Appendix S3).

These data were used to calculate an overall diet for each bee species, with each collected pollen recorded as a percentage. For example, across all samples, *Osmia atriventris* collected 34.6% of its pollen from *Trifolium repens*-type, 27.8% of its pollen from *Vaccinium*-type, 12.3% of its pollen from *Fragaria*, and so on. For each species, these dietary percentages were then multiplied by their abundance during specimen collection as a way of weighting for their relative importance to wild bee species. The final scores for each pollen type were then summed and calculated as a percentage to show their importance for the wild bee pollinator communities of blueberry and cherry. For example, *A. carolina* was netted 34 times from blueberry flowers and dietary analysis showed that it collected 100.0% of its pollen from *Vaccinium*. *Bombus impatiens* was collected 88 times from blueberry flowers and dietary analysis showed that it collected 9.3% of its pollen from *Vaccinium*. Therefore, *A. carolina* generates a *Vaccinium* score of 3,400 and *B. impatiens* generates a *Vaccinium* score of 819.3. This was done for each pollen type collected by each of the bee species providing the top 90% of

wild bee visits to blueberry and cherry flowers. The final weighting of the importance of each pollen type to the whole wild bee pollinator community is therefore dependent on both the relative contribution each pollen type makes to the pollen diet of each species and the relative importance of each bee species as a pollinator of blueberry or cherry.

Herbaceous enhancement surveys

In 2015–2017, blueberry sites were visited four times each year, in June, July, August, and September. One control and one enhanced site were not surveyed for flowers in 2015 due to invasion by weedy species. In 2015–2017, cherry sites were visited three times each year, in June, July, and late August/ early September. One control site was not surveyed for flowers in 2016. In each enhanced or control area, two 50 m transects were randomly placed within each plot. Each 50-m transect was surveyed for 20 min with the observer hand netting any wild bee recorded visiting a flower within 1 m on either side of the transect. Specimens were killed and identified as per the crop pollinator surveys. Total survey time was contingent on the number of observers, with one observer surveying for 40 min, two observers each surveying for 20 min concurrently, up to a maximum of four observers. Following the transect surveys, a 10-min opportunistic sampling period was conducted, collecting from wild flower species that were not found during the transect surveys in order to fully characterize the bee diversity present at each site. After bee surveys, every 5 m on alternating sides along this transect a 1 × 1 m quadrat was placed on the ground. Each flowering plant species present in the quadrat was identified to species. The number of flowers of each flowering plant species was also counted, or estimated depending on abundance, with flowers grouped into manageable units such as racemes, heads, clusters, or umbels (Carvell et al. 2007).

Statistical analysis

All analyses were conducted in R version 3.3.2 (R Development Core Team 2016). Generalized linear mixed-effect models (GLMMs) were used to test for differences in abundance and richness of bee species visiting crop flowers, wild bee species visiting herbaceous areas, and flowering plant species between enhanced and control sites. Models were fitted with Gaussian error distributions where appropriate, but most observations and collected specimen data were not normally distributed or could not be transformed to normality and so models were fitted with Poisson or negative binomial error distributions. Models were tested for overdispersion using the dispersion_glmer function in the package blmeco to ensure appropriate choice of error structure. Data were summed within each year for both on-crop and enhancement analyses. Sampling year was included as a random factor, and models were compared by ANOVA to a null model to obtain final *P* values. Differences in honey bee abundance between sites were not investigated.

Using the package vegan, nonmetric multidimensional scaling plots were constructed using Bray-Curtis dissimilarity scores to determine whether the wild bee pollinator communities visiting blueberry and cherry flowers were different from the wild bee communities visiting enhanced and

control areas. These plots used the abundance data from specimens collected during bloom and from the herbaceous areas during the summer. Differences between the communities were tested using PERMANOVAs.

