*Environmental Entomology*, 50(4), 2021, 821–831
doi: 10.1093/ee/nvab036
Advance Access Publication Date: 26 April 2021
Research

ENTOMOLOGICAL SOCIETY OF AMERICA
SHARING INSECT SCIENCE GLOBALLY

OXFORD

Community Ecology

# Landscape Context Influences the Bee Conservation Value of Wildflower Plantings

**Christopher T. McCullough,[1,2,5] Gina M. Angelella,[1,3] and Megan E. O'Rourke[1,4]**

[1]School of Plant and Environmental Sciences, Virginia Tech, Blacksburg, VA, USA, [2]Current address: Department of Entomology, Virginia Tech, Blacksburg, VA, USA, [3]Current address: USDA, Agricultural Research Service, Temperate Tree Fruit and Vegetable Research Unit, 5230 Konnowac Pass Road, Wapato, WA, 98951, USA, [4]Current address: USDA, National Institute of Food and Agriculture, Kansas City, MO, USA, and [5]Corresponding author, e-mail: ctmccull@vt.edu

Subject Editor: Juliana Rangel

Received 15 December 2020; Editorial decision 17 March 2021

## Abstract

Pollination provided by bees is a critical ecosystem service for agricultural production. However, bee populations are at risk from stressors such as habitat loss, pesticides, and disease. On-farm wildflower plantings is one mitigation strategy to provide habitat and resources for bees. In many instances, government programs can subsidize the installation of these plantings for private landowners. Semi-natural habitat (SNH) in the landscape is also important for bee conservation and may alter the effectiveness of wildflower plantings. In this study, we tested the effectiveness of wildflower plantings and interactions with SNH in the landscape for promoting bee abundance and richness. Bee surveys were conducted over 2 yr at 22 sites in eastern Virginia and Maryland. Wildflower plantings, averaging 0.22 ha in size, were installed and maintained by cooperators at 10 of the sites. In total, 5,122 bees were identified from 85 species. Wildflower plantings did not alter bee communities independently, but bee abundance was greater on farms with plantings and 20–30% SNH in the landscape. Bee abundance and richness had nonlinear responses to increasing SNH in the landscape. The positive effects for richness and abundance peaked when SNH was approximately 40% of the landscape. Similar to predictions of the intermediate-landscape complexity hypothesis, increases in bee abundance at wildflower sites were only detected in simplified landscapes. Results indicate that small wildflower plantings in the Mid-Atlantic U.S. only provided conservation benefits to bee communities under specific circumstances on the scale studied, and that conserving SNH across the landscape may be a more important strategy.

**Key words:** pollinator, natural habitat, community, private land, abundance

Pollination services provided by pollinators are a vital ecosystem service for the production of food and fiber: animal pollination improves yield in 39 of the 57 leading crops in the world (Klein et al. 2007). Diverse and abundant pollinator communities are needed to maintain and enhance crop yields (Woodcock et al. 2019). Native bees, in particular, can provide sufficient pollination for many pollinator-dependent crop species (Winfree et al. 2007, 2008), and can further enhance pollination in the presence of managed species like *Apis mellifera* L. (Hymenoptera: Apidae) (Garibaldi et al. 2013). However, the continued delivery of pollination services is at risk as bee populations face threats from pesticides, habitat loss, pests, and pathogens (Potts et al. 2010, Goulson et al. 2015).

Creating on-farm pollinator refuges by planting wildflowers is one commonly used strategy to mitigate the decline of pollinators and conserve pollination services (Williams et al. 2015, Venturini et al. 2017). In 2014, a presidential memorandum was issued in the United States to enhance or restore seven million acres of land for pollinator habitat (US EPA 2017). The U.S. Department of Agriculture's (USDA) Natural Resources Conservation Service (NRCS) manages 13 programs that can be utilized to conserve and create pollinator habitat on privately owned agricultural lands (NRCS 2015). These programs provide technical assistance and subsidies for the creation or conservation of habitat. As the majority of the land area in the United States is privately owned, these programs provide a critical tool for conserving and creating pollinator habitat (U.S. Forest Service 2016). The Environmental Quality Incentives Program (EQIP) has been used to pay for pollinator conservation efforts on over 16,000,000 acres from 2009 to 2018 (Vaughn and Skinner 2015, USDA 2018).

Given the political, ecological, and agronomic importance of conserving pollinators, it is imperative to understand the effectiveness of these publicly funded conservation programs. One study on an NRCS administered program to conserve Karner blue butterflies, *Lycaeides melissa samuelis* Nabakov (Lepidoptera: Lycaenidae) found that restored farmland sites did not increase Karner blue populations but did increase overall butterfly richness compared to native prairie sites (Kleintjes Neff et al. 2017). The Conservation Reserve Program (CRP) pays landowners to take land out of agricultural production and plant cover of conservation value (USDA 2019). This program is currently implemented on more than 20 million acres (USDA 2019). Studies in North Dakota and Texas found that native habitats had greater bee abundance than CRP land (Otto et al. 2017, Begosh et al. 2020). In Colorado, CRP land enhanced with wildflowers did not increase bee abundance or richness relative to control CRP sites dominated by grasses (Arathi et al. 2019). The effectiveness of CRP land may be limited by the wide variation in management practices, size, or age (Otto et al. 2017). Studies focused on the effectiveness NRCS and other publicly available programs are lacking.

The context of the surrounding landscape may moderate the effectiveness of farm-scale measures to promote bee communities and pollination services. Increasing semi-natural habitat (SNH) in the landscape has been shown to increase bee species richness, abundance, and pollinator visitation rates to nearby crops (Ricketts et al. 2008, Kennedy et al. 2013). Agricultural land surrounding farms, on the other hand, has been shown to have negative effects on bee species richness and pollination services (Dainese et al. 2019, Grab et al. 2019). As predicted by the intermediate landscape complexity hypothesis, farm-scale conservation strategies are most effective when located in simplified landscapes, such as areas where SNH is 1–20% of the surrounding landscape (Tscharntke et al. 2005). Outside of this range, landscapes either have too few species to conserve or already have species rich communities (Tscharntke et al. 2005). Studies that tested this interaction have found that increasing SNH limits the effectiveness of on-farm measures (Scheper et al. 2013, Garratt et al. 2017, Grab et al. 2018, Herbertsson et al. 2018, Krimmer et al. 2019). One study (Grab et al. 2018), which investigated this interaction using nonlinear analyses, found wildflower sites had a positive effect on bee visitation relative to control sites where SNH was between ~25 and 50% of the surrounding landscape.

Wildflower planting specific factors such as bloom density, flower diversity, plot size, or the time since planting may alter the effectiveness of wildflower plantings. Blaauw and Isaacs (2014a) found that the number of flower species blooming at the time of sampling increased wild bee abundance and richness. The floral area or bloom abundance of wildflowers in mixes can also have positive effects on wild bee abundance and richness (Tuell et al. 2008, Balzan et al. 2014, Williams et al. 2015). Wild bee richness and abundance had a positive response to increasing wildflower planting size; however, this effect plateaued as the 10 $m^2$ plot has similar responses as the 100 $m^2$ plot (Blaauw and Isaacs 2014b). There can also be a time lag from when the wildflower plot is planted to when effects are detected, with Blaauw and Isaacs (2014a) detecting increases in bee abundance only 3 yr after planting wildflowers. Accounting for these factors may help refine expectations for pollinator conservation from pollinator habitats.

The objectives of this study were to: 1) assess the effectiveness of NRCS designed wildflower mixes for conserving bees in eastern Virginia and Maryland; 2) understand how SNH interacts with wildflower plantings and bee communities; and 3) investigate what factors are impacting the effectiveness of the wildflower plantings to conserve native bees. We expected that wildflower plantings would enhance bee communities relative to control fields by increasing species richness and abundance. Furthermore, we expected that wildflower plantings will be affected by the amount of SNH in the landscape and the amount of floral resources provided by the plantings.

