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RESEARCH PAPER

Proximity to wildflower strips did not boost crop pollination on small, diversified farms harboring diverse wild bees

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Abstract

The yield of many agricultural crops depends on pollination services provided by wild and managed bees, many of which are experiencing declines due to factors such as reductions in floral resources. Thus, improving pollinator habitat on farmlands using management strategies like planting wildflower strips is vital for wild bee conservation and sustainable crop pollination. Yet, few studies have examined whether and at what spatial scales wildflower strips enhance crop pollination and yields, and most research has been conducted in large-scale commercial agriculture. Therefore, we investigated the effects of wildflower strips on crop pollination on small, diversified farms (i.e., those growing a variety of crop species) where wild bee diversity and abundance is predicted to be comparatively high. Over three years, on four diversified farms in Montana USA, we tested the hypothesis that distance (20, 60, and 180 m) of crops from native perennial wildflower strips planted alongside crop fields affected wild bee visitation, pollination, and yields of squash and sunflower crop plants. We found that distance to wildflower strips did not affect bee visitation or pollination in crops. Squash yield was pollen-limited in the growing season prior to wildflower strip establishment, and in one of the two years after wildflower strip establishment, but proximity to wildflower strips did not influence the magnitude of pollen limitation. Sunflower seed production was not pollen-limited in any year. Our findings demonstrate that even on diverse farms with wildflower strips and a demonstrated high diversity of bees, some crops do not necessarily receive maximum pollination, regardless of distance from the wildflower strips. However, the value of wildflower strips for supporting wild bee diversity, and other ecological or economic benefits, needs consideration for a full understanding of this pollinator habitat management strategy.

Keywords: Agroecosystem; Competition for pollinators; Distance effects; Floral enhancements; Habitat management; Hedgerows; Native plants; Native bee conservation; Pollinator conservation; Pollen limitation

Introduction

Pollination is a vital ecosystem service and of great economic value in agriculture because most of the world's leading non-grain food crops grown for seed and fruit

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production benefit from insect pollinators, making the long-term health and stability of pollination systems an important priority for both food security and economic sustainability (Gallai, Salles, Settele & Vaissière, 2009; IPBES, 2016; Klein et al., 2007). Bees are the primary pollinators of flowering plants, including crop species (Michener, 2007). Managed European honey bees (*Apis mellifera* L.) top the list of crop pollinators globally, though wild bees are more efficient pollinators for some crops (Garibaldi et al., 2011a, 2013; Klein et al., 2007; Reilly et al., 2020; Winfree, Williams, Dushoff & Kremen, 2007).

Given the value of pollinators, it is of great concern that honey bees (e.g., Ellis, Evans & Pettis, 2010) and some wild bee species (e.g., Bartomeus et al., 2013; Burkle, Marlin & Knight, 2013; Cameron et al., 2011; Potts et al., 2010) have experienced population declines due to factors such as the loss of important non-crop floral resources in simplified, large-scale, intensively-managed agroecosystems (Biesmeijer et al., 2006; Goulson, Nicholls, Botías & Rotheray, 2015; Winfree, Bartomeus & Cariveau, 2011). Whether bee declines result in decreases in crop pollination and yields is not well-understood because research on pollen limitation (i.e., the degree that seed production is limited by pollen availability; Knight et al., 2005) has focused more on wild plants (Bennett et al., 2020) than crops (Benjamin & Winfree 2014; Garratt et al., 2018; Groeneveld, Tscharntke, Moser & Clough, 2010). But, a recent experimental study of seven pollinator-dependent crops in the U.S. and British Columbia found evidence of pollen limitation in five of the crops, suggesting that lower bee numbers could impact crop yields (Reilly et al., 2020). This finding supports other works indicating pollen limitation of crops globally (e.g., Garibaldi, Aizen, Cunningham & Klein, 2009, Garibaldi, Aizen, Klein, Cunningham & Harder, 2011b). Reilly et al. (2020) also found that the contribution of wild bees to crop pollination in the U.S. has been underestimated. Therefore, measures aimed at conserving or enhancing wild bee communities and their pollination services in agricultural landscapes should be prioritized.

