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Flower plantings increase wild bee abundance and the pollination services provided to a pollination-dependent crop

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Summary

1. Pollination services from wild insects contribute to crop productivity around the world, but are at risk of decline in agricultural landscapes. Using highbush blueberry as a model system, we tested whether wildflower plantings established adjacent to crop fields would increase the abundance of wild pollinators during crop bloom and enhance pollination and yield.
2. Plantings were seeded in 2009 with a mix of 15 perennial wildflower species that provided season-long bloom and increased plant density and floral area during the subsequent 3 years.
3. Honeybees visiting blueberry flowers had similar abundance in enhanced and control fields in all 4 years of this study, whereas wild bee and syrphid abundance increased annually in the fields adjacent to wildflower plantings.
4. Crop pollination parameters including percentage fruit set, berry weight and mature seeds per berry were significantly greater in fields adjacent to wildflower plantings 3 and 4 years after seeding, leading to higher crop yields and with the associated revenue exceeding the cost of wildflower establishment and maintenance.
5. *Synthesis and applications*. We suggest that provision of forage habitat for bees adjacent to pollinator-dependent crops can conserve wild pollinators in otherwise resource-poor agricultural landscapes. Over time, these plantings can support higher crop yields and bring a return on the initial investment in wildflower seed and planting establishment, also insuring against loss of managed pollinators. Further understanding of the importance of planting size, location and landscape context will be required to effectively implement this practice to support crop pollination.

Key-words: abundance, diversity, native, perennial, fruit, yield, syrphid, conservation, ecosystem services

Introduction

Many arthropods provide valuable ecosystem services, such as those that support human food production. Pollination services have been estimated at over US$200 billion annually around the world (Gallai *et al.* 2009), which includes the contribution of wild bees to crop productivity (Klein *et al.* 2007). However, wild insect pollinators and the pollination services they provide have declined in agricultural landscapes in some regions (Biesmeijer *et al.* 2006; Potts *et al.* 2010). Several factors associated with increased farming intensity to support growing human populations can limit the suitability of farm environments for insect pollinators, including reduction in natural areas, habitat fragmentation and scarcity of flowering food and nesting resources (Carvell *et al.* 2006). Monoculture plantings of crops lack floral diversity and can limit the provision of resources for pollinators throughout the season. Compared with more diverse landscapes, the lack of resources in intensively managed agricultural landscapes can reduce insect pollinator diversity (O'Toole 1993) and potentially decrease wild bee contributions to crop pollination (Potts *et al.* 2010).

Many pollinator-dependent crops are pollinated by the European honeybee, *Apis mellifera* (Free 1993; Delaplane & Mayer 2000), due to their ease of management and high abundance during crop bloom, achieved by bringing hives to fields. Dependence on this single species puts over a third of the world's food supply (Klein *et al.* 2007) at risk from the challenges facing honeybees (Neumann & Carreck 2010). In addition to the ongoing efforts to sustain honeybee populations, there is growing interest in practices that diversify the sources of crop pollination,

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such as integrating floral resources into farms to promote wild pollinators (Isaacs *et al.* 2009; Winfree 2010). Enhancement of structurally resource-poor environments through the establishment of habitats containing flowering plants and grasses can support beneficial insects in agricultural landscapes (Long *et al.* 1998; Kells, Holland & Goulson 2001; Sheffield *et al.* 2008). These agricultural restoration programmes are expected to provide greatest support for bees in simple landscapes with the greatest floral contrast to the background landscape (Scheper *et al.* 2013). Wildflower plantings can provide pollen and nectar resources when the crop is not in bloom and, depending on the bee species biology, may also provide nesting habitat (Carreck & Williams 2002; Kremen *et al.* 2004; Heard *et al.* 2007).

Plants that are dependent on bees for pollination can benefit from the proximity of floral resources at the field scale and from greater resources for bees at landscape scales. Larger flower plantings can support greater bee density and diversity plus improved wildflower pollination (B.R. Blaauw & R. Isaacs, unpublished), and higher proportions of natural area within landscapes are associated with improved crop pollination (Kremen, Williams & Thorp 2002; Holzschuh, Dudenhöffer & Tscharntke 2012). For crop systems in which pollination is provided by eusocial or multivoltine wild bees, flowering borders that bloom before and after the crop may be a precondition for maintaining diverse bee populations (Roulston & Goodell 2011). Adjacent wild habitat can increase pollinator abundance in almond (Klein *et al.* 2012) and mango (Carvalheiro *et al.* 2012) orchards, but direct positive influence on pollination was found only in the latter system where habitat was tailored to support pollinators. There is relatively little information on how local-scale improvement (Murray *et al.* 2012) of resource-poor areas using optimized mixes of wildflowers will affect pollination services in adjacent crop fields, although recent evidence from hedgerow plantings indicates that these act as net exporters of bees into adjacent farmland (Morandin & Kremen 2013). If such habitats can support crop pollination, adoption of these practices on farms will also depend on determining the economics of establishment and the expected returns from investment in the improvement practice.

To determine how wild bees respond to local habitat manipulation with native perennial wildflowers, we measured pollinator abundance within wildflower plantings on marginal land and in adjacent crop fields at blueberry farms in Michigan, USA. We tested the hypothesis that wild pollinator abundance, crop pollination parameters and yield would be higher in blueberry fields adjacent to wildflower plantings compared with fields adjacent to grass perimeters. Finally, we compared the value of investment in pollinator habitat establishment and the revenue generated by pollination-driven changes in blueberry yield under different fruit pricing and subsidy scenarios.

Materials and methods

EXPERIMENTAL DESIGN

In May 2009, we established wildflower plantings using fifteen Midwestern US native and perennial wildflower species at five highbush blueberry *Vaccinium corymbosum* L. farms in southwest Michigan, USA (details in Supporting Information). These plant species have previously been evaluated for their attraction to bees (Tuell *et al.* 2008). The plantings ranged from 0·06 to 1·01 ha, with dimensions from 15·2 × 36·6 m to 91·4 × 111·3 m, and these were established within 3 m of the crop fields, which had an average area (± standard error) of 3·1 ± 0·8 ha. Due to land development at one farm, only four sites were sampled in 2012. At each site, the field adjacent to the wildflower planting was paired with a control field of the same cultivar (Duke, Bluecrop, Jersey, or Elliott) adjacent to a regularly mown grassy field margin that was not sown with native seeds, that is, the typical field perimeter. Control fields were 175–470 m from the enhanced field border, and farm sites were separated by at least 9·6 km. The landscapes within a 1-km radius of the sampled sites were 55·3 ± 4·1% semi-natural habitat (forest and grassland) around the plantings and 59·3 ± 8·1% around the control sites. The densities of plants and blooms were sampled in the wildflower plantings and in the corresponding control perimeters, using the methods described in Appendix S1 (Supporting information). Flower bloom density was very low in the first season after seeding, with the percentage coverage of seeded species increasing annually as the plantings established (see Appendix S1, Supporting information).