RESULTS

Bees observed during bloom

Observations during blueberry bloom recorded 13,028 honey bee visits (95.1%), 210 bumble bee visits (1.5%), and 460 other wild bee visits (3.4%). There was no significant difference in the number of bumble bees observed on-crop between enhanced and control sites (3.9 ± 2.2 against 4.5 ± 1.6 bumble bees per site per year [mean ± SD], GLMM, $\chi^2 = 0.03$, $P = 0.872$). There was also no significant difference in the number of other wild bees observed on-crop between enhanced and control sites (9.2 ± 4.5 against 9.2 ± 2.4 other wild bees per site per year, GLMM, $\chi^2 = 0.00$, $P = 0.973$).

Observations during cherry bloom recorded 8,711 honey bee visits (49.1%), 434 bumble bee visits (2.4%), and 8,609 other wild bee visits (48.5%). There was no significant difference in the number of bumble bees observed on-crop between enhanced and control sites (9.8 ± 2.4 against 7.9 ± 2.0 bumble bees per site per year, GLMM, $\chi^2 = 0.55$, $P = 0.461$). There was also no significant difference in the number of other wild bees observed on-crop between enhanced and control sites (143.8 ± 39.7 against 270.9 ± 86.0 other wild bees per site per year, GLMM, $\chi^2 = 2.89$, $P = 0.089$).

Wild bees collected during bloom

During blueberry bloom, a total of 468 bees belonging to 52 species was collected visiting blueberry flowers (see Appendix S2). Two specimens (0.42%) could not be identified to species. Based on collected specimens, 12 species (22.2%) provided 80% of all wild bee crop flower visits (Table 1a). This community was evenly balanced, with 52.1% of individuals classified as long-season and 47.9% as short-season bees. *Andrena* was the most abundant genus (38.0%), followed by *Bombus* (30.6%) and *Lasioglossum* (8.3%). During cherry bloom, a total of 2,714 bees belonging to 78 species was collected visiting cherry flowers. Four specimens (0.15%) could not be identified to species. Based on collected specimens, 12 species (15.4%) provided 80% of all wild bee crop flower visits (Table 1a). This community was dominated by short-season bees comprising 73.1% of individuals compared to the 26.9% long-season bees. *Andrena* was the most abundant genus (67.2%), followed by *Ceratina* (13.7%) and *Lasioglossum* (7.4%).

For blueberry, there was no significant difference in the number of wild bees collected on-crop between enhanced and control sites (9.7 ± 4.8 against 9.0 ± 2.9 wild bees per site per year, GLMM, $\chi^2 = 0.08$, $P = 0.783$). There was no difference in the richness of wild bee species collected on-crop between enhanced and control sites (5.2 ± 1.4 against 5.3 ± 1.0 species of wild bee per site per year, GLMM, $\chi^2 = 0.01$, $P = 0.930$). For cherry, there was also no significant difference between enhanced sites and control sites (46.8 ± 12.5 against

TABLE 1. The top 10 most abundant wild bee pollinators visiting (a) blueberry and tart cherry flowers and (b) herbaceous enhancements adjacent to blueberry fields and tart cherry orchards.

	No. recorded	Flight period
(a) Bee species visiting crop flowers		
Blueberry (*Vaccinium corymbosum*)		
Bombus impatiens	88	long
Andrena vicina	83	short
Andrena carolina	34	short
Andrena carlini	31	short
Bombus bimaculatus	28	long
Augochlora pura	23	long
Xylocopa virginica	21	long
Bombus griseocollis	20	long
Colletes inaequalis	14	short
Andrena imitatrix	13	short
Tart cherry (*Prunus cerasus*)		
Andrena miserabilis	481	short
Ceratina calcarata	361	long
Andrena forbesii	283	short
Andrena barbilabris	281	short
Andrena crataegi	213	short
Colletes inaequalis	130	short
Andrena imitatrix	121	short
Andrena vicina	101	short
Andrena nasonii	79	short
Andrena rugosa	53	short
(b) Bee species collected from enhancements		
Adjacent to blueberry fields		
Ceratina calcarata	125	long
Bombus impatiens	116	long
Halictus ligatus	111	long
Ceratina mikmaqi	98	long
Bombus bimaculatus	83	long
Bombus vagans	49	long
Lasioglossum leucozonium	43	long
Ceratina strenua	39	long
Bombus griseocollis	27	long
Andrena wilkella	23	short
Adjacent to tart cherry orchards		
Bombus impatiens	121	long
Bombus griseocollis	105	long
Bombus bimaculatus	92	long
Halictus ligatus	45	long
Bombus vagans	42	long
Ceratina calcarata	29	long
Lasioglossum pectorale	18	long
Melissodes communis	14	short
Melissodes subillatus	13	short
Andrena crataegi	12	short