## Materials and Methods

### Field Sites

Bee communities were sampled at 20 sites in 2017 and 2018. Two control sites were added from 2017 to 2018, to replace two sites that dropped out of the study. A total of 22 sites were sampled. These sites were located on the Delmarva Peninsula in Virginia and Maryland and within the locality of Virginia Beach, Virginia. The majority of these sites were small-scale diversified farms that sold direct-to-market. Only two of these farms were certified 'USDA Organic', but others utilized a diversity of management strategies. Of the sites sampled, nine of them had wildflower plantings seeded in the spring of 2016. While the fields with wildflower plantings were not formally enrolled in any cost-sharing program, the installation and management of wildflower plantings followed guidelines similar to those used in the Environmental Quality Incentives Program for the region. Two different wildflower mixes were used to match soil drainage characteristics at each field. Seven fields were planted with a mix adapted for well-draining soils, and two were planted with a mix for poorly draining soil. The mixes included grasses and forbs that were perennials, annuals, and biennials (Supp Table 1 [online only]). Plant species chosen were based on the recommendation of the local NRCS private lands biologist to provide continuous blooms throughout the growing season (B. Glennon, personal communication). All plantings were installed and maintained by cooperators. Generally, site preparation included tillage, an optional application of an herbicide, seeding, and then packing of the soil bed. For further details on site preparation at the well-draining sites, see Angelella and O'Rourke (2017). Further information on the abundance of the flowering forb species is given in Supp Appendix 1 (online only). One site was added to the study that had a wildflower planting installed in the spring of 2015. A total of nine wildflower species were used at this site, seven of which were used in the well-draining mix (Supp Appendix 1 [online only]). Cooperators selected the site and size of the plantings on their land. Wildflower plantings ranged in size from 561 to 8,600 $m^2$.

### Bee Sampling

To balance the needs of collection effort and acknowledging the biases of different sampling techniques, blue-vane and pan traps were used to sample the bee community (Wood et al. 2015, Gibbs et al. 2017, O'Connor et al. 2019). At each site, bees were sampled using blue-vane traps and pan traps. Pan traps were 7.5 cm by 7.5 cm plastic dishes (Rubbermaid, Atlanta, GA) painted with UV-reflective yellow, blue, or white (Blick Art Materials, Galesburg, IL). Pan traps were placed on the ground, and blue-vane traps (Springstar Inc., Woodinville, WA) were attached to poles with the base of the trap 50 cm above the ground. At each field site, a total of 12 traps were placed, three of each pan trap color and three blue-vane traps. Traps were spaced 5 m apart along transects in an alternating sequence of trap type. At fields with wildflower plantings, traps were placed along the edge of the wildflower plot. At control fields, traps were placed along field edges or roads.

All traps were filled with water and a drop of nonscented dish soap. Traps were left in the field for 48 h. Three rounds of sampling took place each year. Sampling was done during the weeks of May 15th, June 19th, and August 14th in 2017. In 2018, sampling was conducted during the weeks of June 4th, July 23rd, and August 13th. Collected bees were processed and identified after the conclusion of the field season. Final species determinations were provided by Sam Droege of the United States Geological Survey. Vouchers are deposited in the Virginia Tech Entomology Collection, accession numbers VTEC000005705-6043.

### Habitat Measurements

Bloom density was measured during the same weeks as bee sampling. Bloom density was recorded within three 1 $m^2$ quadrats randomly placed within wildflower plantings. Landscape data were obtained from the 2017 data layer from USDA Cropscape. The cover classes of deciduous forest, evergreen forest, mixed forest, shrubland, woody wetland, and herbaceous wetland were aggregated into semi-natural habitat. The percent area of semi-natural habitat was calculated within 250, 500, and 1,000 m radii buffers surrounding each field site. At the 1,000 m radius, the range of SNH surrounding was 10.5–69.2% for control sites and 21–59.9% for wildflower sites.

### Statistical Analysis

For all analyses, *Apis mellifera* L. and bees that could not be identified to species were excluded. *Apis mellifera* is a managed species, a total of 66 were caught during the study. Sampled *A. mellifera* were assumed to be from managed hives as indicated by another study in the area (Angelella et al. 2021). Bees not identified to species, ~1.5% of all bees sampled, either have unresolved taxonomy or were in too poor of condition for species determination. A nonmetric multidimensional scaling (NMDS) plot was created to visualize the bee communities sampled at control and wildflower sites each year. The NMDS was performed using the Bray-Curtis dissimilarity matrix. To test for differences between bee communities at wildflower and control fields, a permutation multivariate analysis of variance (PERMANOVA) was performed.

Linear mixed-effects models were used to test for differences between wildflower and control fields on species richness and the Shannon-Wiener diversity index. The effects of wildflower plantings on aggregate bee abundance and for each of the three most abundant species were tested with generalized linear mixed-effects models with a negative binomial distribution. For all models, wildflower plot by year interaction and their main effects were fixed effects, with field as a random effect. Abundance, richness, and the Shannon-Wiener diversity index were summed across each year.

Bee abundance, the abundance of the three most abundant species, species richness, and the Shannon-Wiener diversity index were the response variables used to test the interaction between wildflower plots and the amount of SNH in the landscape at 250, 500, and 1,000 m radii scales. Model types and random effects are the same as previously described. The landscape by wildflower plot interaction, their main effects, and a quadratic term of landscape were the fixed effects. The linear and quadratic landscape terms were centered to reduce collinearity. Year was included as a covariate. The scale with the lowest Akaike Information Criterion, adjusted for small sample size, (AICc) value is presented. Other scales within 2 AICc points are included in Supp Appendix 2 (online only).

Bloom abundance, plot area, and % area of SNH were used as predictors of wildflower planting quality. Bee abundance, species richness, and the Shannon-Wiener diversity index were used as response variables. A multi-model approach was used to test what factors had an effect on the ability of wildflower plantings to attract bees. Seven a priori models were tested, each factor alone, the two-way interactions between each factor, and an intercept only model to serve as a null comparison. Year was included as a covariate in each model, and field was treated as a random effect. Starting with the model with the most weight, models were included to construct a 95% confidence set of models for model averaging (Harrison et al. 2018b).

All analyses were performed in 'R' Studio v3.5.2 (R Core Team 2018). The NMDS and PERMANOVA were done using the functions *MetaMDS* and *anisom* in the 'R' package 'Vegan' (Oksanen et al. 2018). Linear mixed-effects models were analyzed with the *lmer* function in the package 'LmerTest' (Kuznetsova et al. 2017). Generalized linear mixed-effects models were performed with the *glmmadmb* function in the package 'GLMMADMB' (Skaug et al. 2016). Multi-model analyses were done using the package 'MuMIn' (Barton 2018).

## Results

A total of 5,122 bees were identified from 85 species (Table 1). A total of 1,892 bees were caught in 2017 and 3,230 in 2018. *Agapostemon virescens* Fabricius (Hymenoptera: Halictidae), *Eucera pruinosa* (Say) (Hymenoptera: Apidae), and *Melissodes bimaculatus* Lepeletier (Hymenoptera: Apidae) were the three most abundant species sampled, with 1,786, 451, and 395 individuals caught from each species respectively. These three species accounted for 49% of the total bees sampled. Bee communities sampled from sites with and without wildflower plantings were the same. The 95% confidence intervals around the bee communities sampled at control and wildflower fields in 2017 and 2018 greatly overlap each other (Fig. 1). The similarity in communities between the treatments was quantitatively verified by the PERMANOVA (2017, $P = 0.78$; 2018, $P = 0.66$). No differences were detected between wildflower and control fields for species richness, Shannon-Wiener diversity index, and overall bee abundance (Tables 2 and 3). No treatment by year interactions were detected for any bee community metric (Tables 2 and 3). Wildflower plantings did not affect the abundance of *A. virescens* or *E. pruinosa*, but significantly fewer *M. bimaculatus* were sampled from sites with wildflower plantings compared to control sites (Table 3).