POLLINATOR SAMPLING

To determine the response of pollinators to wildflower plantings, we sampled the pollinator community within crop fields, wildflower plantings and control field perimeters in years 1–4 (2009–2012). During peak crop bloom, observations were made on 30 blueberry bushes in each of the crop fields adjacent to the wildflower plantings and the control perimeters. Insects visiting blueberry flowers were observed on 15 bushes spaced between 1 and 4 m along the edge of the crop field for 15 min. This was repeated 15 m into the crop interior parallel to the border. Observers walked along the bushes stopping and recording the identity and number of insects observed visiting blueberry flowers during warm, calm and sunny days between 10:00 and 17:00 h. With the exception of honeybees *Apis mellifera* and bumblebees *Bombus* spp., all other bees and hoverflies (Syrphidae) were identified to family (Borror & White 1998; Ascher & Pickering 2012).

The abundance of each pollinator group observed visiting blueberry flowers per observation was compared between treatments using a generalized linear mixed model (GLMM) with treatment (wildflowers or control) as the fixed factor, farm site as a random factor, Poisson distribution and a log link function (Bolker *et al.* 2009). For this and the subsequent analyses, unless otherwise noted, we used SPSS, version 20; IBM Corp., Armonk, NY, USA. Data were analysed separately for each year, pooling the abundance data for observations taken along the crop edge and those taken within the interior for each of the two treatments. The bee community was analysed by determining the proportion of wild bees of all bees observed visiting blueberry flowers, and comparing between treatments using a two-tailed Fisher's exact test for each year (JMP, Version 8; SAS Institute Inc., Cary, NC, USA).

Corresponding with the sampling for wildflower bloom density, in the years after planting establishment, pollinator abundance in the wildflower plantings and control perimeters were sampled once a month from May to September. Each month, the area was sampled using five 30 s (2·5 min total) passes with a modified reversed-flow leaf blower (BG 56 C-E; Stihl, Waiblingen, Germany) with a fine mesh bag (150 μm; The Cary Company, Addison, IL, USA) placed over the intake to capture insects (Fiedler 2006). To limit the bias of sampling due to vegetation height (Hossain, Gurr & Wratten 1999), samples were distributed throughout the wildflower planting and control perimeter, from areas that were in bloom. Collected insects were later separated from plant matter, and pollinators were identified as described above. The abundance of each pollinator group collected was compared separately for each year between the two treatments using a GLMM as described previously for pollinator observations.

To determine the relationship between the average number of wild pollinators per sample and the average number of native wildflowers in bloom per 1 m^2, we calculated the Pearson product-moment correlation of average wild bees with native wildflower bloom density.

MEASURING POLLINATION

In years 1–4, components of crop yield were measured in the fields adjacent to wildflower plantings and in those adjacent to control perimeters. To measure pollination in each sampled blueberry field, 15 bushes along the crop edge and also 15 m within the interior of the crop field were randomly selected in each field. Prior to bloom, one flower cluster on each bush was randomly designated to be open pollinated (hereafter, open) while a similar cluster on a separate shoot was excluded from animal pollinators (hereafter, bagged) by enclosing it with a fine mesh bag (150 μm; The Cary Company) attached to the stem with a twist tie. The total number of blueberry flower buds in each cluster was counted just prior to bloom each year.

After bloom, open clusters were also enclosed with mesh bags to control for potential effects of bags on berry maturation. Prior to harvest, when *c.* 50% of the fruit per cluster were ripe, the open and bagged berry clusters were collected and the number of fruit recorded to calculate percentage fruit set. Seed number and berry weight are directly related to pollination success in this crop (Brewer & Dobson 1969), so average berry weight was determined for each cluster and the largest berry from each cluster was squashed inside a plastic bag and the number of mature seeds recorded. To account for parthenocarpy, the differences in fruit set, fruit weight and number of mature seeds between open and bagged samples were calculated for each sampling location to estimate the magnitude of pollination provided by insect pollinators. For each year, we compared the changes in pollination parameters (open minus bagged values) between blueberry fields adjacent to wildflower plantings and fields adjacent to control perimeters using a GLMM with treatment as a fixed factor, farm site as a random factor, a normal distribution and an identity link function. In Year 4, we compared the change in pollination parameters between treatments (flower and control) for the crop edge and interior with a GLMM as described above.

Using the change in average percentage fruit set and fruit weight between open and bagged treatments, and calculating fruit abundance per hectare based on bush spacing and flowers per bush, crop yield for the crop edge and interior was compared between fields adjacent to wildflower plantings and those adjacent to control perimeters. The number of bushes per hectare was calculated individually for each farm, and the average number of flowers per bush was determined from previously collected data for different blueberry cultivars [Jersey = 5556, Duke2944, Bluecrop = 3628 and Elliott = 2540 flowers per bush (A. Kirk unpublished)]. Yield (kg ha^{-1}) was estimated by multiplying bushes per hectare, flowers per bush, percentage fruit set and berry weight. Yields from the crop edge and interior were compared between the wildflower planting and control treatments using a GLMM as described previously. Yield data for the edge and interior positions were then combined for each year, and crop yield was compared between treatments for each year separately using a GLMM, as described above.

To understand the overall costs and benefits of wildflower plantings, all expenses involved in their establishment, including preparation, wildflower seeds, site maintenance and labour were recorded during the 4 years of this study. Using the estimated yield calculated from each year and the expenses, we determined the costs and profits, assuming 0·8 ha wildflower plantings placed in marginal land adjacent to 4-ha highbush blueberry fields over a 10-year period (see Appendix S2, Supporting information). To determine the potential yield benefits over this time span, changes in yield in response to wildflower plantings were determined for the first 4 years based on our data. To avoid unrealistic yield predictions, we then assumed that by Year 10, the expected yield would increase by roughly 30% and that the change in percentage yield between the wildflower and control treatments would increase by 4% from Year 4 to Year 5 and then decrease by half sequentially each year thereafter. Expenses for establishment and maintenance were calculated separately for scenarios with or without government cost sharing for pollinator habitat, and using published prices and yields of highbush blueberry (Joshua 2011). See Appendix S2 (Supporting information) for detailed wildflower planting costs and estimated profit.