Note: Flight period refers their respective flight season, short (April–June) and long (April–August/September).

65.3 ± 14.8 wild bees per site per year, GLMM, $\chi^2 = 0.95$, $P = 0.330$). There was no difference in the richness of wild bee species collected on-crop between enhanced and control sites (12.4 ± 1.2 against 13.4 ± 1.8 species of wild bee per site per year, GLMM, $\chi^2 = 0.18$, $P = 0.668$).

Overall, neither long-season or short-season bees showed a significant response to the presence of herbaceous enhancements. In blueberry, there was no difference in the

number of long-season bees recorded on crop flowers at enhanced sites compared to control sites (5.1 ± 2.2 against 4.6 ± 1.2 long-season bees per, GLMM, $\chi^2 = 0.16$, $P = 0.691$). There was also no difference for short-season bees at enhanced sites compared to control sites (4.6 ± 2.6 against 4.4 ± 1.6 short-season bees per year, GLMM, $\chi^2 = 0.01$, $P = 0.916$). In cherry, long-season bees were less abundant on crop flowers at enhanced sites compared to control sites, though this was not significant (8.2 ± 1.9 against 22.1 ± 12.7 long-season bees per year, GLMM, $\chi^2 = 3.79$, $P = 0.051$). Short-season bees were also less abundant, but not significantly so, on crop flowers at enhanced sites (38.6 ± 10.7 against 43.1 ± 6.5 short-season bees per year, GLMM, $\chi^2 = 0.12$, $P = 0.728$).

Pollen diet analysis

In both blueberry and cherry, 21 species of wild bee accounted for 90% of total visits. Ten species were found only in blueberry, 10 only in cherry, and 11 species were important wild pollinators for both crops. In total, 471 pollen loads from these 31 bee species were analysed. All species were polylectic with the exception of *Andrena carolina*, which only collected pollen from *Vaccinium*.

In total, 87 and 82 plant pollen groups were collected by the 21 most important wild bee species visiting blueberry and cherry flowers, respectively (Table 2). Woody plants comprised 67.6% and herbaceous plants 32.4% of the pollen diet of the wild bee blueberry pollinator community.

TABLE 2. Top 10 most important pollen host plants by percentage of diet for the blueberry and cherry wild bee pollinator communities based on pollen load identification and weighting by relative on-crop abundance.

Host plant	Plant type	Diet (%)
Blueberry (*Vaccinium corymbosum*)		
Vaccinium-type[†]	woody	21.90
Salix	woody	8.74
Prunus-type[†]	woody	7.39
Acer	woody	5.50
Solanum	woody	4.47
Rubus	woody	4.24
Centaurea	herbaceous	3.21
Trifolium repens-type	herbaceous	3.16
Rhus	woody	3.11
Lonicera	woody	2.91
Tart cherry (*Prunus cerasus*)		
Prunus-type[†]	woody	21.78
Acer	woody	18.24
Salix	woody	10.37
Rubus	woody	7.43
Rosa	woody	4.70
Malus-type[†]	woody	4.02
Rhus	woody	3.50
Rhamnus	woody	3.26
Melilotus	herbaceous	3.22
Viburnum	woody	3.08

Notes: Plant species are characterized as woody or herbaceous based on the growth type of the majority or dominant Michigan species in that genus.

