

Mass Flowering Crops as a Conservation Resource for Wild Pollinators (Hymenoptera: Apoidea)

KATHERINE J. TODD,^{1*},² MARY M. GARDINER,¹ AND ERIK D. LINDQUIST²

ABSTRACT: Habitat management within agroecosystems can conserve wild pollinator communities by providing nesting and floral resources. However, demarcating arable land for conservation may reduce farm income. A conciliatory habitat management plan thus consists of planting harvestable commodities which offer pollinator resources. This study's goal was to determine whether a single species annual flowering crop could support an abundant and diverse wild pollinator community despite its own uniformity. Local bee communities were sampled using pan traps and hand collection within sixty 10 m² plots of a sunflower, *Helianthus annuus* L., field and thirty 10 m² plots within a meadow three times throughout August, 2012. In total, 2316 bees were collected with *Bombus impatiens* Cresson constituting 81.5% of sampled bees. Examined collectively, hand collections yielded significantly higher bee abundances in the sunflower field ($P < 0.01$) across every sampling date. Conversely, an equivalent number of pan-trapped bees occurred among habitats for all sampling dates except week three ($P = 0.02$) when a greater abundance was observed in the sunflower habitat. Species diversity did not differ ($P_{\text{hand}} = 0.99$, $P_{\text{pan}} = 0.97$) between habitats although community composition differed with high significance ($P < 0.01$) indicating that these habitats had comparable diversity levels but attracted particular bee assemblages. Our study identifies sunflower crops as useful pollinator resources, especially for *Bombus* species, and provides insight into single species annual crops' potential contribution to pollinator conservation.

KEY WORDS: Sunflower, *Bombus*, ecosystem services, habitat management

Much of agricultural production depends on insect pollination for crop success; estimates suggest that insect pollination provides a \$361 billion service to the global agricultural industry (Lautenbach *et al.*, 2012). Although managed honey bees, *Apis mellifera* L., are important crop pollinators, recent evidence suggests that wild pollinators can be critical for crop yield despite honey bee abundance (Garibaldi *et al.*, 2013). Increased diversity and abundance of wild pollinators has also been shown to enhance plant productivity in agricultural production sites (Albrecht *et al.*, 2012; Garibaldi *et al.*, 2014). Furthermore, even self-pollinating crops, such as some sunflower cultivars, exhibit improved yield quantity, quality, and heat-shock resistance when wild bees are present (Parker, 1981; DeGrandi-Hoffman and Chambers, 2006). Unfortunately, such wild bee benefits to agriculture are threatened by bee population declines which have been documented across several countries (Beismejjer *et al.*, 2006; Colla and Packer, 2008; Goulson *et al.*, 2008; Gallai *et al.*, 2009; Grixti *et al.*, 2009; Potts *et al.*, 2010; Bommarco *et al.*, 2012; Dirzo *et al.*, 2014). Moreover, intensively managed agroecosystems often lack suitable nesting habitat and floral resources to attract those pollinators which are present within a surrounding landscape (Kremen *et al.*, 2002; Williams *et al.*, 2010; Kennedy *et al.*, 2013).

Conservationists and farmers alike have attempted to address pollinator decline and support future agricultural production by promoting pollinator biodiversity and planting native

¹ Department of Entomology, The Ohio State University, Columbus, Ohio 43210, e-mail: todd.489@osu.edu, gardiner.29@osu.edu

² Department of Biology, Messiah College, Mechanicsburg, Pennsylvania 17055, quist@messiah.edu

* 216 Kottman Hall, 2021 Coffey Rd Columbus, Ohio 43210, (860) 367-3300

Received 23 August 2015; Accepted 2 June 2015

© 2016 Kansas Entomological Society

wildflower habitats in agricultural sites (Tuell *et al.*, 2008; Isaacs *et al.*, 2009; Winfree and Kremen, 2009; Korpela *et al.*, 2013; Blaauw and Isaacs, 2014). Although governmental programs exist to subsidize the cost of wildflower plantings (Vaughan and Skinner, 2008), farmers must still reserve a portion of their arable land to participate in such programs. Long-term, these subsidies may not be reliable, and so it is necessary to investigate whether mass flowering, annual crops, such as canola or sunflower, could support wild bees while still producing a marketable commodity for farmers.

Mass flowering crops are known to benefit bumble bee populations at a landscape scale (Westphal *et al.*, 2003; Westphal *et al.*, 2009) and research suggests that mass flowering crops interact with semi-natural habitats to support populations of cavity nesting wasps and bees despite their brief bloom duration (Holzschuh *et al.*, 2013; Diekötter *et al.*, 2014). Yet, it is still unclear if patch-scale habitat management for a mass flowering crop can support a bee community in a comparable manner to that of a native wildflower habitat.