Results

HABITAT ESTABLISHMENT

In all 4 years of this study, the density of seeded plant species per square metre within the wildflower plantings was greater than the density of seeded plant species in the control mown grass field margins (Table S1b, Supporting information; Blaauw & Isaacs 2014). The percentage cover of the seeded plants was also significantly greater within the wildflower plantings during each of the 4 years (Table S1b, Supporting information).

POLLINATOR ABUNDANCE AND COMMUNITY

During all 4 years of this experiment, there was no significant difference in the abundance of honeybees in blueberry fields adjacent to wildflower plantings compared with fields adjacent to control perimeters (Fig. 1a; Year 1: $F_{1,38} = 2{\cdot}27$, $P = 0{\cdot}14$; Year 2: $F_{1,38} = 0{\cdot}088$, $P = 0{\cdot}77$; Year 3: $F_{1,38} = 1{\cdot}89$, $P = 0{\cdot}18$; Year 4: $F_{1,30} = 0{\cdot}98$, $P = 0{\cdot}33$). In years 1 and 2, there was no significant difference in the

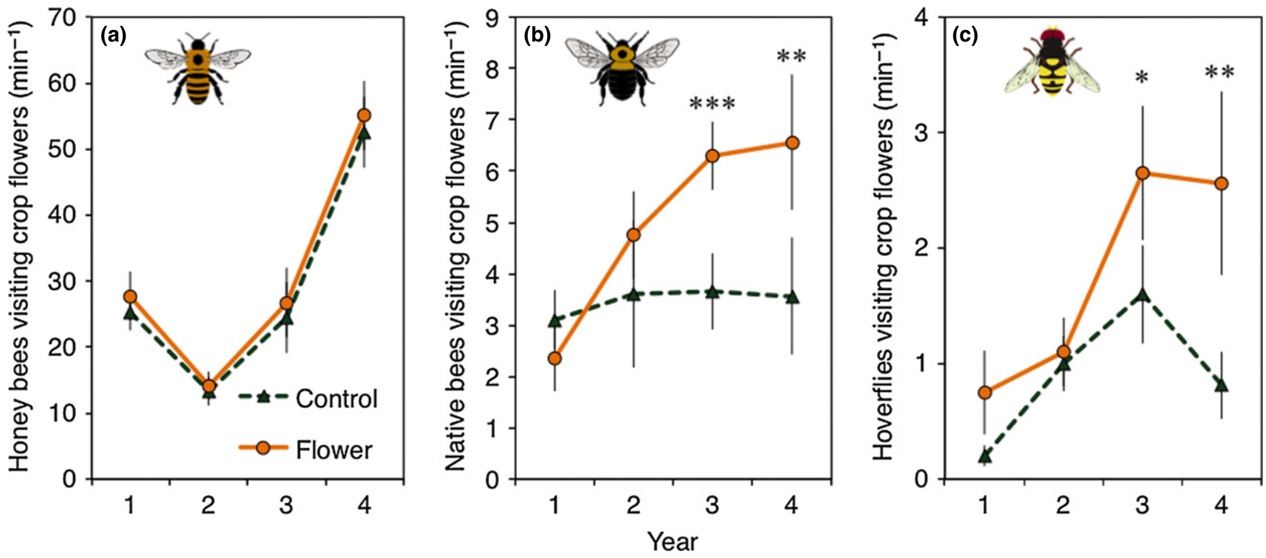

Fig. 1. Mean ± SE abundance of (a) honeybees, (b) wild bees and (c) hoverflies observed visiting blueberry flowers during 15 min observational samples. Asterisks indicate levels of significance (*$P < 0{\cdot}05$, **$P < 0{\cdot}01$, ***$P < 0{\cdot}001$) for difference between control and flower treatments.

number of wild bees observed between the two treatment fields (Fig. 1b; $F_{1,38} = 2{\cdot}1$, $P = 0{\cdot}16$, and $F_{1,38} = 1{\cdot}5$, $P = 0{\cdot}23$, respectively). Thereafter, relative bee abundance increased in the fields adjacent to the plantings, and in Year 3, almost twice as many wild bees were observed compared with fields adjacent to control perimeters ($F_{1,38} = 14{\cdot}7$, $P = 0{\cdot}0008$). The average number of wild bees visiting crop flowers did not increase greatly in Year 4, but remained significantly higher adjacent to wildflower plantings ($F_{1,38} = 13{\cdot}8$, $P = 0{\cdot}001$). The abundance of hoverflies visiting blueberry flowers exhibited a similar trend where the treatments were not significantly different until years 3 and 4 (Fig. 1c; Year 1: $F_{1,38} = 1{\cdot}5$, $P = 0{\cdot}054$; Year 2: $F_{1,38} = 0{\cdot}39$, $P = 0{\cdot}53$: Year 3, $F_{1,38} = 5{\cdot}1$, $P = 0{\cdot}03$: Year 4, $F_{1,38} = 13$, $P = 0{\cdot}001$).

Blueberry flowers were visited by a variety of wild pollinators, including bumblebees, sweat bees (Halictidae), mining bees (Andrenidae) and hoverflies (Fig. 2). Growers stocked fields with honeybees, which were the dominant pollinator visiting crop flowers, comprising at least 74% of the observed visitors. In Year 1, when the wildflowers were still seedlings, the proportions of wild pollinators to all pollinators were similar ($P = 0{\cdot}071$) between treatments (Fig. 2; control = 12% and flower = 10%). In Year 2, 22% of the pollinators observed visiting blueberry flowers adjacent to the control perimeters were unmanaged, compared with 31% in crop fields adjacent to wildflower plantings ($P = 0{\cdot}385$). In Year 3, the proportion of wild pollinators visiting blueberry flowers was significantly higher in fields adjacent to the wildflower plantings (25%) compared with the control (17%) ($P = 0{\cdot}002$). The proportion of wild pollinators decreased in both treatments in Year 4 (control = 6% and flower = 11%), but remained significantly higher in the crop fields adjacent to the wildflower plantings ($P = 0{\cdot}001$).