Landscape effects were detected for species richness, aggregate bee abundance, *A. virescens* abundance, and *M. bimaculatus* abundance (Figs. 2 and 3). No effects were detected for the Shannon-Wiener index. Both the linear and quadratic terms of SNH in the landscape at the 250 m scale had significant effects on species richness. Species richness peaked when SNH is approximately 40% of the land cover (Table 4, Fig. 2). Linear and quadratic effects of landscape at the 1,000 m scale were detected for aggregate bee, as well as the abundance of *A. virescens,* and *M. bimaculatus* abundance (Table 5, Figs. 2 and 3). Abundance peaked when SNH made up about 40% of the landscape. A landscape by wildflower planting interaction was only significant for aggregate bee abundance, abundance was greater at wildflower sites than control sites when SNH was between 20 and 30% of the surrounding landscape. Wildflower planting effects that were dependent on landscape context were detected for *E. pruinosa* and *M. bimaculatus.* When conditioned over landscape, *E. pruinosa* were more abundant at wildflower sites compared to control sites

**Table 1.** List of species and the number caught over the duration of the study at wildflower and control sites

| Family | Species | Wildflower | Control |
|---|---|---|---|
| Halictidae | | | |
| | *Agapostemon sericeus* (Forster) | 5 | 1 |
| | *Agapostemon splendens* (Lepeletier) | 7 | 9 |
| | *Agapostemon texanus* Cresson | 1 | 1 |
| | *Agapostemon virescens* (Fabricius) | 736 | 1,050 |
| | *Augochloropsis metallica metallica* (Fabricius) | 3 | 0 |
| | *Augochloropsis metalluca fulgida* (Smith) | 0 | 1 |
| | *Augochlora pura* (Say) | 8 | 5 |
| | *Augochlorella aurata* (Smith) | 134 | 45 |
| | *Augochlorella gratiosa* (Smith) | 0 | 3 |
| | *Halictus confusus* Smith | 20 | 5 |
| | *Halictus parallelus* Say | 0 | 3 |
| | *Halictus poeyi/ligatus* Say/Lepeletier | 108 | 46 |
| | *Halictus rubicundus* (Christ) | 0 | 10 |
| | *Lasioglossum admirandum* (Sandhouse) | 2 | 8 |
| | *Lasioglossum birkmanni* (Crawford) | 0 | 1 |
| | *Lasioglossum bruneri* (Crawford) | 10 | 37 |
| | *Lasioglossum callidum* (Sandhouse) | 66 | 56 |
| | *Lasioglossum coreopsis* (Robertson) | 5 | 5 |
| | *Lasioglossum cressoni* (Robertson) | 1 | 3 |
| | *Lasioglossum flordanum* (Robertson) | 0 | 1 |
| | *Lasioglossum hitchensi* Gibbs | 31 | 43 |
| | *Lasioglossum illinoense* (Robertson) | 1 | 1 |
| | *Lasioglossum imitatum* (Smith) | 1 | 1 |
| | *Lasioglossum leucocomum* Gibbs | 0 | 18 |
| | *Lasioglossum lustrans* (Cockerell) | 3 | 0 |
| | *Lasioglossum nelumbonis* (Robertson) | 1 | 0 |
| | *Lasioglossum oblongum* (Lovell) | 2 | 8 |
| | *Lasioglossum pectorale* (Smith) | 49 | 10 |
| | *Lasioglossum pilosum* (Smith) | 74 | 91 |
| | *Lasioglossum rozeni* Gibbs | 1 | 0 |
| | *Lasioglossum tegulare* (Robertson) | 44 | 47 |
| | *Lasioglossum trigeminum* Gibbs | 48 | 21 |
| | *Lasioglossum versatum* (Robertson) | 15 | 17 |
| | *Lasioglossum vierecki* (Crawford) | 35 | 0 |
| | *Lasioglossum weemsi* (Mitchell) | 0 | 6 |
| | *Lasioglossum zephyrum* (Smith) | 1 | 0 |
| Andrenidae | | | |
| | *Andrena carlini* Cockerell | 0 | 1 |
| | *Andrena nasonii* Robertson | 1 | 1 |
| | *Andrena perplexa* Smith | 2 | 2 |
| | *Calliopsis andreniformis* Smith | 56 | 6 |
| Apidae | | | |
| | *Anthophora abrubta* Say | 7 | 2 |
| | *Bombus bimaculatus* Cresson | 5 | 2 |
| | *Bombus fervidus* (Fabricius) | 0 | 1 |
| | *Bombus griseocollis* (De Geer) | 14 | 2 |
| | *Bombus impatiens* Cresson | 24 | 36 |
| | *Bombus pensylvanicus* (De Geer) | 108 | 83 |
| | *Ceratina calcarata* Robertson | 14 | 28 |
| | *Ceratina dupla* Say | 39 | 12 |
| | *Ceratina floridana* Mitchell | 0 | 2 |
| | *Ceratina mikmaqi* Ren and Sheffield | 0 | 3 |
| | *Ceratina strenua* Smith | 3 | 1 |
| | *Eucera hamata* (Bradley) | 55 | 81 |
| | *Eucera pruinosa* (Say) | 296 | 155 |
| | *Eucera rosae* (Robertson) | 1 | 4 |
| | *Florilegus condignus* (Cresson) | 3 | 0 |
| | *Holcopasites calliopsidis* (Linsley) | 0 | 1 |
| | *Melissodes agilis* Cresson | 1 | 0 |
| | *Melissodes bimaculatus* (Lepeletier) | 112 | 283 |
| | *Melissodes communis* Cresson | 60 | 57 |
| | *Melissodes comptoides* Robertson | 75 | 127 |

**Table 1.** Continued

| Family | Species | Wildflower | Control |
|---|---|---|---|
| | *Melissodes denticulatus* Smith | 1 | 0 |
| | *Melissodes desponsus* Smith | 0 | 1 |
| | *Melissodes trinodis* Robertson | 83 | 12 |
| | *Ptilothrix bombiformis* (Cresson) | 55 | 57 |
| | *Svastra atripes* (Cresson) | 35 | 55 |
| | *Svastra obliqua* (Say) | 6 | 1 |
| | *Triepeolus concavus* (Cresson) | 1 | 0 |
| | *Triepeolus lunatus* (Say) | 0 | 1 |
| | *Triepeolus simplex* Robertson | 2 | 0 |
| | *Xenoglossa strenua* (Cresson) | 1 | 6 |
| | *Xylocopa virginica* (L.) | 14 | 14 |
| Colletidae | | | |
| | *Hylaeus ornatus* Mitchell | 1 | 0 |
| Megachilidae | | | |
| | *Heriades leavitti/variolosa* Crawford/(Cresson) | 1 | 0 |
| | *Hoplitis pilosifrons* (Cresson) | 3 | 1 |
| | *Hoplitis producta* (Cresson) | 1 | 0 |
| | *Hoplitis truncata* (Cresson) | 1 | 0 |
| | *Megachile brevis* Say | 7 | 1 |
| | *Megachile campanulae* (Robertson) | 1 | 1 |
| | *Megachile mendica* Cresson | 3 | 2 |
| | *Megachile rotundata* (Fabricius) | 5 | 1 |
| | *Osmia collinsae* Robertson | 1 | 3 |
| | *Osmia georgica* Cresson | 1 | 0 |
| | *Osmia pumila* Cresson | 4 | 0 |
| | *Osmia sandhouseae* Mitchell | 3 | 0 |
| | *Stelis lateralis* Cresson | 1 | 0 |

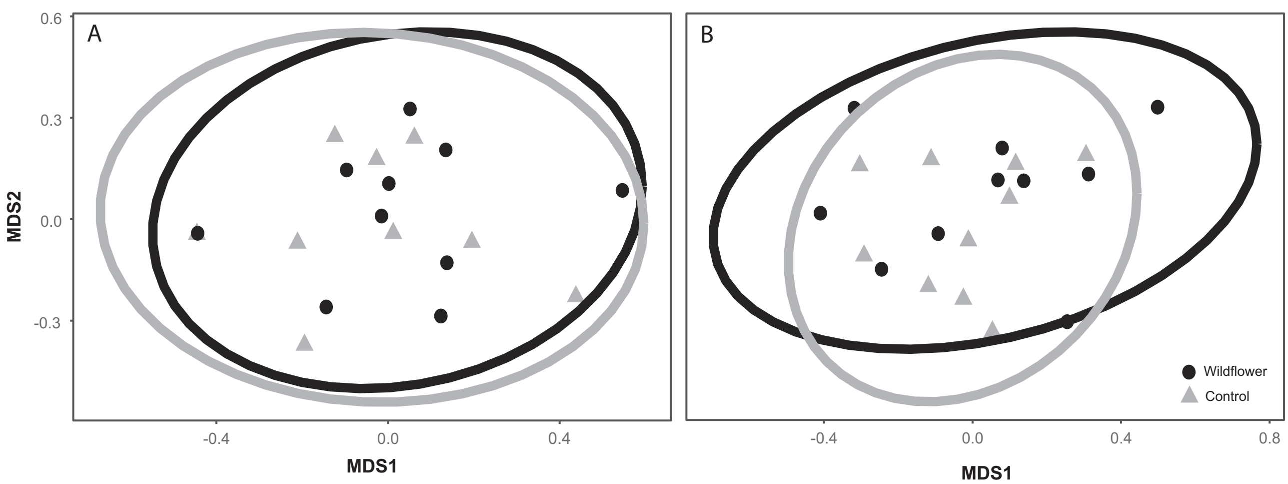


**Fig. 1.** NMDS plot of the of the bee communities sampled in 2017 (A) and 2018 (B) at control and wildflower fields. Circles represent 95% confidence intervals around the centroid of the sampled communities. (Stress values: 2017 = 0.18, 2018 = 0.18).