[†]Genera cultivated as crops.

Blueberry pollen was identified as the most important pollen source for this community, followed by willow (*Salix* spp. 8.7%), cherry/serviceberry (*Prunus*-type 7.4%) and maple (*Acer* spp. 5.5%). Woody plants comprised 81.1% and herbaceous plants 18.9% of the pollen diet of the wild bee cherry pollinator community. Cherry/serviceberry pollen was identified as the most important pollen source for this community (21.8%), followed by maple (18.2%), willow (10.4%) and bramble (*Rubus* spp. 7.4%).

Floristic community change in herbaceous enhancements

In 2015–2017, a total of 151 species or morphospecies of flowering plants with 961,514 flowering units was recorded at blueberry sites. Across all years, flowering species richness (GLMM, $\chi^2 = 18.09$, $P < 0.001$) and floral abundance (GLMM, $\chi^2 = 13.58$, $P < 0.001$) were significantly higher in enhanced areas compared to control areas (29.3 ± 3.9 against 16.4 ± 2.5 flowering plant species per site per year; 60,113 ± 46,542 against 4,874 ± 1,933 floral units per site per year). In 2015–2017, a total of 89 species or morphospecies of flowering plants with 412,256 flowering units was recorded at cherry sites. Across all years, flowering species richness (GLMM, $\chi^2 = 24.80$, $P < 0.001$) and floral abundance (GLMM, $\chi^2 = 34.94$, $P < 0.001$) were significantly higher in enhanced areas compared to control areas (20.7 ± 2.5 against 7.2 ± 1.7 flowering plant species per site per year; 11,565 ± 5,172 against 743 ± 528 floral units per site per year).

Wild bee communities visiting enhanced and control areas

In 2015–2017, a total of 2,386 bees belonging to 134 species was collected from floral enhancements (115 species) and herbaceous controls (78 species) adjacent to blueberry fields and cherry orchards. Six specimens of *Nomada* (0.25%) could not be identified to species. At blueberry sites, 1,546 bees belonging to 109 species were collected. Eighty-eight species were collected from enhancements and 71 species were collected from herbaceous controls. Across all years, significantly more bees were captured at the enhancements adjacent to blueberry fields compared to controls (69.9 ± 13.5 against 33.2 ± 7.3 wild bees per site per year, GLMM, $\chi^2 = 8.00$, $P = 0.005$). Significantly more species of bee were captured at enhancements compared to controls (19.3 ± 3.0 against 13.9 ± 2.8 wild bees species per site per year, GLMM, $\chi^2 = 4.26$, $P = 0.039$).

In cherry, a total of 840 bees belonging to 79 species was collected. Seventy-five species were collected from enhancements and 28 from herbaceous controls. Across all years, significantly more bees were captured at the enhancements adjacent to cherry orchards compared to controls (45.1 ± 10.5 against 10.9 ± 4.1 wild bees per site per year, GLMM, $\chi^2 = 9.29$, $P = 0.002$). Significantly more species of bee were captured at enhancements compared to controls (15.6 ± 1.2 against 6.4 ± 2.3 wild bees species per site per year, GLMM, $\chi^2 = 13.31$, $P = 0.001$).

Across both crops, 19 species were collected exclusively from herbaceous controls, of which only one was a floral specialist. In contrast, 56 species were collected exclusively from enhancements with 16 floral specialists. Fifty-nine

species containing 13 floral specialists were found in both habitat types (Table 3). There was a significant positive relationship between the number of flowering plant species and the number of bee species recorded in enhanced and control areas adjacent to blueberry fields (GLMM, $\chi^2 = 10.98$, $P < 0.001$, Fig. 2a) and cherry orchards (GLMM, $\chi^2 = 22.81$, $P < 0.001$, Fig. 2b).