One on-farm habitat management strategy to support pollinators that has received attention recently is providing diverse, alternative non-crop floral resources such as wildflower strips or hedgerows, which can also provide valuable nesting sites (e.g., hollow plant stems) and nesting resources (e.g., leaves, plant trichomes, resin) (Albrecht et al., 2020; Requier & Leonhardt 2020; Venturini, Drummond, Hoshide, Dibble & Stack, 2017a). The main assumption behind these approaches is that wildflower plantings will increase wild bee populations, leading ultimately to higher crop yields. Incorporation of wildflower plantings into agriculture can increase local diversity, abundance, and reproductive success of wild bees (e.g., Blaauw & Isaacs 2014; Carvell, Meek, Pywell, Goulson & Nowakowski, 2007; Graham et al., 2020; Klatt, Nilsson & Smith, 2020; Williams et al., 2015). But, few studies have examined whether wildflower strips increase pollination of crops (e.g., Blaauw & Isaacs 2014; Carvalheiro, Seymour, Nicolson & Veldtman, 2012; Kleijn et al., 2019; Pywell et al., 2015; Uyttenbroeck et al., 2016; Venturini, Drummond, Hoshide, Dibble & Stack, 2017b). A recent synthesis found no overall effect of flower strips on crop pollination or yields, though pollination services were higher for crops closer to flower strips (Albrecht et al., 2020). Whether or how changes in bee measures affect crop pollination and yield at varying distances from wildflower plantings is not well understood and multiple hypotheses exist regarding these distance effects of wildflower plantings on crop pollination. For example, if wildflower plantings facilitate pollinator visits to adjacent crops via spillover effects from the floral enhancements (Morandin & Kremen 2013), then we would expect crops closest to the plantings to have the lowest level of pollen limitation. Alternatively, if wildflower plantings outcompete and draw pollinators away from nearby crops (Lander, Bebber, Choy, Harris & Boshier, 2011; Nicholson et al., 2019), then we would expect crops closest to the plantings to have the highest level of pollen limitation. Additionally, these contrasting distance effects of wildflower plantings on crop pollination are likely restricted to small spatial scales (Ganser, Mayr, Albrecht & Knop, 2018) and may vary with timing of crop and wildflower bloom (Grab, Blitzer, Danforth, Loeb & Poveda, 2017) and with landscape context (Grab, Poveda, Danforth & Loeb, 2018) among many other factors.

Most research on wildflower strips has been conducted on large commercial farms planted to monocultures, which represent most food production systems, as they are expected to have the greatest impact by providing wild bees with high-value food resources in otherwise simplified, resource-limited landscapes (Kennedy et al., 2013; Kremen, Williams & Thorp, 2002; Scheper et al., 2013, 2015). Much less is known about the potential for wildflower strips to benefit bees on small-scale, diversified farms (i.e., those growing a diversity of crops), which have inherently higher crop heterogeneity compared to large-scale simplified farms. Increasing crop heterogeneity (e.g., increasing crop diversity and decreasing farm size) can have positive effects on biodiversity similar to increasing semi-natural habitat (i.e., increasing agricultural landscape heterogeneity) (Sirami et al., 2019). For example, irrespective of the amount of semi-natural habitat between fields, decreasing mean field size benefited farmland biodiversity (Sirami et al., 2019). Due to higher biodiversity, including pollinators, crops on small, diversified farms may not be pollen-limited (depending on the abundance of crop pollinators and the crop species) independent of the surrounding landscape context, and therefore may not benefit from the addition of wildflower strips. But, neither pollen limitation of crops nor the effects of proximity to wildflower strips on crop pollination have been previously studied on small, diversified farms. Thus, additional research is needed before generalizations can be made about this local-scale management practice for increasing pollination by wild bees.

We previously reported that over 200 species of wild bees were found on four small, diversified farms in southwest Montana, U.S.A. (Delphia, Griswold, Reese, O'Neill & Burkle, 2019b). Further, perennial wildflower strips that we planted were visited by more than 65% of those bee species, including rare species (Burkle, Delphia & O'Neill, 2020). As part of the same study on these four diversified farms, we explored the potential benefits of wildflower strips for increasing crop pollination and yields in diverse agroecosystems. Over three years, we tested the hypothesis that distance from wildflower strips influenced (1) pollinator visitation rates and (2) pollen limitation of reproductive success (i.e., yield) in squash and sunflower crops. We hypothesized that if crops were pollen-limited, then crops positioned closer to the wildflower strips would experience higher rates of bee visitation, lower pollen limitation, and greater yields than crops positioned further away.

Materials and methods

Study sites and wildflower strips

This research was conducted over three years (2013−2015) at four small, diversified vegetable farms (ca. 3−7 acres in vegetable production) growing a variety of crops that require or benefit from pollinators for fruit set (e.g., summer squashes, tomatoes, beans, and strawberries) as well as crops that do not require pollination (e.g., herbs, lettuce, carrots, onions) in southwest Montana USA (all sites were within 24 km of Bozeman, Gallatin County, MT; 45.6770° N, 111.0429° W). Farms varied in micro-climate, weed densities, management practices, and surrounding landscape among many other factors (see Appendix A: Farm details).