($z$ = 2.32, $P$ = 0.02), and *M. bimaculatus* were more abundant at control sites than sites with wildflower plantings (z = −1.11, $P$ = 0.03; Fig. 3).

In examining the factors that affect the abilities of the wildflower plantings to attract bee species, the intercept only models were the only ones selected for predicting changes in species richness and the Shannon-Wiener index (Table 6, Supp Appendix 2 [online only]). Each scale analyzed for bee abundance selected multiple factors; however, each included the intercept only models (Table 6, Supp Appendix 2 [online only]). Percent SNH in the landscape was the top factor at the 500 m scale. SNH in the landscape had a significant negative effect on bee abundance at sites with wildflower plantings (Table 7).

## Discussion

When considered by themselves, wildflower plantings did not have an effect on the bee community sampled. This contrasts with much of the published literature showing that wildflower plantings and other restoration efforts are beneficial to bee communities (Williams

**Table 2.** Results of linear mixed effects models on the effect of wildflower plantings on the Shannon-Wiener diversity index and bee richness

| Response | Parameter | Estimate | Std. error | df | *t*-value | *P*-value |
|---|---|---|---|---|---|---|
| Shannon | | | | | | |
| | Intercept | 1.92 | 0.16 | 34.3 | 12.2 | <0.0001* |
| | Year | 0.03 | 0.19 | 20.2 | 0.14 | 0.88 |
| | Wildflower | 0.16 | 0.22 | 33.5 | 0.70 | 0.48 |
| | Year × Wildflower | 0.08 | 0.26 | 18.4 | 0.32 | 0.75 |
| Richness | | | | | | |
| | Intercept | 13.2 | 1.59 | 34.5 | 8.28 | <0.0001* |
| | Year | 5.18 | 2.06 | 20.5 | 2.51 | 0.02* |
| | Wildflower | 2.99 | 2.55 | 35.1 | 1.32 | 0.19 |
| | Year × Wildflower | −0.88 | 2.88 | 18.5 | −0.31 | 0.76 |

*Significant at $P < 0.05$.

**Table 3.** Results of generalized linear mixed effects model on the effect of wildflower plantings on the abundance of all bees and the three most abundant species sampled

| Species | Effect | Estimate | Std. error | z-value | *P*-value |
|---|---|---|---|---|---|
| All bees | | | | | |
| | Intercept | 4.28 | 0.24 | 17.5 | <0.0001* |
| | Year | 0.66 | 0.22 | 2.92 | 0.003* |
| | Wildflower | 0.29 | 0.35 | 0.85 | 0.39 |
| | Year × Wildflower | −0.30 | 0.31 | −0.97 | 0.33 |
| *A. virescens* | | | | | |
| | Intercept | 1.77 | 0.66 | 2.70 | 0.007* |
| | Year | 0.91 | 0.35 | 2.64 | 0.008* |
| | Wildflower | 0.32 | 0.92 | 0.34 | 0.73 |
| | Year × Wildflower | −0.69 | 0.47 | −1.48 | 0.14 |
| *E. pruinosa* | | | | | |
| | Intercept | 1.46 | 0.65 | 2.23 | 0.03* |
| | Year | −0.98 | 0.64 | −1.54 | 0.12 |
| | Wildflower | 0.29 | 0.86 | 0.34 | 0.73 |
| | Year × Wildflower | 1.18 | 0.85 | 1.40 | 0.16 |
| *M. bimaculatus* | | | | | |
| | Intercept | 2.23 | 0.54 | 4.07 | <0.0001* |
| | Year | 0.33 | 0.77 | 0.43 | 0.67 |
| | Wildflower | −1.93 | 0.79 | −2.43 | 0.02* |
| | Year × Wildflower | 1.53 | 1.06 | 1.45 | 0.15 |

*Significant at $P < 0.05$.

et al. 2015, Venturini et al. 2017, Tonietto and Larkin 2018, Nicholson et al. 2020). Year by wildflower plot interactions were not approaching significance, indicating that the lack of differences is not likely caused by plot age. It may be that the small-scaled diverse nature of many of the sites was already harboring robust bee communities. Having more unmanaged areas on farms and using less pesticides leads to having more speciose and abundant bee communities (Nicholson et al. 2017). Increasing plant diversity on farms is shown to increase the abundance and richness of pollinators (Lichtenberg et al. 2017). With many operations using practices that already benefit bee communities, it may have been difficult for wildflower plantings to have a detectable effect that was beneficial for bee communities. Conservation efforts may need to consider the resources already present at potential restoration locations to better ensure their effectiveness.

The amount of SNH in the landscape around wildflower plantings modulated their effectiveness in promoting bee communities. Keeping with the intermediate landscape complexity hypothesis, we found that wildflower plantings enhanced bee abundance within a range of 20–30% SNH in the landscape at the 1,000 m scale. This range falls between the one proposed by Tscharntke et al. (2005) of 1–20% and the one observed in New York of 25–55% SNH (Grab et al. 2018). A meta-analysis of on-farm actions to promote pollinators showed diminished effectiveness as SNH increased (Scheper et al. 2013). The success of on-farm actions in simplified landscapes is due to the ability to provide resources in an area that is not entirely devoid, but lacking in resources (Scheper et al. 2013). Stronger effects of wildflower plots may be detected if plot locations can be situated in areas where SNH is less than 20% of the landscape, which we were unable to do in this study. The visual attraction methods used to sample bees in this study may have also dampened the detected effects, as they must compete with other resources in the area to attract bees. Increases in floral resources at the local and landscape scales can negatively affect trap catch (Wood et al. 2015, O'Connor et al. 2019). The influences of these two factors may have also caused the seemingly negative effect if wildflower plots at the higher levels of SNH. Regardless of the sampling methodology,

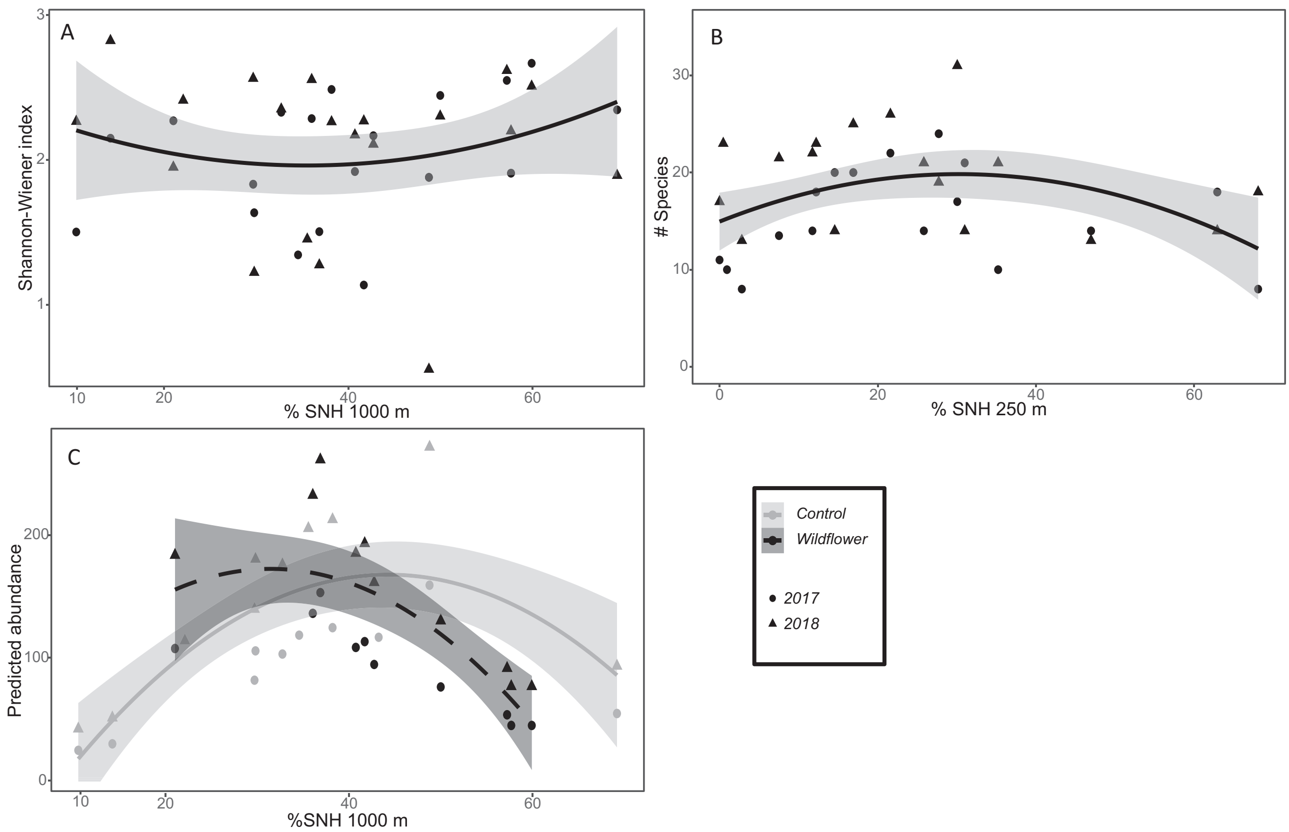


**Fig. 2.** The effects of the interaction of wildflower plots and the amount of SNH in the landscape on the Shannon-Wiener diversity index (A), bee species richness (B), and abundance (C). The scale presented has the lowest AICc score of the scales tested.