Our study focuses on sunflowers as they are a prominent mass flowering crop in the United States with an average of 1,023,045 hectares harvested each year from 1980–2013 (Ash, 2015). The first objective of our study was to compare bee abundance and community composition supported by patch-scale production of sunflowers versus a meadow habitat. We hypothesized that a sunflower planting would provide foraging resources to a high abundance and diversity of wild bees, as sunflowers have abundant pollen and nectar resources (Neff and Simpson, 1990; Minckley *et al.*, 1994), and a variety of bees are known to visit sunflowers (Hurd *et al.*, 1980). Secondly, we examined how sunflower densities may impact bee foraging. Sunflowers are grown as both a confection and biofuel crop and these two crops are respectively seeded at low and high densities (Berglund, 2007). Thus, investigating floral density is relevant to determining conservation potential of sunflower plantings.

Methods and Materials

STUDY SITES: Two sites were used in the course of this study, a sunflower field and an old field meadow, located in Mechanicsburg, Pennsylvania (Cumberland County) within 1.6 km of each other. All data was collected from sixty 10 m² plots of varying floral density (25–400 inflorescences) within the sunflower habitat and thirty 10 m² plots within the meadow habitat. Additional plots were sampled in the sunflower habitat to measure the influence of floral density on pollinator abundance and diversity. Plots were located at the edge of their respective habitats and represent likely placement within an agroecosystem. The sunflower field (40°9'41.01"N, 76°59'35.06"W) was planted with Pioneer® Sunflower Hybrid 63N82 (DuPont, Wilmington, DE) sunflowers and consists of 5.9 hectares of agricultural property owned by Messiah College. The field lays adjacent to a residential area and is lined by trees at its west and east edges and a small cemetery at its southern border. The meadow control site (40°9'18.17"N, 76°58'42.63"W) is located within an 11.3 hectare undeveloped property owned by Messiah College and consists of both a wetland and an old field meadow. The meadow is managed with mowing every 2–5 years in order to control invasive autumn olive, *Elaeagnus umbellata* Thunb. Hardwood forest borders the meadow to its north, south, and west with a residential area to its east. Dominant plants in this habitat included: *Solidago canadensis* L., *Erigeron strigosus* Muhl. ex Willd., *Asclepias syriaca* L., *Daucus carota* L., *Trifolium pratense* L., *Alliaria petiolata* (M.Bieb.) Cavara & Grande, and *Lonicera maackii* (Rupr.) Maxim. Less common plant species included: *Symphotrichum lateriflorum* (L.) Á. & D. Löve, *Cirsium arvense* (L.) Scop., and *Solidago gigantea* Ait.

BEE COLLECTION: Our study was informed by LeBuhn *et al.*'s (2003) standardized methodology for bee inventory. For every plot, both pan traps and hand collection were utilized to determine the composition of the pollinator community over the course of sunflower bloom. Collection occurred once a week for three weeks during the period August 06 to 22, 2012 and was initiated during peak sunflower bloom. The weather on all collection days was sunny to partly cloudy with a wind speed of less than 4.8 kph and no precipitation. Mean daytime temperatures varied between 21 and 27°C.

On collection days, hand collection occurred during the early afternoon, from 1300–1600 h and was limited to 3 minutes per plot. During this sampling, bees were collected by one field worker with both nets and small glass vials. When collecting, workers walked through a plot looking at all floral resources, and would pause their stopwatch if transferring a bee from a net to a vial. In order to pan trap bees, bamboo stakes were placed in the center of each 10 m² plot and supported a 1.2 m high platform with three pan traps at the height of the sunflower heads. Pan traps consisted of Solo[®] soufflé cups in three colors: fluorescent blue, fluorescent yellow, and white, and were filled 1/3 with soapy water. Soapy water was composed of approximately 1 ml of Ultra Blue Dawn[®] liquid soap per 3.8 liters of water. Pan traps were put into the field at 1700–1800 P.M. following the completion of hand collection and left for 24 hours. All pan-trapped specimens were washed with water and stored in 70% ethanol; hand-collected specimens were frozen until further pinning and identification. Online keys from DiscoverLife.org were used for identification with all species verified by Leo R. Donovall at the Pennsylvania Department of Agriculture's Entomology Program. Voucher specimens are available in the collections of the Oakes Museum of Natural History at Messiah College in Mechanicsburg, Pennsylvania.

DATA ANALYSIS: Bee species diversity for both pan and hand-collected samples was calculated separately using a Simpson's Diversity Index ($D = 1 - \frac{\sum n_i(n_i-1)}{N(N-1)}$) and then compared among meadow and sunflower habitats using a General Linear Model (GLM) with a Poisson distribution in SAS version 9.4 (SAS Institute Inc., 2013). The fixed factors within this model were habitat (sunflower or meadow) and sampling week (1–3). The interaction term habitat*week was also included in the model. Additional GLM analyses were conducted for the response variables bee abundance and *Bombus impatiens* Cresson abundance, both with a negative binomial distribution. These models also included the fixed factors habitat (sunflower or meadow) and sampling week (1–3) as well as the interaction term habitat*week.