We chose plant species for the wildflower strips that varied in flower color, morphology, and bloom phenology (Tuell, Fiedler, Landis & Isaacs, 2008), and that would succeed in typical agricultural field conditions in this area (full sun, drought tolerance). Our list included the following nine native perennials: *Campanula rotundifolia* L. (Campanulaceae), *Erigeron speciosus* (Lindl.) (Asteraceae), *Gaillardia aristata* Pursh (Asteraceae), *Geranium viscosissimum* Fisch. & C.A. Mey. Ex C.A. Mey. (Geraneaceae), *Helianthus maximiliani* Schrad. (Asteraceae), *Heterotheca villosa* (Pursh) Shinners (Asteraceae), *Monarda fistulosa* L. (Lamiaceae), *Penstemon confertus* Douglas ex Lindl. (Plantaginaceae), and *Phacelia hastata* Douglas ex Lehm. (Boraginaceae). In early June 2013 at each farm, we established one wildflower strip measuring ca. 1 × 33 m using plugs of each plant species (5, 6, or 9 plugs of each species depending on the species' growth characteristics; 153 total plugs for each strip) started from seed in the greenhouse (additional details in Delphia, O'Neill & Burkle, 2019a). We planted three, ca. 1 m^2 -replicates of each of the nine species for a total of 27 plots per strip with ca. 0.22 m paths between plots (see Appendix A: Fig. 1). The order of the nine species within strips was randomly selected then replicated for each of three blocks on each farm. The wildflower strips were positioned at one edge of each farm to keep from interfering with farming activities and planted according to each farms' planting bed preparation methods (additional details in Delphia et al., 2019a). In previous studies, we sampled bees from the wildflower strips because we were interested in evaluating whether wildflower strips attracted wild bees that might also pollinate nearby crops (additional details in Burkle et al., 2020; Delphia et al., 2019a, Delphia et al., 2019b). Briefly, though some flowering by some species occurred in 2013 during the wildflower strip establishment phase, it was minimal (ca. 15% of the floral abundance) and,

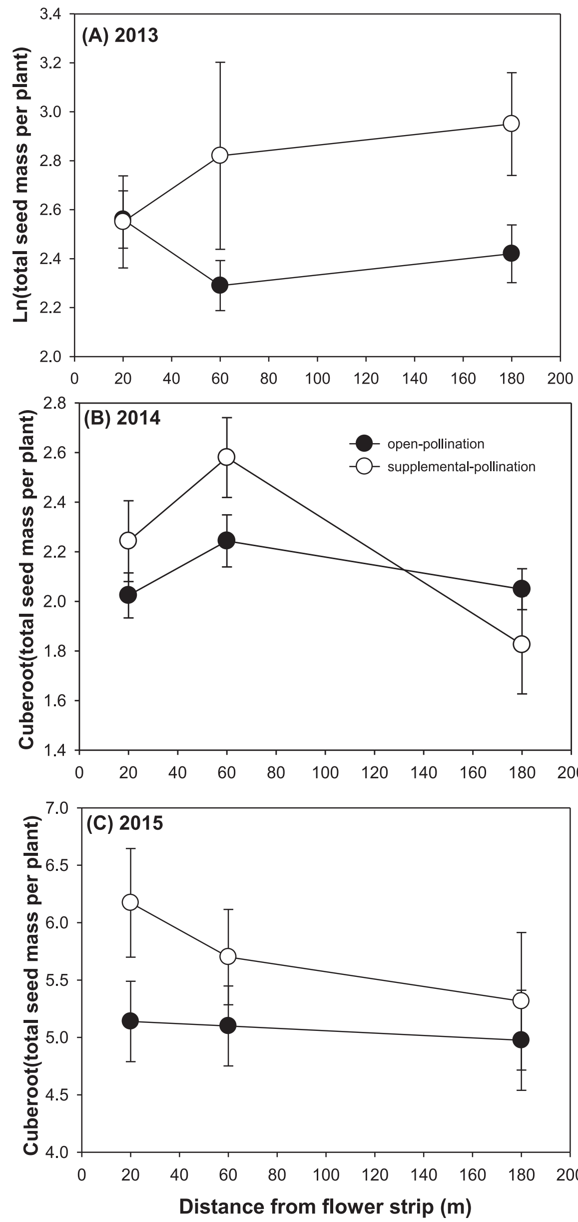

Fig. 1. Least-square mean (±SE) squash seed mass per plant among farms for open and supplemental pollination treatments by distance from wildflower strips in (A) 2013, (B) 2014, and (C) 2015.

on average, 6 weeks later than in 2014 and 2015 with most blooms in mid- to late-August through September. Wildflower strip establishment was successful, and, the following year (2014), all nine plant species bloomed, and we quantified floral abundance, date of initiation of bloom, date of peak bloom, and duration of bloom for each plant species in 2014 and in 2015 (see Burkle et al., 2020; Delphia et al., 2019a). In 2014 and 2015, plants bloomed during their typical bloom times from late-May through September, produced abundant seed (see Delphia et al., 2019a), and wildflower strips were visited by more than 130 wild bee species (see Burkle et al., 2020; Delphia et al., 2019b).