Vacuum sampling in the habitat immediately adjacent to blueberry fields revealed greater abundance of wild pollinators, including bees and hoverflies, in the presence of wildflowers. In Year 2, there was an average ± standard error of $0{\cdot}4 \pm 0{\cdot}27$ wild bees and $2{\cdot}65 \pm 1{\cdot}59$ hoverflies per 2·5 min sampling period within the control perimeters compared with $1{\cdot}4 \pm 0{\cdot}27$ bees and $4{\cdot}35 \pm 1{\cdot}6$ hoverflies within the wildflower plantings. The following year, only $0{\cdot}48 \pm 0{\cdot}35$ wild bees and $1{\cdot}8 \pm 0{\cdot}92$ hoverflies were collected within the control perimeter, whereas $2{\cdot}16 \pm 0{\cdot}34$ bees and $4{\cdot}12 \pm 0{\cdot}92$ hoverflies were collected from wildflower plantings. In both years, the number of wild bees was significantly greater in wildflower plantings (Year 2: $F_{1,38} = 9{\cdot}8$, $P = 0{\cdot}003$; Year 3: $F_{1,48} = 22{\cdot}8$, $P = 0{\cdot}0009$). Hoverfly abundance did not vary significantly between treatments in Year 2 ($F_{1,38} = 3{\cdot}09$, $P = 0{\cdot}07$), but in Year 3, significantly more hoverflies were collected in the wildflower plantings ($F_{1,48} = 21{\cdot}5$ $P = 0{\cdot}0001$). Also in Year 3, there was a significant positive correlation between the average number of blooms per square metre of the seeded forb species within the wildflower plantings and the average total number of wild pollinators collected ($r = 0{\cdot}75$, d.f. = 23, $P < 0{\cdot}0001$).

POLLINATION AND YIELD

In Year 1 of this study, the difference in average fruit set between open and bagged treatments was 7.6% greater in blueberry fields adjacent to the wildflower plantings (Table 1). However, average berry weight was 0.11 g higher in fields adjacent to the control perimeter, and there was no significant difference in average number of mature blueberry seeds (Table 1), resulting in an estimated yield that was similar for both treatments (Table 1). In Year 2, there was no significant difference

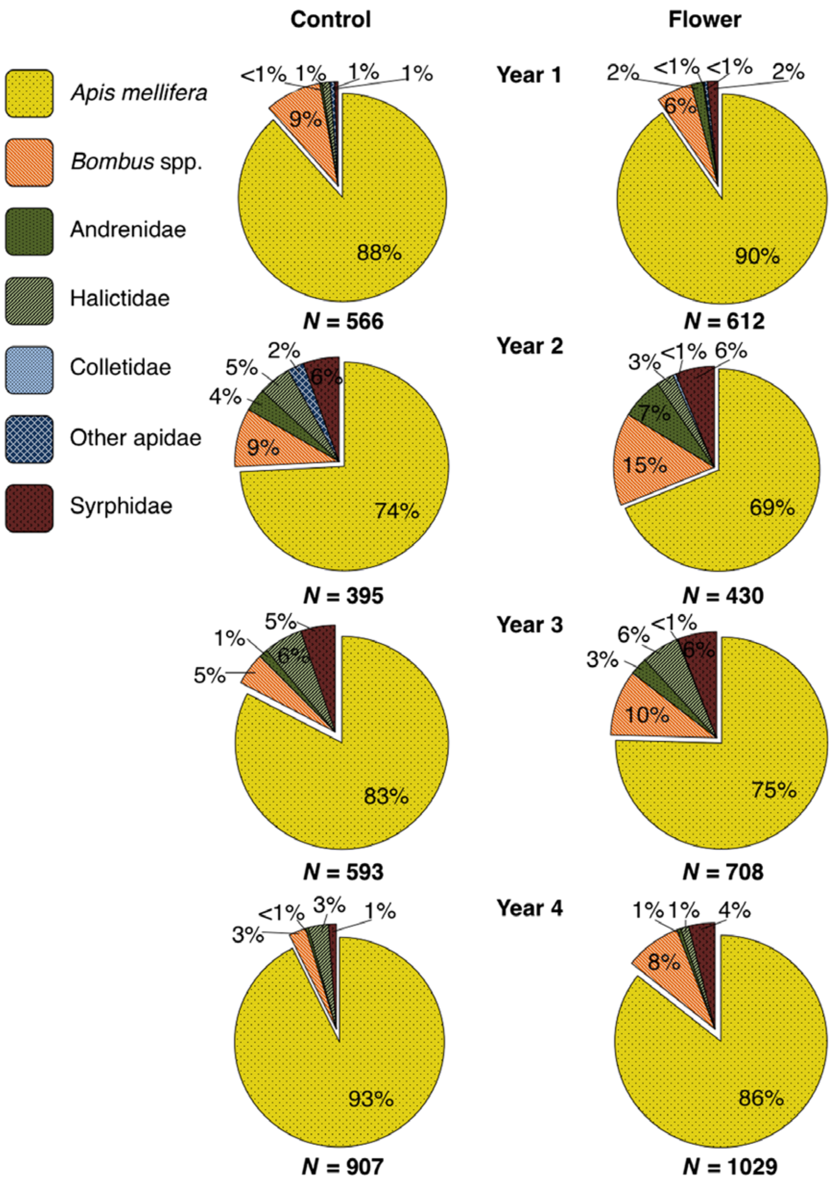

Fig. 2. Bee community observed in blueberry fields with or without adjacent wildflower habitat over 4 years.

between treatments in any of the pollination parameters or the yield. In Year 3, the changes in percentage fruit set, average berry weight and number of mature seeds were all significantly greater in blueberry fields adjacent to the wildflower plantings (Table 1), and this pattern continued in Year 4, resulting in significantly higher yield adjacent to wildflower plantings (Table 1).

Estimated blueberry yields were higher in crop fields adjacent to wildflower plantings than controls in years 3 and 4 (Table 1). By examining the two regions of the crop field separately (edge and interior), we found that in years 1 and 2, there were no differences in estimated crop yield along the edge or interior between the flower and control treatments (Table 2). In Year 3, the estimated yield was significantly higher along the edge, but not within the crop interior (Table 2), whereas in Year 4, the increase in pollination was more evenly distributed, with greater yield in both regions of the fields adjacent to the wildflower plantings (Table 2).

Expenses for establishment and maintenance were calculated for scenarios with or without cost sharing for pollinator habitat, and as expected, the time to reach positive profit was greater for the unsubsidized scenario receiving low to average berry prices (4–5 years) than for a subsidized planting at a farm receiving high prices (3 years, Fig. 3). For all scenarios, it is expected that the increase in yield benefit from pollination will reach a plateau within several years. See Appendix S2 (Supporting information) for a more detailed explanation of wildflower planting costs and estimated profit.