The impact of sunflower density on bee abundance and diversity was measured using simple linear regression. Sunflower density was regressed separately against pan and hand-collected bee abundance, pan and hand-collected bee diversity, and *Bombus impatiens* abundance using Minitab version 17 (Minitab, 2014). Finally, bee community composition among habitat types and sampling methods was compared via a Nonmetric Multidimensional Scaling (NMDS) analysis and a Permutational Multivariate Analysis of Variance (PERMANOVA) using distance matrices in the vegan package of R version 3.1.1 (Oksanen *et al.*, 2013). To spatially represent the communities through a NMDS analysis, a *metaMDS* function with a Bray-Curtis distance distribution and three dimensions was plotted in R. To test for statistical significance between these communities, an *adonis* function with a Bray-Curtis distance distribution was employed.

Results

BEE COMMUNITY COMPOSITION: Bees collected during the sampling period numbered 2316 (Table 1). Of this total count, 111 were *Apis mellifera* and 2205 were wild bees. One

Table 1. Total species collected in Cumberland County, PA from 06–22 August 2012.

Family	Genus	Species	Sunflower	Meadow	Total
Apidae	<i>Anthophora</i>	<i>terminalis</i>	1	-	1
Apidae	<i>Apis</i>	<i>mellifera</i>	103	8	111
Apidae	<i>Bombus</i>	<i>bimaculatus</i>	1	-	1
Apidae	<i>Bombus</i>	<i>fervidus</i>	7	-	7
Apidae	<i>Bombus</i>	<i>griseocollis</i>	10	1	11
Apidae	<i>Bombus</i>	<i>impatiens</i>	1868	19	1887
Apidae	<i>Bombus</i>	<i>perplexus</i>	6	-	6
Apidae	<i>Ceratina</i>	<i>calcarata / mikmaqi</i>	1	35	36
Apidae	<i>Ceratina</i>	<i>dupla</i>	6	12	18
Apidae	<i>Ceratina</i>	<i>strenua</i>	-	11	11
Apidae	<i>Melissodes</i>	<i>bimaculata</i>	14	1	15
Apidae	<i>Melissodes</i>	<i>denticulata</i>	-	1	1
Apidae	<i>Melissodes</i>	<i>nivea</i>	1	-	1
Apidae	<i>Peponapis</i>	<i>pruinosa</i>	-	2	2
Apidae	<i>Xylocopa</i>	<i>virginica</i>	3	2	5
Colletidae	<i>Hylaeus</i>	<i>affinis</i>	-	6	6
Halictidae	<i>Agapostemon</i>	<i>virescens</i>	2	3	5
Halictidae	<i>Augochlora</i>	<i>pura</i>	29	40	69
Halictidae	<i>Augochlorella</i>	<i>aurata</i>	4	6	10
Halictidae	<i>Augochloropsis</i>	<i>metallica</i>	-	2	2
Halictidae	<i>Halictus</i>	<i>confusus</i>	-	7	7
Halictidae	<i>Halictus</i>	<i>ligatus</i>	14	17	31
Halictidae	<i>Halictus</i>	<i>rubicundus</i>	1	-	1
Halictidae	<i>Lasioglossum</i>	<i>admirandum</i>	20	9	29
Halictidae	<i>Lasioglossum</i>	<i>caeruleum</i>	1	-	1
Halictidae	<i>Lasioglossum</i>	<i>imitatum</i>	4	1	5
Halictidae	<i>Lasioglossum</i>	<i>pilosum</i>	15	5	20
Halictidae	<i>Lasioglossum</i>	sp.	-	1	1
Halictidae	<i>Lasioglossum</i>	<i>tegulare</i>	2	-	2
Halictidae	<i>Lasioglossum</i>	<i>versatum</i>	3	2	5
Megachilidae	<i>Anthidium</i>	<i>manicatum</i>	1	-	1
Megachilidae	<i>Megachile</i>	<i>companulae</i>	-	1	1
Megachilidae	<i>Megachile</i>	<i>inimical</i>	1	-	1
Megachilidae	<i>Megachile</i>	<i>mendica</i>	2	1	3
Megachilidae	<i>Megachile</i>	<i>rotundata</i>	-	1	1
Megachilidae	<i>Osmia</i>	<i>texana</i>	-	1	1
Megachilidae	<i>Pseudoanthidium</i>	<i>nanum</i>	-	1	1
			2120	196	2316

species, *Bombus impatiens*, dominated the collection and constituted 81.5% of the total count or 1887 bees in total. Comparatively, other *Bombus* spp. only comprised $\leq 0.5\%$ of total bees. Apart from the halictid *Augochlora pura* (Say), which comprised 3.0% of total bees, all other wild bee species were present at less than < 1.5 (Table 1). Curiously, our two most abundant species (*B. impatiens* and *A. pura*) are polyleges determined as only casually associated with sunflower (Hurd *et al.*, 1980), while the regular sunflower associate *Bombus griseocollis* (DeGeer) was collected only 11 times.