Crop strips to evaluate bee visitation rates and pollen limitation of yields

On each farm in each year, we established three 1 × 5 m annual crop strips each comprised of both acorn winter squash (Honey bear F1; *Cucurbita pepo* L. [Cucurbitaceae]) and sunflower (Royal Hybrid [RH] 1121 F1; *Helianthus annuus* L. [Asteraceae]) planted next to one another within the crop strip at 20, 60, and 180 m from the wildflower strip (see Appendix A: Fig. 1). We chose these common crop species because they require or benefit from pollinators for seed and fruit set (Bomfim, Freitas, de Aragão & Walters, 2016; Degrandi-Hoffman & Chambers 2006; Gallai et al., 2009; Mallinger, Bradshaw, Varenhorst & Prasifka, 2019). Squash has an estimated 95% dependance on insect pollination versus 25% in sunflower (Gallai et al., 2009), and, for the sunflower cultivar we used, yields improved with bee visitation (Mallinger et al., 2019). These crops also represent different plant families with distinct floral morphologies and bloom times, so likely attract different guilds of bees. Each year we grew squash and sunflower plants from seeds in the greenhouse for transplantation onto farms in mid-June. We transplanted eight squash and eight sunflower plants at each crop strip for a total of 24 plants of each species at each farm. Our experimental crop strips were planted in the same location on each farm in each year but owing to each farm's crop rotation schedule and within season succession planting, our crop strips were positioned next to different crops in each year and different crops within the same season.

To determine the degree to which reproduction of crops was pollen-limited, we performed standard supplemental pollinations on half of the squash and half of the sunflower plants in each crop strip, allowing the remaining half to be open-pollinated. We randomly assigned plants to open versus supplemental pollination treatments as flowers opened to ensure that treatments were equally distributed through time. Treatments were performed weekly throughout flowering (mid-July to early September). For squash, we used open male flowers of the same cultivar from another individual plant from the crop strip for supplemental pollinations. After pollinating, we left female flowers open (not bagged) allowing for additional pollination services. Similarly, for sunflower, we used pollen collected from another individual plant from the crop strip of the same cultivar for supplemental pollinations and, after pollinating, plants were left open allowing for additional pollinator visits. At the end of each growing season, we harvested all plants from crop strips and measured average fruit mass (g), fruit and seed set, and dry seed mass (g) for each squash and sunflower plant. For squash plants, we also measured dry plant biomass (g). For sunflowers, we used the product of plant height (mm) and maximum stem width (mm) as an index of biomass following Nezami, Khazaei, Boroumand and Hosseini (2008).

We recorded the species composition of bee assemblages visiting crop strips and bee-visitation rates. On calm, sunny days between 09:00 and 17:00 h, we conducted timed observations (10 min per crop strip) every other week in 2013 (sunflower only) and weekly in 2014 and 2015 (squash and sunflower) during the flowering period and captured all bees visiting flowers for identification to species in the lab (see Appendix A: Taxonomic keys).

Statistical analyses

Bee visitation rates

Bee visitation rates for squash (2014 and 2015) and sunflower (2013−2015) were calculated as total bee visits per open flower per minute in each crop strip on observation days. To determine how bee visitation rates to squash and sunflower varied with distance from wildflower strip and among farms, we used separate linear mixed-effects models for each year (flower strips were not yet established in 2013). We included distance from flower strip as a fixed effect and farm as a random effect. To account for differences among farms in landscape context (see percentage ranges for landscape types in Appendix A: Farm details), we included the percentage of surrounding semi-natural land cover within 1000 m (calculated using caltopo.com; for more details see Burkle et al., 2020) as a covariate.

Pollen limitation of squash and sunflower yields

For squash and sunflower, we measured multiple metrics of reproductive success, including the total number of seeds per plant, total seed mass per plant, and mass per seed; for squash we also measured total fruit mass per plant. Squash yield is typically measured by growers as total fruit mass per plant. However, squash fruit mass was highly correlated with the other seed-related measures of reproductive success and yield across plants ($r > 0.74$, $P < 0.0001$ in each year). Because seed metrics were correlated across plant individuals (squash: $r > 0.73$, $P \langle 0.0001$; sunflower: $r \rangle 0.56$, $P < 0.0001$ in all cases) and we observed the same responses to our supplemental pollination treatment for each of these metrics (see Appendix A: Tables 1−5), we report results for total seed mass per plant only as a measure of yield.