Discussion

The expected increase in global demand for agricultural products will likely result in further intensification of agricultural land use (Godfray *et al.* 2010). Finding ways to do this sustainably will require the design of farm systems that can support biodiversity while also enhancing crop

Table 1. Comparison of the average (± SE) changes (open-bagged) in pollination parameters for blueberry fields adjacent to control or flower treatments over 4 years

Pollination Parameter	Treatment	Year 1	2	3	**4**
Δ %Fruit Set	Control	30·1 ± 2·9	30·9 ± 2·7	26·5 ± 3·4	38·1 ± 2·9
	Flower	37·7 ± 3·0	32·9 ± 2·5	37·9 ± 3·1	50·3 ± 2·8
	F	3·7	0·29	8·4	9·3
	P	0·056	0·58	0·004	0·003
Δ Berry Weight (g)	Control	0·63 ± 0·08	0·52 ± 0·03	0·56 ± 0·05	0·47 ± 0·04
	Flower	0·52 ± 0·07	0·53 ± 0·03	0·62 ± 0·04	0·64 ± 0·04
	F	1·1	0·18	1·1	9·4
	P	0·29	0·67	0·3	0·002
Δ Mature Seeds	Control	20·7 ± 1·8	19·5 ± 0·8	15·0 ± 1·0	20·1 ± 1·2
	Flower	21·2 ± 1·4	19·5 ± 1·0	19·5 ± 1·0	23·6 ± 1·2
	F	0·05	0·001	11	5·1
	P	0·83	0·97	0·001	0·025
Estimated Yield (kg ha^{-1})	Control	7291·1 ± 496·9	4377·1 ± 218·7	6147·3 ± 462·9	3171·3 ± 237·4
	Flower	6887·4 ± 408·2	4610·62 ± 224·2	6995·1 ± 424·4	4148·1 ± 268·8
	F	0·79	0·65	11	39·3
	P	0·37	0·97	0·001	0·003

Table 2. Comparison of the average (± SE) estimated blueberry yield (kg ha^{-1}) for the different sampling regions (edge and interior) within crop fields adjacent to control or flower treatments over 4 years

Region	Treatment	Year 1	2	3	4
Edge	Control	7266·7 ± 661·4	4782·1 ± 339·9	5156·4 ± 498·3	2839 ± 314·3
	Flower	6576·1 ± 592·2	5104·4 ± 342·4	6734·9 ± 563·9	3940·5 ± 360·3
	F	1·1	0·61	10·3	8·7
	P	0·29	0·43	0·027	0·004
Edge	Control	7315·4 ± 746·4	3972·1 ± 269·4	7138·1 ± 767·1	3490·7 ± 351·6
	Flower	7198·6 ± 563·8	4116·9 ± 280·4	7255·3 ± 636·8	4372·6 ± 402·8
	F	0·03	0·15	0·03	10·9
	P	0·86	0·7	0·87	0·001

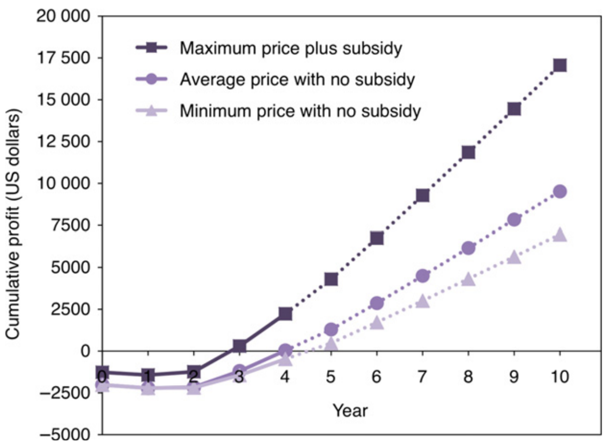

Fig. 3. Measured (solid line) and predicted (dashed line) profits from a 4-ha highbush blueberry field adjacent to a 0·8-ha wildflower planting. Scenarios provided are for minimum, average or maximum price of blueberries (Joshua 2011) and under conditions with or without pollinator habitat subsidy.

yield (Bommarco, Kleijn & Potts 2012; Tscharntke *et al.* 2012). Our study suggests that use of marginal land to establish wildflower plantings that provide season-long floral resources can support wild bees and enhance pollination in adjacent blueberry crop fields. This was seen even in situations where honeybees dominate the floral visitor community, which is consistent with previous findings that honeybees can supplement pollination from wild bees (Garibaldi *et al.* 2013).

Conserving a range of beneficial insects is important for reliably providing ecosystem services in agricultural settings (Naeem 1998; Kleijn & Sutherland 2003). The enhancement of wild bee abundance from wildflower plantings is likely due in part to the additional nesting and food resources provided, which can support their growth and persistence (Potts *et al.* 2005; Roulston & Goodell 2011). Because wild bee populations fluctuate from year to year and take time to colonize habitats (Williams, Minckley & Silveira 2001), the abundance of wild bees observed at wildflower-enhanced farms may be partially dependent on the flower abundance from the previous year. Establishing natural habitat in farms by removing vegetation may initially hinder pollinator populations, but the substantial increase in floral abundance, and thus greater food resources (i.e. pollen and nectar), in subsequent years likely explains the observed increase in wild bee abundance in years 3 and 4. It is also possible that these perennial plantings increase local nesting resources to further support wild bee populations.

The addition of floral resources also enhanced the abundance of hoverflies in adjacent blueberry fields. Although hoverflies are not effective pollinators of blueberry, they are efficient pollinators of other crops, such as mango (Dag & Gazit 2001) and oilseed rape (Jauker & Wolters 2008), and the larvae of aphidophagous species are also biological control agents of many soft-bodied arthropods (Bugg *et al.* 2008; Smith, Chaney & Bensen 2008), thus providing an additional ecosystem service to crops. The impact of flowering resources and their associated ecosystem service, such as pollination or pest control, will likely change depending on the type of crop. Further work is needed to better understand which crops are best suited for this approach and the extent to which multiple services might vary with plot size, configuration and distribution of these plantings (Brosi, Armsworth & Daily 2008). Larger wildflower plantings are expected to have more resources and hence higher capacity to support populations of beneficial insects (Slobodkin 1980; Kruess & Tscharntke 2000). Furthermore, increasing the size of the habitat can positively impact the services provided by insects supported by the additional floral resources (Blaauw & Isaacs 2012).

Floral diversity also increases pollinator diversity (O'Toole 1993), and thus, additional methods to determine species-specific responses to supplementary habitat are needed, as it is possible that these plantings function by attracting pollinator populations away from the control perimeters and the surrounding landscape. Such an aggregation of bees within plantings could negatively affect pollination in nearby fields without wildflower enhancements, if abundance of pollinators in the surrounding landscape was relatively low. Although we did not detect a decrease in pollination in control fields, our project was not designed to determine whether plantings act as concentrators or sources of pollinators, and further studies will be needed to determine the mechanism of pollinator enhancement (Kleijn *et al.* 2011). This can help determine the most appropriate strategies for implementing pollinator habitat on farms for potential restoration goals and to support crop yields (Brosi, Armsworth & Daily 2008; Morandin & Kremen 2013).