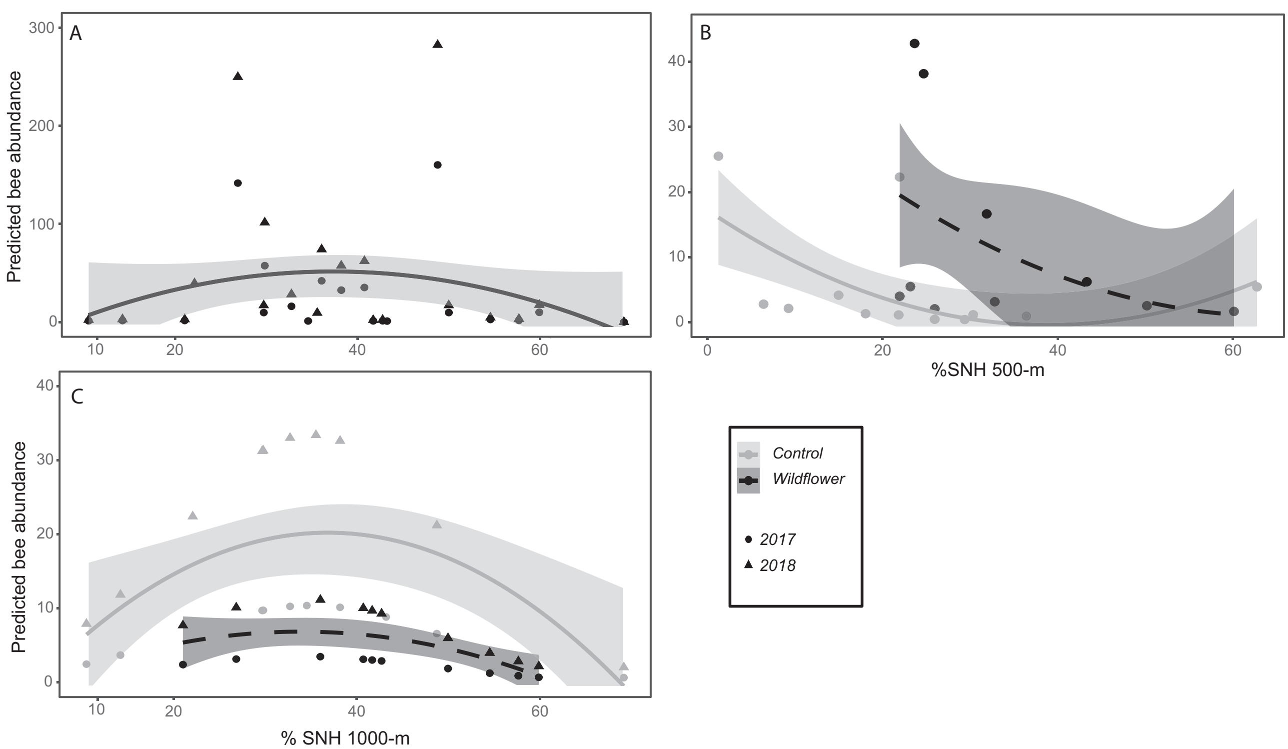


**Fig. 3.** The effects of the interaction of SNH in the landscape and wildflower plots on the abundance of three most common bee species sampled (A) *A. virescens*, (B) *E. pruinosa*, (C) *M. bimaculatus*. The scale presented has the lowest AICc score of the scales tested.

**Table 4.** Results of linear mixed effects models testing the effects of wildflower plots and the amount of semi-natural habitat in the landscape on the species richness and Shannon-wiener diversity index of sampled bees. Scales presented had the lowest AICc of the three scales analyzed

| Response | Model term | Estimate | Std. error | df | *t*-value | *P*-value |
|---|---|---|---|---|---|---|
| Richness | | | | | | |
| | Intercept | 13.9 | 1.34 | 25.9 | 10.3 | <0.0001* |
| | Year | 4.96 | 1.43 | 18.2 | 3.45 | 0.003* |
| | Wildflower | 1.72 | 1.66 | 13.7 | 1.04 | 0.31 |
| | SNH 250 | 0.29 | 0.13 | 14.8 | 2.23 | 0.04* |
| | WF × SNH 250 | −0.04 | 0.09 | 13.4 | −0.55 | 0.59 |
| | SNH $250^2$ | −0.004 | 0.002 | 13.8 | −2.21 | 0.04* |
| Shannon | | | | | | |
| | Intercept | 1.85 | 0.14 | 25.2 | 12.7 | <0.0001* |
| | Year | 0.06 | 0.13 | 19.8 | 0.49 | 0.62 |
| | Wildflower | 0.22 | 0.20 | 17.3 | 1.13 | 0.27 |
| | SNH 1000 | −0.04 | 0.02 | 16.8 | −1.51 | 0.15 |
| | WF × SNH 1000 | 0.017 | 0.014 | 15.9 | 1.22 | 0.24 |
| | SNH $1000^2$ | 0.0004 | 0.0003 | 16.6 | 1.34 | 0.20 |

*Significant at $P < 0.05$.

**Table 5.** Results of generalized linear mixed effects models testing the effects of wildflower plots and the amount of semi-natural habitat in the landscape on total bee abundance and the three most abundant species sampled

| Species | Term | Estimate | Std. error | z-value | *P*-value |
|---|---|---|---|---|---|
| All bees | | | | | |
| | Intercept | 4.53 | 0.18 | 24.7 | <0.0001* |
| | Year | 0.53 | 0.18 | 3.05 | 0.002* |
| | Wildflower | −0.06 | 0.22 | −0.25 | 0.80 |
| | SNH 1000 | 0.13 | 0.03 | 4.12 | <0.0001* |
| | WF × SNH 1000 | −0.04 | 0.02 | −2.55 | 0.01* |
| | SNH $1000^2$ | −0.001 | 0.0001 | −3.72 | 0.0002* |
| *A. virescens* | | | | | |
| | Intercept | 1.61 | 0.68 | 2.35 | 0.02* |
| | Year | 0.56 | 0.26 | 2.16 | 0.03* |
| | Wildflower | 0.20 | 0.90 | 0.22 | 0.83 |
| | SNH 1000 | 0.27 | 0.13 | 1.99 | 0.04* |
| | WF × SNH 1000 | 0.02 | 0.07 | 0.34 | 0.73 |
| | SNH $1000^2$ | −0.004 | 0.001 | −2.18 | 0.03* |
| *E. pruinosa* | | | | | |
| | Intercept | 0.82 | 0.59 | 1.40 | 0.16 |
| | Year | −0.39 | 0.44 | −0.89 | 0.37 |
| | Wildflower | 1.88 | 0.81 | 2.32 | 0.02* |
| | SNH 500 | −0.15 | 0.08 | −1.81 | 0.07 |
| | WF × SNH 500 | −0.06 | 0.05 | −1.19 | 0.24 |
| | SNH $500^2$ | 0.002 | 0.002 | 1.69 | 0.09 |
| *M. bimaculatus* | | | | | |
| | Intercept | 1.77 | 0.40 | 4.40 | <0.0001* |
| | Year | 1.17 | 0.48 | 2.40 | 0.02* |
| | Wildflower | −1.11 | 0.50 | −2.21 | 0.03* |
| | SNH 1000 | 0.17 | 0.06 | 2.62 | 0.01* |
| | WF × SNH 1000 | −0.01 | 0.03 | −0.17 | 0.87 |
| | SNH $1000^2$ | −0.002 | 0.001 | −2.85 | 0.004* |

*Significant at $P < 0.05$.

conservation efforts may need to consider the broader context of the surrounding landscape to better situate wildflower plantings to better ensure their value.