To assess the degree of pollen limitation of reproduction at varying distances from the wildflower strips in each year (2013−2015), total seed mass per plant for squash and sunflower were analyzed using separate linear mixed-effects models. Distance and pollination treatment were included as fixed effects, and farm was included as a random effect to account for potential non-independence among experimental crop plants on a farm (e.g., local soil conditions, differences in wildflower strip establishment). We also included the interaction between distance and pollination treatment to test whether pollen limitation of reproduction varied by distance from the wildflower strip. The majority of crop plants produced a single fruit (squash) or one main flowerhead (sunflower); in a few cases, large squash plants produced two or three fruits and a few large sunflower plants produced auxiliary flower heads, and we included plant biomass (ln-transformed for squash) as a covariate. Percentage surrounding semi-natural land cover was also included as a covariate to account for variation among farms in landscape context. Sunflowers at one farm were destroyed by deer in 2014 and 2015, thus were excluded from our analyses. Squash total seed mass was ln-transformed in 2013, and cube-root transformed in 2014 and 2015 to meet the assumptions of normality. Sunflower total seed mass was square-root transformed in 2013 and 2014. The degrees of freedom reflect data collected at the individual plant level (the level at which the pollination treatments were implemented, and thus the unit of replication; this is standard methodology in experimental tests of pollen limitation [e.g., Burkle & Irwin 2010; Knight, 2004]). In years in which we detected pollen limitation of reproduction, we investigated correlations between the mean magnitude of pollen limitation of total seed mass per plant (log response ratio) and mean bee visitation rates to determine whether low visitation was related to strong pollen limitation.

Results

Squash: bee visitation rates and pollen limitation of yields

We observed 101 bee visitors of 11 species visiting experimental squash plants over two years (see Appendix A: Table 6). On all farms combined, *A. mellifera* were the most common bee visitors to squash flowers in the experimental crop strips, making up 88% of 68 visitors in 2014 and 73% of 33 visitors in 2015.

Bee visitation rates

Bee visitation rates to squash flowers did not differ with distance from wildflower strips or with percentage surrounding natural habitat in either 2014 or 2015 (Table 1).

Table 1. Mixed-effects linear model results of the influence of distance from wildflower strip and surrounding semi-natural habitat on bee visitation rates to squash in 2014 (R^2 = 0.11) and 2015 (R^2 = 0.20). *P*-values in boldface are significant at α = 0.05.

Source	DF	F	*P*-value	Estimate
2014				
Habitat	1, 40	0.45	0.57	0.00009
Distance	1, 40	0.63	0.43	0.00030
2015				
Habitat	1, 42	5.65	0.16	0.00043
Distance	1, 42	2.74	0.11	−0.00013

Pollen limitation of yields

Reproductive success (i.e., total seed mass per plant; yield) declined with distance of squash plants from the wildflower strips only in 2014 (Table 2, Fig. 1B). Supplemental pollination increased squash reproductive success by 14−15% in 2013 and 2015, but not in 2014 (Table 2; Fig. 1A−C). The percentage of surrounding semi-natural habitat did not influence squash reproductive success and there were no interactive effects in any year between pollination treatment and distance from wildflower strips on squash reproductive success (Table 2). Bee visitation rates to experimental squash strips were not related to the mean magnitude of pollen limitation of squash reproduction in 2015 (r = 0.19, P = 0.62).

Sunflower: bee visitation rates and pollen limitation of yields

We observed 185 bee visitors of 22 species visiting experimental sunflower plants over three years (see Appendix A: Table 6). The solitary bee *Melissodes agilis* Cresson was the most abundant sunflower visitor, accounting for 32% of bee visits, followed by *A. mellifera* (26%), *Bombus huntii* Greene (15%), and the sweat bee *Halictus ligatus* Say (6%).

Bee visitation rates

There were no differences in bee visitation rates to sunflowers across distances from the wildflower strips or with percentage surrounding semi-natural habitat (Table 3).

Pollen limitation of yields

Reproductive success (i.e., total seed mass per plant; yield) varied as a function of distance from the wildflower strips in two of three years (Table 4; Fig. 2A, C). But, across years, the distance-effects on reproductive success were not consistent (Fig. 2). Pollination treatment had no effect on reproductive success (Table 4). The percentage of surrounding semi-natural habitat did not influence sunflower reproduction and there were no interactive effects in any year between pollination treatment and distance from wildflower strips on sunflower reproductive success (Table 4).

Table 2. Mixed-effects linear model results of the influence of surrounding semi-natural habitat, distance from wildflower strip, supplemental pollination treatment, squash plant biomass, and the interaction between distance and supplemental pollination treatment on squash plant reproductive success (total seed mass) in 2013 ($R^2 = 0.68$), 2014 ($R^2 = 0.64$), and 2015 ($R^2 = 0.52$). *P*-values in boldface are significant at $\alpha = 0.05$.