Crop yield can also be directly or indirectly affected by weather conditions (Retamales & Hancock 2012). During Year 4 (2012) of this study, there were atypically cool temperatures during blueberry bloom (Marino 2012), including periods of temperatures below freezing, which may have substantially influenced fruit production (Gough 1994). Indeed, in Year 4, there was a drop in percentage fruit set, berry weight and consequently crop yield for all blueberry sites adjacent to both wildflower plantings and control perimeters compared with previous years (Table 1). Year 4 also had uncharacteristically high temperatures and low precipitation during the summer months, likely causing considerable decrease in fruit yield from Year 3 to Year 4. Despite these conditions, fruit set and berry weight were not as negatively affected by the conditions in the crop fields adjacent to the wildflower plantings, suggesting that increased abundance of wild bees can provide insurance against potential yield loss from poor conditions (Naeem 1998; Winfree *et al.* 2007).

As with pollinator abundance, it took multiple years after wildflower establishment to detect a significant change in pollination within the adjacent blueberry fields. It is expected that as the wildflower plantings continue to establish, the crop pollination benefits will also continue to increase until reaching a maximum benefit. Over time, even a slight increase in fruit yield in high value crops such as blueberry can cover the costs of establishing and maintaining these wildflower plantings (Table S2, Supporting information).

Beneficial insects respond positively to the presence of flowering resources, but different insect taxa respond to these manipulations in varying ways (Tscharntke *et al.* 2007; Osborne *et al.* 2008) and may also respond to habitat at different scales (Steffan-Dewenter *et al.* 2002) or to the complexity of the surrounding landscape (Tscharntke *et al.* 2002). Recently, Carvalheiro *et al.* (2012) demonstrated that within large mango farms surrounded by natural habitat, the addition of small patches of native flowers can increase crop yield, but this small-scale habitat manipulation may only attract and concentrate beneficial insects that are already present in the surrounding landscape (Gurr, van Emden & Wratten 1998; Kleijn *et al.* 2011). At the landscape scale, natural habitat is necessary to support a diverse pool of wild pollinators and their services to crop fields (Carvalheiro *et al.* 2010; Klein *et al.* 2012), while at the field scale, the addition of floral resources may locally augment bee density and diversity. This is supported by the results from Heard *et al.* (2007) where landscape context, rather than local-scale forage resources, was the major influence on bee density in habitats restored with floral resources. Conversely, Meyer, Gaebele and Steffan-Dewenter (2007) observed that the density and diversity of insect pollinators increased with the size of flowering habitat. Similarly, in our study, bee abundance in blueberry fields during bloom increased with the size of adjacent pollinator plantings (data not shown), suggesting that there is benefit to establishing larger plantings. This is also expected to affect the magnitude of the return on investment, but with conflicting results in the literature on the importance of local-scale habitat manipulation, it is crucial that future studies address the combined influence of landscape context and local habitat manipulation on distribution and dispersal of beneficial insects and their ecosystem services within agricultural landscapes (Murray *et al.* 2012).

While there can be benefits for pollinators and crop yield from adding floral resources to agricultural landscapes, the costs of establishment and maintenance of those habitats might discourage farmers from adopting this approach. Even within agricultural landscapes surrounded by natural habitats, fruit production can be highly dependent on managed honeybees for crop pollination (Isaacs & Kirk 2010). However, we show here that providing habitat with season-long floral resources optimized for wild bees can provide yield benefits, with values exceeding the cost of habitat establishment and maintenance, even where honeybees are supplied for pollination. Thus, with the potential declines in biodiversity from agricultural intensification (Godfray *et al.* 2010), establishment of floral resources can be an important strategy in the conservation of wild bees, enhancing crop yield, and positively impacting the surrounding environment (Bommarco, Kleijn & Potts 2012; Tscharntke *et al.* 2012). Furthermore, financial incentive programmes to motivate landowners to undertake practices that support beneficial insects (EEC 1992; NRCS 2010), along with evidence for positive effects of pollinator abundances and crop yield enhancement, may make this strategy more economically attractive to growers (Kennedy *et al.* 2013). Thus, the results of this study have value to growers and conservationists alike, and can help guide future policy in the conservation and support of plant–pollinator interactions to help create more sustainable agricultural practices.

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References

Ascher, J.S. & Pickering, J. (2012) Discover life bee species guide and world checklist (Hymenoptera: Apoidea: Anthophila). http://www.discoverlife.org/mp/20q?guide=Apoidea_species. [Accessed 28 January 2009].

Biesmeijer, J., Roberts, S., Reemer, M., Ohlemüller, R., Edwards, M., Schaffers, A. *et al.* (2006) Parallel declines in pollinators and insect-pollinated plants in Britain and the Netherlands. *Science*, **313**, 351–354.

Blaauw, B.R. & Isaacs, R. (2012) Larger wildflower plantings increase natural enemy density, diversity, and biological control of sentinel prey, without increasing herbivore density. *Ecological Entomology*, **37**, 386–394.

Blaauw, B.R. & Isaacs, R. (2014) Wildflowers enhance pollinator services. figshare. http://dx.doi.org/10.6084/m9.figshare.966566.

Bolker, B.M., Brooks, M.E., Clark, C.J., Geange, S.W., Poulsen, J.R., Stevens, H.H. & White, J.S.S. (2009) Generalized linear mixed models: a practical guide for ecology and evolution. *Trends in Ecology and Evolution*, **24**, 127–135.

Bommarco, R., Kleijn, D. & Potts, S.G. (2012) Ecological intensification: harnessing ecosystem services for food security. *Trends in Ecology and Evolution*, **28**, 230–238.

Borror, D.J. & White, R.E. (1998) *A Field Guide to Insects: America North of Mexico*, 2nd edn. Houghton Mifflin Harcourt, New York, NY, USA.

Brewer, J.W. & Dobson, R.C. (1969) Seed count and berry size in relation to pollinator level and harvest date for the highbush blueberry, *Vaccinium corymbosum*. *Journal of Economic Entomology*, **62**, 1253–1256.

Brosi, B.J., Armsworth, P.R. & Daily, G.C. (2008) Optimal design of agricultural landscapes for pollination services. *Conservation Letters*, **1**, 27–36.