Similarity between on-crop and enhancement bee communities

There was limited overlap between the wild bee communities visiting the crops and herbaceous areas. In blueberry,

TABLE 3. Floral specialists recorded visiting either enhanced plantings or control areas only, and species common to both habitat types.

Species	Floral specialization
Recorded in enhanced areas only	
Andrena aliciae	Asteraceae
Andrena helianthi	Asteraceae (*Helianthus*)
Andrena rudbeckiae	Asteraceae (*Rudbeckia* and *Ratibida*)
Dianthidium simile	Asteraceae
Dieunomia heteropoda	Asteraceae
Dufourea monardae	Lamiaceae
Megachile pugnata	Asteraceae
Melissodes agilis	Asteraceae (*Helianthus*)
Melissodes desponsus	Asteraceae (*Cirsium*)
Melissodes druriellus	Asteraceae
Melissodes tinctus	Asteraceae
Melissodes trinodis	Asteraceae (*Rudbeckia* and *Ratibida*)
Peponapis pruinosa	Cucurbitaceae (*Cucurbita*)
Perdita bequaerti	Asteraceae (*Helianthus*)
Perdita halictoides	Solanaceae (*Physalis*)
Pseudopanurgus aestivalis	Asteraceae (*Solidago* and *Symphyotrichum*)
Recorded in control areas only	
Colletes americanus	Asteraceae
Recorded in both habitat types	
Andrena asteris	Asteraceae (*Solidago* and *Symphotrichum*)
Andrena canadensis	Asteraceae (*Solidago* and *Symphotrichum*)
Andrena hirticincta	Asteraceae (*Solidago* and *Symphotrichum*)
Andrena nubecula	Asteraceae (*Solidago* and *Symphotrichum*)
Andrena placata	Asteraceae (*Solidago* and *Symphotrichum*)
Andrena simplex	Asteraceae (*Solidago* and *Symphotrichum*)
Andrena wilkella	Fabaceae
Lasioglossum lustrans	Asteraceae (Cichorioideae)
Melissodes denticulatus	Asteraceae (*Vernonia*)
Melissodes illatus	Asteraceae (*Solidago* and *Symphotrichum*)
Melissodes subillatus	Asteraceae
Osmia georgica	Asteraceae
Pseudopanurgus andrenoides	Asteraceae (*Solidago* and *Symphotrichum*)

Note: All species are short-season bees of the summer, with the exception of *Osmia georgica*, which is a spring bee, and the introduced *Andrena wilkella*, which overlaps the spring and summer seasons.
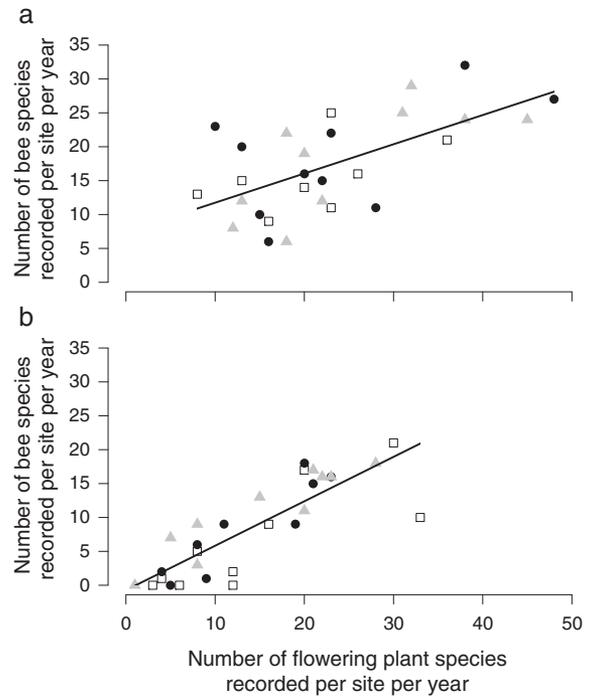

FIG. 2. Relationship between plant species richness and bee species richness in enhanced and unenhanced areas adjacent to (a) blueberry fields and (b) cherry orchards. Open squares, 2015; black circles, 2016; gray triangles, 2017.