In addition to landscape context surrounding wildflower plots, the quality of the plots themselves could be a factor. Plot area and bloom density were included in model averaging, but were never significant. Bloom density and plot area can be important factors in determining the effectiveness of the plot (Blaauw and Isaacs 2014b, Krimmer et al. 2019), but landscape effects may be stronger (Kleijn et al. 2018). Time since planting was also not a factor, as no changes were seen from year to year for these wildflower plots. The inclusion of intercept-only models indicates there could be other factors that were not measured or analyzed affecting the plots. Floral area and the number of flowering species in bloom both can have a positive effect on bee communities (Blaauw and Isaacs 2014b and Williams et al. 2015). Crop production practices at wildflower sites could be impacting the effectiveness of the wildflower planting. *Eucera pruinosa* was three

**Table 6.** Results of model selection for factors affecting the effectiveness of wildflower plots for the Shannon-Wiener index, species richness, and abundance. The scale with the lowest average AICc is presented. All other scales are presented in Supp Appendix 2 (online only)

| Response | Scale (m) | Model | k | logLik | AICc | Δ AICc | Weight |
|---|---|---|---|---|---|---|---|
| Shannon | 1,000 | | | | | | |
| | | Intercept only | 4 | −11.36 | 33.38 | - | 0.969* |
| | | Avg. blooms | 5 | −13.42 | 41.12 | 7.737 | 0.02 |
| | | % SNH | 5 | −14.08 | 42.46 | 9.073 | 0.01 |
| | | Plot area | 5 | −20.17 | 54.62 | 21.241 | 0 |
| | | Avg. blooms × % SNH | 7 | −23.05 | 69.44 | 36.06 | 0 |
| | | Avg. blooms × area | 7 | −32.26 | 87.85 | 54.473 | 0 |
| | | Plot area × % SNH | 7 | −32.93 | 89.19 | 55.803 | 0 |
| Richness | 250 | | | | | | |
| | | Intercept only | 4 | −57.24 | 125.15 | - | 0.917* |
| | | % SNH | 5 | −58.52 | 131.32 | 6.175 | 0.042 |
| | | Avg. blooms | 5 | −58.55 | 131.39 | 6.242 | 0.04 |
| | | Plot area | 5 | −62.77 | 139.83 | 14.678 | 0.001 |
| | | Avg. blooms × % SNH | 7 | −63.3 | 149.94 | 24.786 | 0 |
| | | Plot area × % SNH | 7 | −70.82 | 164.97 | 39.817 | 0 |
| | | Avg. blooms × area | 7 | −72.33 | 167.99 | 42.845 | 0 |
| Abundance | 500 | | | | | | |
| | | % SNH | 5 | −107.5 | 229.29 | - | 0.836* |
| | | Avg. blooms × % SNH | 7 | −105.89 | 235.12 | 5.834 | 0.045* |
| | | Intercept only | 4 | −112.3 | 235.26 | 5.969 | 0.042* |
| | | Avg. blooms | 5 | −110.74 | 235.76 | 6.474 | 0.033 |
| | | Plot area | 5 | −111.2 | 236.68 | 7.394 | 0.021 |
| | | Plot area × % SNH | 7 | −106.73 | 236.79 | 7.496 | 0.02 |
| | | Avg. blooms × area | 7 | −108.56 | 240.46 | 11.172 | 0.003 |

K is the number of parameters in the model.
*Models selected for averaging.

**Table 7.** Results of model averaging for factors affecting the effectiveness of wildflower plots in promoting bee abundance at the 500 m scale. Other scales analyzed are presented in Supp Appendix 2 (online only)

| Term | Estimate | Std. error | z-value | *P*-value |
|---|---|---|---|---|
| Intercept | 5.72 | 0.53 | 10.7 | <0.0001* |
| Year | 0.36 | 0.25 | 1.45 | 0.14 |
| % SNH | −0.037 | 0.01 | 2.85 | 0.004* |
| Avg. blooms | 0.68 | 0.04 | 1.46 | 0.14 |
| % SNH × Blooms | −0.002 | 0.001 | 1.27 | 0.20 |

*Significant at $P < 0.05$.

times more abundant on farms that practiced no-till than farms that used tillage (Shuler et al. 2005). Increased pesticide usage and more mowing of non-crop areas decreased on-farm bee abundance and richness (Nicholson et al. 2017). Conservation efforts may need to consider the quality of the wildflower plantings themselves to better ensure their success.

Of the three most abundant species sampled, only *E. pruinosa* had a positive response to the wildflower plantings. These three species, *A. virescens*, *E. pruinosa*, and *M. bimaculatus* are often sampled from or associated with agriculturally dominated landscapes (Wheelock et al. 2016, Buchanan et al. 2017, Harrison et al. 2018a, Collado et al. 2019), which likely already provide all the resources these species need. *Agapostemon virescens* is a generalist that has been documented on more than 50 species of plants (Pickering et al. 2020). *Eucera pruinosa* is a cucurbit specialist that evolved with humans and squash, as it followed the cultivation of cucrbits out of Central America and across the rest of the continent (López-Uribe et al. 2016). *Eucera pruinosa* could be utilizing the wildflower plantings as nesting habitats that is proximate to crop plantings of cucurbits and undisturbed. These factors can be beneficial for *E. pruinosa* abundance (Shuler et al. 2005, Julier and Roulston 2009). *Melissodes bimaculatus* has shown a strong preference for agricultural land and avoided forests in a survey using 15 yr of geo-referenced bee data (Collado et al. 2019). *Melissodes bimaculatus* and *E. pruinosa* are two of top 10 most commonly reported bee species foraging on pollinator dependent crops in agricultural systems (Klein et al. 2018). With regard to *A. virescens* and *M. bimaculatus*, these two species are likely providing the bulk of the pollination services in study area because of their abundance (Winfree et al. 2015). The nonlinear effects detected in relation to SNH in the landscape for these two common agricultural species, may provide further insight into how these species could be promoted to provide pollination services. To measure the success of conservation efforts, assessments may need to consider what species are being targeted rather than bee communities as a whole.

Variable management of wildflower plantings may have affected our findings. The wildflower plantings in this study represent a real-world situation where grower-cooperators would have utilized a government program to install the plantings. Cooperators decided the locations and size of the wildflower plantings. Cooperators also differed in their approach to seedbed preparation, as three used tillage and an herbicide compared to the others who used only tillage. This difference in preparation resulted in more wildflower biomass at the sites where herbicides were used for the well-draining mix (Angelella and O'Rourke 2017). It was also recommended that the plots be mowed during the dormant season to promote growth for the following year. Two sites were never mowed after planting, and another was only mowed once after establishment. This lack of mowing may have altered the effectiveness of the plantings as it led to increased weed pressure and woody plant encroachment (Angelella, personal observation). Another wildflower site was mowed twice during the growing season. In addition to providing financial support, engaging with farmers about their experiences in using government conservation programs can lead to better conservation outcomes (McCracken et al. 2015).

When considered alone, wildflower plantings did not enhance the bee communities sampled. However, when SNH in the landscape was considered, there is a range in which the wildflower plantings enhanced bee abundance relative to control fields, suggesting bee populations on farms in the Mid-Atlantic with an intermediate level of surrounding SNH are most likely to benefit from the plantings. While on-farm wildflower plantings may be able to sometimes enhance bee communities, larger, landscape-scale, conservation efforts may be needed to better conserve bee communities. Further studies are needed in real world situations in the United States to better understand the effectiveness of on-farm efforts, such as establishing wildflower plantings. Assessing these situations is important, as the research team is not in control of certain aspects of the experiment. Allowing cooperating farmers to install and manage their wildflower plantings better reflects the reality and decision making of farmers as they seek to balance goals of conservation and production. Better understanding how private land pollinator conservation efforts play out will be critical to ensuring the success of pollinator conservation efforts more broadly.

## Supplementary Data

Supplementary data are available at *Environmental Entomology* online.