Bugg, R.L., Colfer, R., Chaney, W.E., Smith, H.A. & Cannon, J. (2008) Flower flies (Syrphidae) and other biological control agents for aphids in vegetable crops. *Agriculture and Natural Resources Publication*, **8285**, 1–25.

Carreck, N.L. & Williams, I.H. (2002) Food for insect pollinators on farmland: insect visits to flowers of annual seed mixtures. *Journal of Insect Conservation*, **6**, 13–23.

Carvalheiro, L.G., Seymour, C.L., Veldtman, R. & Nicolson, S.W. (2010) Pollination services decline with distance from natural habitat even in biodiversity-rich areas. *Journal of Applied Ecology*, **47**, 810–820.

Carvalheiro, L.G., Seymour, C.L., Nicolson, S.W. & Veldtman, R. (2012) Creating patches of native flowers facilitates crop pollination in large agricultural fields: mango as a case study. *Journal of Applied Ecology*, **49**, 1373–1383.

Carvell, C., Roy, D., Smart, S., Pywell, R., Preston, C. & Goulson, D. (2006) Declines in forage availability for bumblebees at a national scale. *Biological Conservation*, **132**, 481–489.

Dag, A. & Gazit, S. (2001) Mango pollinators in Israel. *Journal of Applied Horticulture*, **2**, 39–43.

Delaplane, K.S. & Mayer, D.F. (2000) *Crop Pollination by Bees*. CABI Publishing, New York, NY, USA.

EEC (1992) Council Regulation (EEC) No 2078/92 of 30 June 1992 of agricultural production methods compatible with the requirements of the protection of the environment and the maintenance of the countryside. *Official Journal of the European Communities*, **215**, 85–90.

Fiedler, A.K. (2006) *Evaluation of Michigan Native Plants to Provide Resources for Natural Enemy Arthropods*. MS, Michigan State University, East Lansing, MI, USA.

Free, J.B. (1993) *Insect Pollination of Crops*, 2nd edn, revised. Academic Press, San Diego, CA, USA.

Gallai, N., Salles, J., Settele, J. & Vaissiere, B. (2009) Economic valuation of the vulnerability of world agriculture confronted with pollinator decline. *Ecological Economics*, **68**, 810–821.

Garibaldi, L.A., Steffan-Dewenter, I., Winfree, R., Aizen, M.A., Bommarco, R., Cunningham, S.A. *et al.* (2013) Wild pollinators enhance fruit set of crops regardless of honey bee abundance. *Science*, **339**, 1608–1611.

Godfray, H.C.J., Beddington, J.R., Crute, J.I., Haddad, L., Lawrence, D., Muir, J.F. *et al.* (2010) Food security: the challenge of feeding 9 billion people. *Science*, **327**, 812–818.

Gough, R.E. (1994) *The Highbush Blueberry and its Management*. The Haworth Press, Binghamton, NY, USA.

Gurr, G.M., van Emden, H.F. & Wratten, S.D. (1998) Habitat manipulation and natural enemy efficiency: implications for the control of pests. *Conservation Biological Control* (ed. P. Barbosa), pp. 155–183. Academic Press, San Diego CA, USA.

Heard, M.S., Carvell, C., Carreck, N.L., Rothery, P., Osborne, J.L. & Bourke, A.F.G. (2007) Landscape context not patch size determines bumble-bee density on flower mixtures sown for agri-environment schemes. *Biology Letters*, **3**, 638–641.

Holzschuh, A., Dudenhöffer, J.H. & Tscharntke, T. (2012) Landscapes with wild bee habitats enhance pollination, fruit set and yield of sweet cherry. *Biological Conservation*, **153**, 101–107.

Hossain, Z., Gurr, G.M. & Wratten, S.D. (1999) Capture efficiency of insect natural enemies from tall and short vegetation using vacuum sampling. *Annals of Applied Biology*, **135**, 463–467.

Isaacs, R. & Kirk, A.K. (2010) Pollination services provided to small and large highbush blueberry fields by wild and managed bees. *Journal of Applied Ecology*, **47**, 841–849.

Isaacs, R., Tuell, J.K., Fiedler, A.K., Gardiner, M. & Landis, D.A. (2009) Maximizing arthropod-mediated ecosystem services in agricultural landscapes: the role of native plants. *Frontiers in Ecology and the Environment*, **7**, 196–203.