the wild bee pollinator community was significantly different from the community visiting the enhanced and control areas in the summer (Fig. 3a, PERMANOVA, $F_1 = 6.26$, $P = 0.001$). The wild bee communities visiting the enhanced and control areas in blueberry fields were not significantly different (PERMANOVA, $F_1 = 1.48$, $P = 0.154$). In cherry, the wild bee pollinator community was significantly different from the community visiting the enhanced and control areas in the summer (Fig. 3b, PERMANOVA, $F_1 = 9.22$, $P = 0.001$). The communities visiting the enhanced and control areas in cherry orchards were significantly different (PERMANOVA, $F_1 = 2.15$, $P = 0.009$), though this was partly driven by low sample size at two control sites where only two and seven specimens were collected over three years. Removing these two sites produced non-significant results (PERMANOVA, $F_1 = 1.864$, $P = 0.072$). Comparing enhanced and control areas next to cherry orchards are difficult due to the low number of specimens collected over the three-year sampling period in control areas ($n = 163$).

During sample collection, 24 species of blueberry visiting bees were collected in enhanced areas, comprising five short-season and 19 long-season species. By abundance, these comprised seven and 727 specimens, 0.67% and 67.39% of the total number of bees collected on enhanced areas ($n = 1,048$). Blueberry visiting species were the most commonly collected bees in enhanced areas (Table 1b). Twenty-seven species of cherry visiting bees were collected in enhanced areas, comprising 5 short-season bees and 22 long-season bees. By abundance, these comprised 20 and 475 specimens, 2.95% and 70.2% of the total number of bees collected on enhanced areas ($n = 677$). Cherry visiting
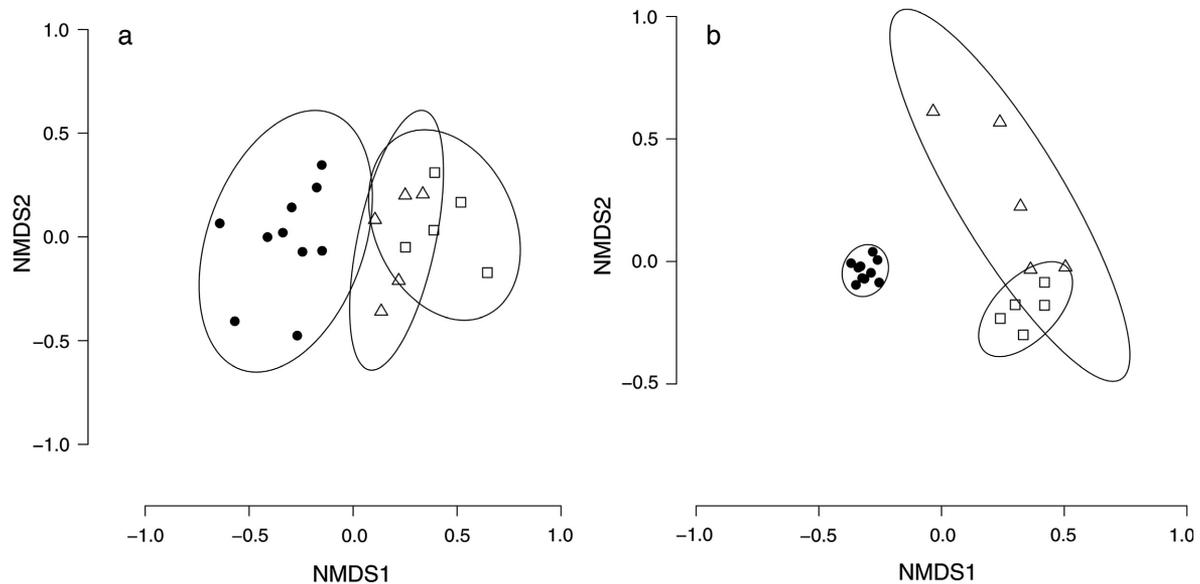
FIG. 3. Nonmetric multidimensional scaling plot using Bray Curtis dissimilarity distances for the spring crop pollinating wild bee community visiting (a) blueberry and (b) tart cherry in May and early June (black circles), and for the wild bees visiting enhanced (open squares) and control (open triangles) herbaceous habitats adjacent to these respective crops during late June–September. Ellipses represent groupings by season and by enhancement type using 95% confidence intervals.

species were the most commonly collected species on enhanced areas (Table 1b).