## Acknowledgments

We thank our cooperators for access to their land to conduct the study. Thank you to Jane Lassiter and Bob Glennon of the NRCS for their time and effort with this project. We greatly appreciate the efforts of our undergraduate assistants Erica, Sarah, Monique, Courtney, Brook, Brian, and Mika for their help collecting and processing all of the samples. We appreciate Sam Droege's time and effort for providing the species determinations. Thank you to Tom Kuhar, Sarah Karpanty, and Jacob Barney for feedback on the manuscript. We would like to acknowledge the two peer-reviewers whose feedback greatly improved the manuscript. Thank you to the Virginia Tech Entomology Collection for the use of reference specimens. United States Department of Agriculture is an equal opportunity provider and employer. The use of trade names or commercial products in this publication is to provide information for the reader and does not imply recommendation or endorsement by the USDA. This work was supported by United States Department of Agriculture National Institute of Food and Agriculture Agroecosystem Management grant, number 2015 67019-23215, to M.O. and by Southern Sustainable Agriculture Research and Education graduate student grant, GS17-176, to C.M.

## Data Availability

These data are available from the Virginia Tech Data Repository. McCullough, C., O'Rourke, M., & Angelella, G. (2021). Landscape context influences the bee conservation value of wildflower plantings [Data set]. University Libraries, Virginia Tech. https://doi.org/10.7294/C1XN-QD46

## References Cited

**Angelella, G. M., and M. E. O'Rourke. 2017**. Pollinator habitat establishment after organic and no-till seedbed preparation methods. HortScience. 52: 1349–1355.

**Angelella, G. M., C. T. McCullough, and M. E. O'Rourke. 2021**. Honey bee hives decrease wild bee abundance, species richness, and fruit count on farms regardless of wildflower strips. Sci. Rep. 11: 3202.

**Arathi, H. S., M. W. Vandever, and B. S. Cade. 2019**. Diversity and abundance of wild bees in an agriculturally dominated landscape of eastern Colorado. J. Insect Conserv. 23:187–197.

**Balzan, M. V., G. Bocci, and A.-C. Moonen. 2014**. Augmenting flower trait diversity in wildflower strips to optimise the conservation of arthropod functional groups for multiple agroecosystem services. J. Insect Conserv. 18: 713–728.

**Barton, K. 2018**. MuMIn: multi-model inference. https://cran.r-project.org/web/packages/MuMIn/index.html

**Begosh, A., L. M. Smith, S. T. McMurry, and J. P. Harris. 2020**. Influence of the Conservation Reserve Program (CRP) and playa wetlands on pollinator communities in the Southern High Plains, USA. J. Environ. Manage. 256: 109910.

**Blaauw, B. R., and R. Isaacs. 2014a**. Flower plantings increase wild bee abundance and the pollination services provided to a pollination-dependent crop. J. Appl. Ecol. 51: 890–898.

**Blaauw, B. R., and R. Isaacs. 2014b**. Larger patches of diverse floral resources increase insect pollinator density, diversity, and their pollination of native wildflowers. Basic Appl. Ecol. 15: 701–711.

**Buchanan, A., J. Gibbs, L. Komondy, and Z. Szendrei. 2017**. Bee community of commercial potato fields in Michigan and *Bombus impatiens* visitation to neonicotinoid-treated potato plants. Insects. 8: 30.

**Collado, M. Á., D. Sol, and I. Bartomeus. 2019**. Bees use anthropogenic habitats despite strong natural habitat preferences. Divers. Distrib. 25: 924–935.

**Dainese, M., E. A. Martin, M. A. Aizen, M. Albrecht, I. Bartomeus, R. Bommarco, L. G. Carvalheiro, R. Chaplin-Kramer, V. Gagic, L. A. Garibaldi, *et al.* 2019**. A global synthesis reveals biodiversity-mediated benefits for crop production. Sci. Adv. 5: eaax0121.

**Garibaldi, L. A., I. Steffan-Dewenter, R. Winfree, M. A. Aizen, R. Bommarco, S. A. Cunningham, C. Kremen, L. G. Carvalheiro, L. D. Harder, O. Afik, *et al.* 2013**. Wild pollinators enhance fruit set of crops regardless of honey bee abundance. Science. 339: 1608–1611.

**Garratt, M. P. D., D. Senapathi, D. J. Coston, S. R. Mortimer, and S. G. Potts. 2017**. The benefits of hedgerows for pollinators and natural enemies depends on hedge quality and landscape context. Agric. Ecosyst. Environ. 247: 363–370.

**Gibbs, J., N. K. Joshi, J. K. Wilson, N. L. Rothwell, K. Powers, M. Haas, L. Gut, D. J. Biddinger, and R. Isaacs. 2017**. Does passive sampling accurately reflect the bee (Apoidea: Anthophila) communities pollinating apple and sour cherry orchards? Environ. Entomol. 46: 579–588.

**Goulson, D., E. Nicholls, C. Botías, and E. L. Rotheray. 2015**. Bee declines driven by combined stress from parasites, pesticides, and lack of flowers. Science. 347: 1255957.

**Grab, H., K. Poveda, B. Danforth, and G. Loeb. 2018**. Landscape context shifts the balance of costs and benefits from wildflower borders on multiple ecosystem services. Proc R Soc B. 285: 20181102.

**Grab, H., M. G. Branstetter, N. Amon, K. R. Urban-Mead, M. G. Park, J. Gibbs, E. J. Blitzer, K. Poveda, G. Loeb, and B. N. Danforth. 2019**. Agriculturally dominated landscapes reduce bee phylogenetic diversity and pollination services. Science. 363: 282–284.

**Harrison, T., J. Gibbs, and R. Winfree. 2018a**. Phylogenetic homogenization of bee communities across ecoregions. Glob. Ecol. Biogeogr. 27: 1457–1466.

**Harrison, X. A., L. Donaldson, M. E. Correa-Cano, J. Evans, D. N. Fisher, C. E. D. Goodwin, B. S. Robinson, D. J. Hodgson, and R. Inger. 2018b**. A brief introduction to mixed effects modelling and multi-model inference in ecology. Peerj. 6: e4794.

**Herbertsson, L., A. M. Jönsson, G. K. S. Andersson, K. Seibel, M. Rundlöf, J. Ekroos, M. Stjernman, O. Olsson, and H. G. Smith. 2018**. The impact of sown flower strips on plant reproductive success in Southern Sweden varies with landscape context. Agric. Ecosyst. Environ. 259: 127–134.

**Julier, H. E., and T. H. Roulston. 2009**. Wild bee abundance and pollination service in cultivated pumpkins: farm management, nesting behavior and landscape effects. J. Econ. Entomol. 102: 563–573.

**Kennedy, C. M., E. Lonsdorf, M. C. Neel, N. M. Williams, T. H. Ricketts, R. Winfree, R. Bommarco, C. Brittain, A. L. Burley, D. Cariveau, *et al.* 2013**. A global quantitative synthesis of local and landscape effects on wild bee pollinators in agroecosystems. Ecol. Lett. 16: 584–599.

**Kleijn, D., T. E. W. Linders, A. Stip, J. C. Biesmeijer, F. L. Wäckers, and T. Bukovinszky. 2018**. Scaling up effects of measures mitigating pollinator loss from local- to landscape-level population responses. Methods Ecol. Evol. 9: 1727–1738.

**Klein, A. M., B. E. Vaissière, J. H. Cane, I. Steffan-Dewenter, S. A. Cunningham, C. Kremen, and T. Tscharntke. 2007**. Importance of pollinators in changing landscapes for world crops. Proc. Biol. Sci. 274: 303–313.

**Klein, A. M., V. Boreux, F. Fornoff, A. C. Mupepele, and G. Pufal. 2018**. Relevance of wild and managed bees for human well-being. Curr. Opin. Insect Sci. 26: 82–88.

**Kleintjes Neff, P., C. Locke, and E. Lee-Mäder. 2017**. Assessing a farmland set-aside conservation program for an endangered butterfly: USDA State Acres for Wildlife Enhancement (SAFE) for the Karner blue butterfly. J. Insect Conserv. 21: 929–941.

**Krimmer, E., E. A. Martin, J. Krauss, A. Holzschuh, and I. Steffan-Dewenter. 2019**. Size, age and surrounding semi-natural habitats modulate the effectiveness of flower-rich agri-environment schemes to promote pollinator visitation in crop fields. Agric. Ecosyst. Environ. 284: 106590.

**Kuznetsova, A., P. B. Brockhoff, and R. H. B. Christensen. 2017**. lmerTest package: tests in linear mixed effects models. J. Stat. Softw. 82: 1–26.