Source	DF	F	*P*-value	Estimate
2013				
Habitat	1, 77	0.03	0.87	−0.00054
Distance	1, 77	0.96	0.33	0.00097
Pollination treatment	1, 77	3.84	**0.050**	0.15
Ln(Plant biomass)	1, 77	91.85	< **0.0001**	0.78
D x PT	1, 77	1.96	0.17	0.0014
2014				
Habitat	1, 69	0.009	0.93	−0.0005
Distance	1, 69	4.25	**0.043**	−0.0018
Pollination treatment	1, 69	0.92	0.34	0.059
Ln(Plant biomass)	1, 69	77.44	< **0.0001**	0.58
D x PT	1, 69	3.06	0.085	−0.0015
2015				
Habitat	1, 49	0.11	0.77	0.0042
Distance	1, 49	1.32	0.26	−0.0014
Pollination treatment	1, 49	5.79	**0.020**	0.17
Ln(Plant biomass)	1, 49	4.46	**0.040**	0.22
D x PT	1, 49	1.11	0.30	−0.0012

Table 4. Mixed-effects linear model results of the influence of surrounding semi-natural habitat, distance from wildflower strip, supplemental pollination treatment, sunflower plant biomass, and the interaction between distance and supplemental pollination treatment on sunflower plant reproductive success (total seed mass) and yield in 2013 ($R^2 = 0.52$), 2014 ($R^2 = 0.56$), and 2015 ($R^2 = 0.25$). *P*-values in boldface are significant at $\alpha = 0.05$.

Source	DF	F	*P*-value	Estimate
2013				
Habitat	1, 89	0.17	0.71	0.018
Distance	1, 89	4.20	**0.043**	0.0068
Pollination treatment	1, 89	0.086	0.77	0.23
Plant biomass	1, 89	8.02	**0.0057**	0.00004
D x PT	1, 89	0.040	0.84	0.0018
2014				
Habitat	1, 50	1.20	0.48	−0.050
Distance	1, 50	0.46	0.50	−0.0029
Pollination treatment	1, 50	0.031	0.86	−0.081
Plant biomass	1, 50	15.96	**0.0002**	0.00011
D x PT	1, 50	0.016	0.90	−0.0003
2015				
Habitat	1, 53	1.39	0.24	−0.40
Distance	1, 53	11.60	**0.0013**	−0.24
Pollination treatment	1, 53	0.28	0.60	−2.20
Plant biomass	1, 53	3.89	0.054	0.00013
D x PT	1, 53	0.084	0.77	−0.019

Discussion

On the four small, diversified farms, proximity to wildflower strips did not enhance pollination services to focal crops. Sunflower reproductive success was not pollen-limited in any year, including the year prior to maturation of the wildflower strips. However, squash reproductive success was pollen-limited both before and after wildflower strip establishment, indicating a potential value of taking steps to attract more pollinators to the farms. Nevertheless, distance from wildflower strips did not influence the magnitude of pollen limitation for squash. This was the case despite the fact that, as part of the same study, we documented more than 130 bee species visiting flowers of the nine species of plants in the wildflower strips (Burkle et al., 2020; Delphia et al., 2019b). Of the 23 wild bee species recorded visiting crop plants, 18 species were also documented visiting the wildflower strips (see Appendix A: Table 6). In addition, the three main wild bee taxa attracted to the sunflowers, *M. agilis, B. huntii*, and *H. ligatus*, were among the ten most abundant species observed in the wildflower strips (Burkle et al., 2020).

Table 3. Mixed-effects linear model results of the influence of surrounding semi-natural habitat and distance from wildflower strip on bee visitation rates to sunflower in 2013 ($R^2 = 0.12$), 2014 ($R^2 = 0.09$), and 2015 ($R^2 = 0.12$). *P*-values in boldface are significant at $\alpha = 0.05$.

Source	DF	F	*P*-value	Estimate
2013				
Habitat	1, 18	0.48	0.50	−0.00012
Distance	1, 18	0.61	0.44	0.000068
2014				
Habitat	1, 27	0.59	0.52	0.00038
Distance	1, 27	1.05	0.32	−0.00017
2015				
Habitat	1, 20	0.45	0.60	−0.00076
Distance	1, 20	0.030	0.86	0.00006

Distance to wildflower strips did not increase pollinator visitation to squash flowers or increase plant reproductive success (i.e., yield). Open-pollinated squash exhibited lower total seed mass compared to hand-pollinated squash before and after wildflower strip establishment, indicating pollen limitation, but proximity to the wildflower strip did not reduce this problem. Unlike squash, sunflower never exhibited pollen limitation of seed production (i.e., neither prior to nor after wildflower strip establishment), and thus could not benefit further from any increases in visitation due to the presence of the wildflower strips. Additional studies are needed to determine whether wildflower strips enhance pollination in other diversified agroecosystems where crops are pollen-limited.