DISCUSSION

In the blueberry and tart cherry farms in this study, we found no difference in the abundance of bees on-crop during bloom regardless of whether there was a pollinator enhancement present. This result was found for both long-season and short-season bees in both blueberry fields and cherry orchards. These results are in direct contrast to previous work in the highbush blueberry system; Blaauw and Isaacs (2014) found that numbers of wild bees visiting blueberry flowers increased adjacent to enhanced areas three and four years after establishment. The pollinator community recorded by Blaauw and Isaacs in 2009–2012 was one in which wild bees were proportionally more abundant, with bumble bees representing 7.9% and other wild bees 4.7% of bee visits to blueberry flowers compared to 1.5% and 3.4%, respectively, for this study during 2013–2017. The 2009–2012 wild bee community was also dominated by long-season bees, predominantly bumble bees, with 86.0% of observed visits compared to 14.0% from short-season bees.

The large difference in relative bumble bee abundance between this study and previous research could potentially explain the difference in the response of wild bee crop visitors between the two studies, since bumble bees are long-season bees that visit the enhancements extensively, and have been demonstrated to respond positively, at the population scale, to an increase in summer resource abundance (Wood et al. 2015, Carvell et al. 2017). Compared to the bees visiting cherry flowers, blueberry flowers attract a more functionally diverse pollinator community, including more long-season bees, which should respond positively to these enhancements. Bumble bees are often recorded as the

most important wild pollinators of blueberry in Michigan (Blaauw and Isaacs 2014) and other parts of North America (Button and Elle 2014, Nicholson et al. 2017). The specific sites used in this study were different from those used by Blaauw and Isaacs (2014), but both studies were conducted in the same region of southwest Michigan. It is therefore concerning that over a period of <10 yr, bumble bees appear to have decreased from 58.1% to 30.6% of the wild bee blueberry pollinating community in this region.

Rapid declines in the wild bee pollinating community have been observed when changes in pesticide management occur, for example in the introduction of the organophosphate fenitrothion to New Brunswick, Canada, which significantly reduced blueberry pollination and yield compared to neighboring provinces (reviewed Kevan and Plowright [1995]). Pesticide use in the Michigan blueberry system has increased since detection of the spotted wing *Drosophila* (SWD), *Drosophila suzukii*, in 2010 (Isaacs et al. 2010). SWD is a significant invasive pest of fruit crops such as blueberry and cherry and is managed through insecticide applications during fruit ripening (Van Timmeren and Isaacs 2013, Diepenbrock et al. 2016). As long-season bees, bumble bees are more likely to be exposed to this increased post-bloom insecticide use than short-season bees, many of which have completed their life cycle by the time bloom ends. Without a long-term monitoring program, it is difficult to determine whether or not bumble bees or other long-season bees have been affected by pest control practices. No baseline data exist for cherry orchards in Michigan so it is also not possible to comment on whether bumble bees have become a less important component of the cherry pollinating wild bee community during this period.

Compared to the blueberry wild bee community, the cherry community was dominated by short-season bees, predominantly *Andrena* species. While wild pollinators of cherry are

relatively understudied, solitary bees, including *Andrena*, have been identified as the most effective and economically important pollinators of apple, *Malus pumila*, a similar flowering Rosaceous crop (Garratt et al. 2016). The importance of short-season bees in this system is reflected in the low overlap between the bee communities visiting the crop and the communities visiting the herbaceous enhancements.