**Lichtenberg, E. M., C. M. Kennedy, C. Kremen, P. Batáry, F. Berendse, R. Bommarco, N. A. Bosque-Pérez, L. G. Carvalheiro, W. E. Snyder, N. M. Williams, *et al.* 2017**. A global synthesis of the effects of diversified farming systems on arthropod diversity within fields and across agricultural landscapes. Glob. Chang. Biol. 23: 4946–4957.

**López-Uribe, M. M., J. H. Cane, R. L. Minckley, and B. N. Danforth. 2016**. Crop domestication facilitated rapid geographical expansion of a specialist pollinator, the squash bee *Peponapis pruinosa*. Proc. R. Soc. B Biol. Sci. 283: 20160443.

**McCracken, M. E., B. A. Woodcock, M. Lobley, R. F. Pywell, E. Saratsi, R. D. Swetnam, S. R. Mortimer, S. J. Harris, M. Winter, S. Hinsley, *et al.* 2015**. Social and ecological drivers of success in agri-environment schemes: the roles of farmers and environmental context. J. Appl. Ecol. 52: 696–705.

**Nicholson, C. C., I. Koh, L. L. Richardson, A. Beauchemin, and T. H. Ricketts. 2017**. Farm and landscape factors interact to affect the supply of pollination services. Agric. Ecosyst. Environ. 250: 113–122.

**Nicholson, C. C., K. L. Ward, N. M. Williams, R. Isaacs, K. S. Mason, J. K. Wilson, J. Brokaw, L. J. Gut, N. L. Rothwell, T. J. Wood, *et al.* 2020**. Mismatched outcomes for biodiversity and ecosystem services: testing the responses of crop pollinators and wild bee biodiversity to habitat enhancement. Ecol. Lett. 23: 326–335.

**NRCS. 2015**. Using 2014 farm bill programs for pollinator conservation. Biology Technical Note No. 78, 2nd Ed. United States Department of Agriculture, Washington D.C.

**O'Connor, R. S., W. E. Kunin, M. P. D. Garratt, S. G. Potts, H. E. Roy, C. Andrews, C. M. Jones, J. M. Peyton, J. Savage, M. C. Harvey, *et al.* 2019**. Monitoring insect pollinators and flower visitation: the effectiveness and feasibility of different survey methods. Methods Ecol. Evol. 10: 2129–2140.

**Oksanen, J., F. G. Blanchete, M. Friendly, R. Kindt, P. Legendre, D. McFlinn, P. R. Minchin, R. B. O'Hara, G. L. Simpson, P. Solymos, *et al.* 2018**. vegan: community ecology package. https://cran.r-project.org/web/packages/vegan/index.html

**Otto, C. R. V., S. O'Dell, R. B. Bryant, N. H. Euliss, R. M. Bush, and M. D. Smart. 2017**. Using publicly available data to quantify plant–pollinator interactions and evaluate conservation seeding mixes in the northern Great Plains. Environ. Entomol. 46: 565–578.

**Pickering, J., J. Ascher, and S. Droege. 2020**. Apoidea, Bees; Apoid Wasps. Discov. Life. https://www.discoverlife.org/20/q?search=Apoidea.

**Potts, S. G., J. C. Biesmeijer, C. Kremen, P. Neumann, O. Schweiger, and W. E. Kunin. 2010**. Global pollinator declines: trends, impacts and drivers. Trends Ecol. Evol. 25: 345–353.

**R Core Team. 2018**. A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.

**Ricketts, T. H., J. Regetz, I. Steffan-Dewenter, S. A. Cunningham, C. Kremen, A. Bogdanski, B. Gemmill-Herren, S. S. Greenleaf, A. M. Klein, M. M. Mayfield, *et al.* 2008**. Landscape effects on crop pollination services: are there general patterns? Ecol. Lett. 11: 499–515.

**Scheper, J., A. Holzschuh, M. Kuussaari, S. G. Potts, M. Rundlöf, H. G. Smith, and D. Kleijn. 2013**. Environmental factors driving the effectiveness of European agri-environmental measures in mitigating pollinator loss – a meta-analysis. Ecol. Lett. 16: 912–920.

**Shuler, R. E., T. H. Roulston, and G. E. Farris. 2005**. Farming practices influence wild pollinator populations on squash and pumpkin. J. Econ. Entomol. 98: 790–795.

**Skaug, H., D. Fournier, A. Nielsen, A. Magnusson, and B. Bolker. 2016**. Generalized linear mixed models using "AD Model Builder". http://www.admb-project.org/

**Tonietto, R. K., and D. J. Larkin. 2018**. Habitat restoration benefits wild bees: a meta-analysis. J. Appl. Ecol. 55: 582–590.

**Tscharntke, T., A. M. Klein, A. Kruess, I. Steffan-Dewenter, and C. Thies. 2005**. Landscape perspectives on agricultural intensification and biodiversity – ecosystem service management. Ecol. Lett. 8: 857–874.

**Tuell, J. K., A. K. Fiedler, D. Landis, and R. Isaacs. 2008**. Visitation by wild and managed bees (Hymenoptera: Apoidea) to eastern U.S. native plants for use in conservation programs. Environ. Entomol. 37: 707–718.

**USDA. 2018**. Environmental Quality Incentives Program (EQIP) | Farm Bill Report (FY 2009 through FY 2018) | NRCS. https://www.nrcs.usda.gov/Internet/NRCS_RCA/reports/fb08_cp_eqip.html.

**USDA. 2019**. Conservation reserve program fact sheet. United States Department of Agriculture. https://www.fsa.usda.gov/Assets/USDA-FSA-Public/usdafiles/FactSheets/2019/conservation-reserve_program-fact_sheet.pdf

**US EPA. 2017**. Federal pollinator health task force: EPA's role. https://19january2017snapshot.epa.gov/pollinator-protection/federal-pollinator-health-task-force-epas-role_.html#:~:text=The%20goals%20of%20the%20National,over%20the%20next%20five%20years

**United States Forest Service. 2016**. Future of America's forests and rangelands: update to the Forest Service 2010 Resources Planning Act Assessment (No. Gen. Tech. Rep. WO-94). United States Department of Agriculture, Washington D.C.

**Vaughn, M., and M. Skinner. 2015**. Using 2014 Farm Bill programs for pollinator conservation (Biology Technical Note No. No. 78). United States Department of Agriculture, Washington D.C.

**Venturini, E. M., F. A. Drummond, A. K. Hoshide, A. C. Dibble, and L. B. Stack. 2017**. Pollination reservoirs for wild bee habitat enhancement in cropping systems: a review. Agroecol. Sustain. Food Syst. 41: 101–142.

**Wheelock, M. J., K. P. Rey, and M. E. O'Neal. 2016**. Defining the insect pollinator community found in Iowa corn and soybean fields: implications for pollinator conservation. Environ. Entomol. 45: 1099–1106.

**Williams, N. M., K. L. Ward, N. Pope, R. Isaacs, J. Wilson, E. A. May, J. Ellis, J. Daniels, A. Pence, K. Ullmann, *et al.* 2015**. Native wildflower plantings support wild bee abundance and diversity in agricultural landscapes across the United States. Ecol. Appl. 25: 2119–2131.

**Winfree, R., N. M. Williams, J. Dushoff, and C. Kremen. 2007**. Native bees provide insurance against ongoing honey bee losses. Ecol. Lett. 10: 1105–1113.

**Winfree, R., N. M. Williams, H. Gaines, J. S. Ascher, and C. Kremen. 2008**. Wild bee pollinators provide the majority of crop visitation across land-use gradients in New Jersey and Pennsylvania, USA. J. Appl. Ecol. 45: 793–802.

**Winfree, R., J. W. Fox, N. M. Williams, J. R. Reilly, and D. P. Cariveau. 2015**. Abundance of common species, not species richness, drives delivery of a real-world ecosystem service. Ecol. Lett. 18: 626–635.

**Wood, T. J., J. M. Holland, and D. Goulson. 2015**. A comparison of techniques for assessing farmland bumblebee populations. Oecologia. 177: 1093–1102.

**Woodcock, B. A., M. P. D. Garratt, G. D. Powney, R. F. Shaw, J. L. Osborne, J. Soroka, S. A. M. Lindström, D. Stanley, P. Ouvrard, M. E. Edwards, *et al.* 2019**. Meta-analysis reveals that pollinator functional diversity and abundance enhance crop pollination and yield. Nat. Commun. 10: 1481.