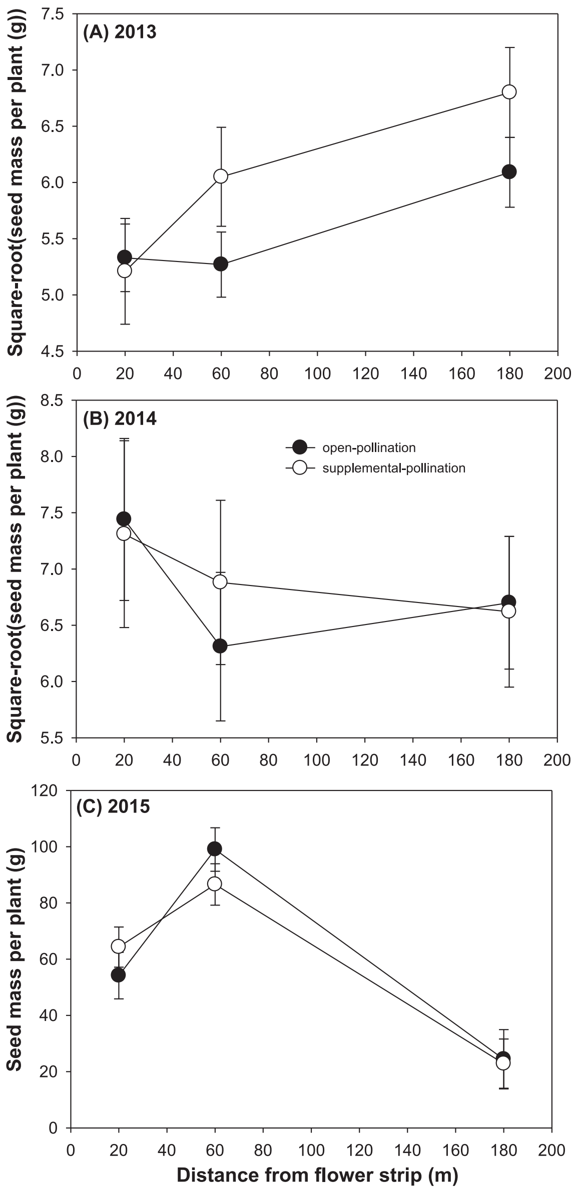

Fig. 2. Least-square mean (±SE) sunflower seed mass per plant among farms for open and supplemental pollination treatments by distance from wildflower strips in (A) 2013, (B) 2014, and (C) 2015.

Given that squash is heavily dependent on animal pollination (an estimated 95%; Gallai et al., 2009), there are several possible explanations for our observation of pollen limitation of squash reproduction, even in the presence of wildflower strips and on diversified farms. First, whereas honey bees (*A. mellifera*) were the most common squash visitors during our study and are important cucurbit pollinators (Bomfim et al., 2016; McGrady, Troyer & Fleischer, 2020), they may not have been abundant enough to provide adequate pollination (Petersen, Reiners & Nault, 2013), given that not all growers in our study had hives on their farms. Whether increased honey bee stocking densities could alleviate pollen limitation of squash reproduction in this system is unknown. In contrast, honey bees can act as nectar robbers, providing no pollination services (Willmer, 2011), and high honey bee densities can negatively impact the presence of wild bee pollinators (Mallinger, Gaines-Day & Gratton, 2017; Russo, 2016). Additional study is needed, including observations of pollinator behavior at squash flowers, for a more complete understanding.

Second, densities of some wild bee species that are efficient squash pollinators may have been too low at our sites and others were completely absent. Several studies have shown that bumble bees are more efficient cucurbit pollinators than are honey bees (Artz & Nault 2011; McGrady et al., 2020; Petersen et al., 2013; Stanghellini, Ambrose & Schultheis, 2002), but we recorded only one individual bumble bee (*B. huntii*) visiting our experimental squash plants. Another important cucurbit pollinator, *Peponapis pruinosa* (Say), is not reported in Montana (López-Uribe, Cane, Minckley & Danforth, 2016). Thus, based on how few wild bees visited experimental squash flowers, honey bees may be the primary pollinators of squash in this region.

Third, it may take longer than three years from wildflower strip planting to observe benefits on squash pollination and yields or on other pollen-limited crops. As with our study, most studies examining the effects of flower strips on crop pollination are limited to three years or less (Albrecht et al., 2020), so long-term data is lacking. Because increases in crop pollination and yield may be observed only after three or more years since flower strip planting (Blaauw & Isaacs 2014), the abundance of short-term studies may underestimate the overall value of flower strips (Albrecht et al., 2020). Additionally, the small size of our wildflower strips may have been a limitation. In studies where positive effects of habitat enhancement on crop pollination have been demonstrated, the wildflower plantings have been considerably larger (e.g., Blaauw & Isaacs 2014).