Even though the blueberry pollinating community was evenly split between long- and short-season bees, pollen dietary analysis suggested that woody plants were the most important food resource for the community as a whole. The native woody plants *Salix*, *Acer*, *Prunus*-type, *Rubus*, and *Rhus* were all ranked in the top 10 pollen types most commonly collected by the wild bees visiting blueberry and cherry. In an assessment of types of pollen collected by wild bee pollinators found visiting crop flowers in New York apple orchards (including both long- and short-season bees), Russo and Danforth (2017) found that, in addition to apple pollen, the majority of other pollen types were collected from early flowering woody plants such as *Prunus* and *Salix*. Long-season crop pollinating bees such as *Bombus*, *Xylocopa*, and *Ceratina* are social or subsocial and require pollen and nectar resources throughout both the spring and the summer in order to found nests and raise workers/subservient daughters (Cardinal and Danforth 2011, Dicks et al. 2015). Bumble bee species can benefit from an increase in spring resource availability, increasing early colony growth (Westphal et al. 2009), so increasing the abundance of flowering woody plants is likely to benefit both the long- and short-season wild bee communities, as well as honey bees that can forage extensively from trees during the spring (Hawkins et al. 2015).

Proximity to seminatural habitat in temperate areas (primarily woodland) has been consistently associated with increased visitation rates of wild bees to spring flowering crops like apple (Joshi et al. 2016) and blueberry (Gibbs et al. 2016, Nicholson et al. 2017). More broadly, the stability of pollination services declines with increasing distance from seminatural habitat (Garibaldi et al. 2011). While the importance of seminatural habitat has been recognized, woody species offer an opportunity for low maintenance plantings that can be integrated into fencerows and hedges within intensive farmland (Hannon and Sisk 2009, Kremen and M'Gonigle 2015). Much of the focus on reversing losses of wild bee populations that have occurred as a result of agricultural intensification has concentrated on herbaceous plantings, in part due to the substantial declines of flower-rich agricultural grasslands in Europe (Carvell et al. 2006) and the loss of prairie habitats in North America (Samson and Knopf 1994, Ramankutty and Foley 1999). The focus on herbaceous plant communities that flower outside of crop bloom is also partly driven by grower concerns that creating patches that flower during crop bloom will reduce the number of bees visiting their crop, though empirical evidence for this is mixed, with a negative impact seen in the tropics (Peters et al. 2012) and no effect was seen in temperate areas (Lundin et al. 2017).

Herbaceous floral enhancements attracted a greater abundance, species richness and number of pollen specialist bee species compared to control areas. Most of the specialist bees found in common between enhanced and control strips collect pollen from *Solidago* and *Symphyotrichum*, plant species that are able to persist as weeds in a variety of grassy habitats and are common throughout the study region. In contrast, the wider selection of prairie plants like *Helianthus*, *Rudbeckia*, *Ratibida*, and *Monarda* was found in greatest abundance in the enhancements and supported a wider variety of summer specialist bees.

Conclusions

Overall, the creation of summer-flowering herbaceous enhancements did not increase the abundance of wild bee pollinators visiting spring-flowering fruit crops in this study. Providing foraging resources for summer-flying bees is an appropriate conservation goal in its own right, and may be preferable since summer bees have declined more than spring bees (Scheper et al. 2014). However, if the goal of implementing herbaceous enhancements is to increase the abundance of wild bees visiting crop flowers, the efficacy of such interventions will be limited if the wild bee pollinator community is dominated by short-season bees that have very limited phenological overlap with such enhancements. Understanding the identity and ecology of crop pollinators is important if appropriate strategies are to be developed to increase their abundance (Garratt et al. 2014). Where the wild bee pollinator community visiting a spring-flowering crop contains a mixture of long- and short-season bees, increasing the availability of flowering woody plants is likely to complement flower-rich grassland habitats for season-long enhancement of bee populations.

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