Jauker, F. & Wolters, V. (2008) Hover flies are efficient pollinators of oilseed rape. *Oecologia*, **156**, 819–823.
Joshua, T.M. (2011) *2011 Blueberry Statistics. (United States Department of Agriculture)*. New Jersey Agricultural Statistics Service, Trenton, NJ, USA.
Kells, A., Holland, J. & Goulson, D. (2001) The value of uncropped field margins for foraging bumblebees. *Journal of Insect Conservation*, **5**, 283–291.
Kennedy, C.M., Lonsdorf, E., Neel, M.C., Williams, N.M., Ricketts, T.H., Winfree, R. *et al.* (2013) A global quantitative synthesis of local and landscape effects on wild bee pollinators in agroecosystems. *Ecology Letters*, **16**, 584–599.
Kleijn, D. & Sutherland, W. (2003) How effective are European agri-environment schemes in conserving and promoting biodiversity? *Journal of Applied Ecology*, **40**, 947–969.
Kleijn, D., Rundlöf, M., Scheper, J., Smith, H.G. & Tscharntke, T. (2011) Does conservation on farmland contribute to halting the biodiversity decline? *Trends in Ecology and Evolution*, **26**, 474–481.
Klein, A.M., Vaissiere, E.B., Cane, J.H., Steffan-Dewenter, I., Cunningham, S.A., Kremen, C. & Tscharntke, T. (2007) Importance of pollinators in changing landscapes for world crops. *Proceedings of the Royal Society B*, **274**, 303–313.
Klein, A.M., Brittain, C., Hendrix, S.D., Thorp, R., Williams, N. & Kremen, C. (2012) Wild pollination services to California almond rely on semi-natural habitat. *Journal of Applied Ecology*, **49**, 723–732.
Kremen, C., Williams, N.M. & Thorp, R.W. (2002) Crop pollination from native bees at risk from agricultural intensification. *Proceedings of the National Academy of Sciences of the United States of America*, **99**, 16812–16816.
Kremen, C., Williams, N.M., Bugg, R.L., Fay, J.P. & Thorp, R.W. (2004) The area requirements of an ecosystem service: crop pollination by native bee communities in California. *Ecology Letters*, **7**, 1109–1119.
Kruess, A. & Tscharntke, T. (2000) Effects of habitat fragmentation on plant-insect communities. *Interchanges of Insects Between Agricultural and Surrounding Landscapes* (eds B.S. Ekbom, M.E. Irwin & Y. Robert), pp. 53–69. Kluwer Academic Publishers, Boston, MA, USA.
Long, R.F., Corbett, A., Lamb, C., Reberg-Horton, C., Chandler, J. & Stimmann, M. (1998) Beneficial insects move from flowering plants to nearby crops. *California Agriculture*, **52**, 23–26.
Marino, W.D. (2012) Spring 2012 Climate Summary for Southwest Lower Michigan. National Weather Service. http://www.crh.noaa.gov/grr/. [Accessed 31 October 2012].
Meyer, B., Gaebele, V. & Steffan-Dewenter, I.D. (2007) Patch size and landscape effects on pollinators and seed set of the horseshoe vetch, *Hippocrepis comosa*, in an agricultural landscape of central Europe. *Entomologia Generalis*, **30**, 173–185.
Morandin, L.A. & Kremen, C. (2013) Hedgerow restoration promotes pollinator populations and exports native bees to adjacent fields. *Ecological Applications*, **23**, 829–839.
Murray, T.E., Fitzpatrick, U., Byrne, A., Fealy, R., Brown, M.J.F. & Paxton, R.J. (2012) Local-scale factors structure wild bee communities in protected areas. *Journal of Applied Ecology*, **49**, 998–1008.
Naeem, S. (1998) Species redundancy and ecosytem reliability. *Conservation Biology*, **12**, 39–45.
Neumann, P. & Carreck, N.L. (2010) Honey bee colony losses. *Journal of Apiculture Research*, **49**, 1–6.
NRCS (2010) Pollinator Habitat Planting: Michigan CRP – SAFE CP-38E Pollinator. *Natural Resources Conservation Service – Conservation Reserve Program*, United States Department of Agriculture, MI, USA.
Osborne, J.L., Martin, A.P., Carreck, N.L., Swain, J.L., Knight, M.E., Goulson, D., Hale, R.J. & Sanderson, R.A. (2008) Bumblebee flight distances in relation to the forage landscape. *Journal of Animal Ecology*, **77**, 406–415.
O'Toole, C. (1993) Diversity of native bees and agroecosystems. *Hymenoptera and Biodiversity* (eds J. LaSalle & I.D. Gauld), pp. 169–196. CAB Int., Wallingford, UK.
Potts, S.G., Vulliamy, B., Roberts, S., O'Toole, C., Dafni, A., Ne'eman, G. & Wilmer, R. (2005) Role of nesting resources in organising diverse bee communities in a Mediterranean landscape. *Ecological Entomology*, **30**, 78–85.
Potts, S.G., Biesmeijer, J.C., Kremen, C., Neumann, P., Schweiger, O. & Kunin, W.E. (2010) Global pollinator declines: trends, impacts and drivers. *Trends in Ecology and Evolution*, **25**, 345–353.
Retamales, J.B. & Hancock, J.F. (2012) *Blueberries*. CABI, Cambridge, MA, USA.
Roulston, T.H. & Goodell, K. (2011) The role of resources and risks in regulating wild bee populations. *Annual Review of Entomology*, **56**, 293–312.
Scheper, J., Holzschuh, A., Kuussaari, M., Potts, S.G., Rundlöf, M., Smith, H.G. & Kleijn, D. (2013) Environmental factors driving the effectiveness of European agri-environmental measures in mitigating pollinator loss – a meta-analysis. *Ecology Letters*, **16**, 912–920.
Sheffield, C.S., Westby, S.M., Smith, R.F. & Kevan, P.G. (2008) Potential of bigleaf lupine for building and sustaining *Osmia lignaria* populations for pollination of apple. *The Canadian Entomologist*, **140**, 589–599.
Slobodkin, L.B. (1980) *Growth and Regulation of Animal Populations*, 2nd edn. Dover Publications Inc., New York, NY, USA.
Smith, H.A., Chaney, W.E. & Bensen, T.A. (2008) Role of syrphid larvae and other predators in suppressing aphid infestations in organic lettuce on California's Central Coast. *Journal of Economic Entomology*, **101**, 1526–1532.
Steffan-Dewenter, I., Münzenberg, U., Buerger, C., Thies, C. & Tscharntke, T. (2002) Scale-dependent effects of landscape context on three pollinator guilds. *Ecology*, **83**, 1421–1432.
Tscharntke, T., Steffan-Dewenter, I., Kruess, A. & Thies, C. (2002) Contribution of small habitat fragments to conservation of insect communities of grassland-cropland landscapes. *Ecological Applications*, **12**, 354–363.
Tscharntke, T., Bommarco, R., Clough, Y., Crist, T.O., Kleijn, D., Rand, T.A., Tylianakis, J.M., van Nouhuys, S. & Vidal, S. (2007) Conservation biological control and enemy diversity on a landscape scale. *Biological Control*, **43**, 294–309.
Tscharntke, T., Clough, Y., Wanger, T.C., Jackson, L., Motzke, I., Perfecto, I., Vandermeer, J. & Whitbread, A. (2012) Global food security, biodiversity conservation and the future of agricultural intensification. *Biological Conservation*, **151**, 53–59.
Tuell, J.K., Fiedler, A.K., Landis, D. & Isaacs, R. (2008) Visitation by wild and managed bees (Hymenoptera: Apoidea) to Eastern US native plants for use in conservation programs. *Environmental Entomology*, **37**, 707–718.
Williams, N.M., Minckley, R.L. & Silveira, F.A. (2001) Variation in native bee faunas and its implications for detecting community changes. *Conservation Ecology*, **5**, 7.
Winfree, R. (2010) The conservation and restoration of wild bees. *Annals of the New York Academy of Sciences*, **1195**, 169–197.
Winfree, R., Williams, N.M., Dushoff, J. & Kremen, C. (2007) Native bees provide insurance against ongoing honey bee losses. *Ecology Letters*, **10**, 1105–1113.

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Supporting Information

Additional Supporting Information may be found in the online version of this article.

Appendix S1. Methods and analysis of establishing and maintaining wildflower plantings.

Appendix S2. Wildflower planting establishment costs and the estimated profits from these plantings.

Table S1. (a) List of native Midwestern perennial wildflowers, grasses, bloom periods and respective seeding rates for seed mix sown in the wildflower plantings. (b) Comparison of the average number of seeded plants per m^2, a comparison of the average percentage coverage of seeded and volunteer plants, and the number of flower blooms per m^2 within the flower and control treatments over 4 years.

Table S2. Estimated costs and profit for the establishment of unsubsidized and subsidized wildflower plantings.