Lastly, it is possible that the wild bee fauna on our study farms were drawn away from the squash by other crops on the farm (e.g., large patches of cucurbits present on all farms; Cresswell & Osborne 2004), the wildflower strips (Lander et al., 2011; Nicholson et al., 2019; Peter, Hoffmann, Donath & Diekötter, 2021), or other plants in the adjacent unmanaged semi-natural habitat (Grab et al., 2018). All farms had some type of *Cucurbita* species planted (e.g., summer squashes, winter squashes, gourds, and pumpkins) each year with patch size and farm placement (layout) varying each year, depending on the farm and crop rotation schedule. It is possible that our small patches of experimental squash offered fewer flowers and were less attractive to pollinators than the relatively larger patches of cucurbits also present on farms, but we do not have the data to support or refute this. Although wild bees were abundant and diverse on the farms we studied (Delphia et al., 2019b), they were less frequent visitors to experimental squash than to the wildflower strips (see Burkle et al., 2020). In general, cucurbits have less attractive floral resources compared to wildflowers (e.g., Williams & Kremen 2007), and this comparatively lower attractiveness of squash is potentially exacerbated by the low number of open squash flowers available each day and relatively lower flower visibility (Bomfim et al., 2016). The potential of wildflower strips to distract pollinators and reduce crop pollination is receiving increased attention recently (Nicholson et al., 2019). Similarly, researchers have explored the use of wildflower strips as an alternative management strategy to intentionally reduce pollinator visitation rates (and ultimately reproductive success) of an unwanted target plant species (Peter et al., 2021). Therefore, adding wildflower strips to support wild bees for enhancing pollination of squash, at least in this region, might not always be useful. However, though this was not our approach for the present study, additional research examining crop pollination on diversified farms in the absence and presence of wildflower strips is needed to determine the degree to which pollinator abundance and crop pollination services may be enhanced by wildflower strips. Future work may also examine non-bee insects (e.g., syrphid flies) known to serve as crop pollinators and provide pest regulation services to crops in some systems (Rader, Cunningham, Howlett & Inouye, 2020).

On the diversified farms we studied, sunflower was not pollen-limited in any year, indicating plants received adequate pollination and could not benefit further from increased bee visitation resulting from the addition of wildflower strips. Though hybrid sunflower cultivars are bred to be self-fertile, different cultivars exhibit varying degrees of self-fertility, and, for the cultivar we studied, yields improved by 22% with bee visitation in the Northern Great Plains (i.e., North Dakota, South Dakota, and Nebraska) (Mallinger et al., 2019). Sunflower supported a diversity of wild bees on farms, including the most abundant visitor *M. agilis*—a native sunflower specialist (Parker, Tepedino & Bohart, 1981). Similarly, a diversity of native bees visited hybrid sunflowers across this region, with the most common and effective pollinators being sunflower specialists (Hurd, LaBerge & Linsley, 1980) including *Melissodes* species and *Andrena helianthi* Robertson (Mallinger et al., 2019). In fact, among ten sunflower hybrids examined by Mallinger et al. (2019), the cultivar that we studied was the second most attractive to pollinators (i.e., high bee visitation rates). Thus, sunflowers have value as pollinator food resources in this region as well as provide a marketable commodity (e.g., Todd, Gardiner & Lindquist, 2016).

Conclusions

Our study was motivated by the growing interest in providing floral resources as a management strategy for supporting wild bees in agroecosystems, as well as the limited number of studies that have tested whether proximity to wildflower plantings increase crop pollination and yields (i.e. farmer profits), which is important for increasing farmer adoption (Albrecht et al., 2020; Garibaldi et al., 2014; Venturini et al., 2017a). With most work being conducted on large, simplified farms, our understanding of the role of wildflower strips in increasing crop pollination and yields on small, diversified farms is especially limited, as is our general knowledge of crop pollen limitation. Given that squash plants were pollen-limited before and after wildflower strip establishment and sunflower was never pollen-limited, our findings suggest that local-scale habitat manipulation on diversified farms may not enhance crop pollination, though further study in other regions is needed. Additionally, despite being located on diversified farms that harbor high wild bee abundance and diversity, some crops may still experience pollen limitation. Our cumulative findings in this system highlight the need to consider other ecological (wild bee diversity; Delphia et al., 2019b) and economic (seed sales; Delphia et al., 2019a) benefits beyond increases in crop yields for a complete understanding of the value of wildflower strips for wild bee conservation on farmlands and for encouraging farmer adoption of this management practice.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

CRediT authorship contribution statement

Casey M. Delphia: Conceptualization, Methodology, Data curation, Investigation. **Kevin M. O’Neill:** Conceptualization, Methodology, Data curation. **Laura A. Burkle:** Conceptualization, Methodology, Data curation, Formal analysis.

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Data will be archived in Dryad.

Supplementary materials

Supplementary material associated with this article can be found, in the online version, at doi:10.1016/j.baae.2022.03.010.

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