BEE DIVERSITY AND ABUNDANCE BY HABITAT: Thirty-seven bee species were collected throughout the duration of this study, of which 27 species were sampled in the wildflower habitat, 26 in the sunflower habitat, and 16 species from both habitats. We found no significant differences in Simpson's diversity for bees within pan ($F_{1,213} = 0.00$, $P = 0.99$) or

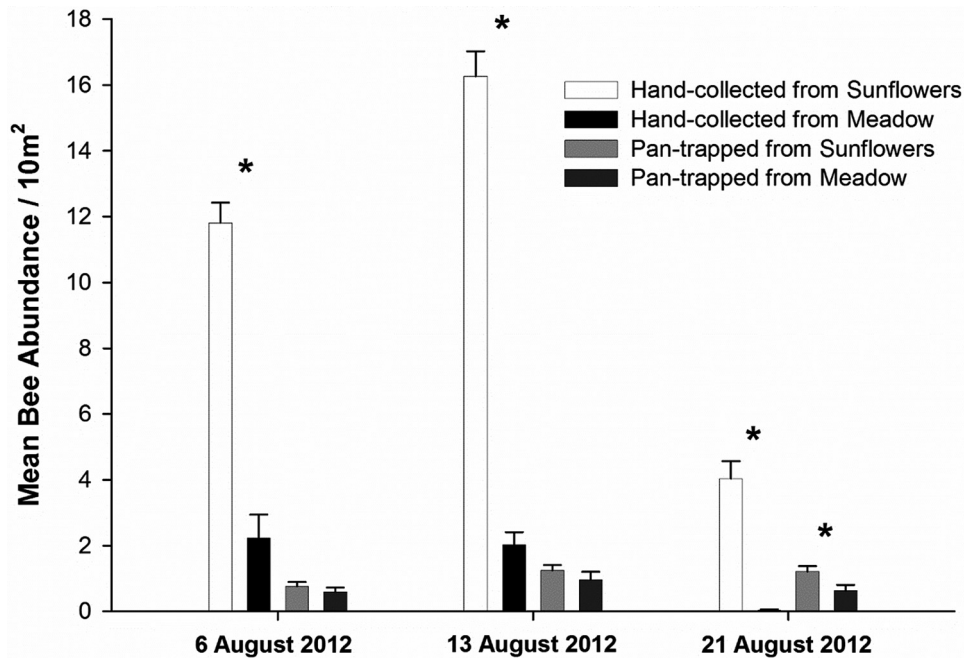


Fig. 1. **Mean bee abundance by habitat and collecting method.** Mean abundance of bees collected in 10 m² of a sunflower habitat versus a meadow habitat during three weeks of sampling. General Linear Model (GLM) regression analysis concluded bees were more abundant within the sunflower field across all weeks for hand-collected samples ($P < 0.01$). For pan-trapped samples, only week three showed a significant difference between meadow and sunflower bee abundance ($P = 0.02$), although statistical differences were only slightly above our chosen level of significance ($\alpha = 0.05$) for week one ($P = 0.053$) and week two ($P = 0.06$).

hand-collected ($F_{1,264} = 0.00$, $P = 0.97$) samples between the two habitats. However, we hand-collected a greater abundance of bees in the sunflower field across all weeks of sampling ($F_{1,264} = 67.81$, $P < 0.01$; Fig. 1).

Hand-collections within a habitat type also varied in abundance by week. All hand-collected samples exhibited an interaction between week and habitat ($F_{2,264} = 5.60$, $P < 0.01$), potentially due to variation in nectar or pollen as sunflower bloom progressed over time. Within meadow samples, significantly fewer bees were hand-collected in week three than in week one and two ($P < 0.01$) while there was no difference in bee abundance between weeks one and two ($P = 0.67$). Similarly, sunflower hand-collected samples varied in abundance across all weeks ($F_{2,264} = 14.52$, $P < 0.01$).

For pan samples, habitat differences were less distinct. A higher abundance of bees occurred in the sunflower field compared to the meadow during week three ($P = 0.02$; Fig. 2A) but bee abundances in weeks one and two were statistically equivalent ($P = 0.053$ and $P = 0.06$). Within the meadow habitat, pan-trapped bee abundances did not vary over our three week sampling period. In the sunflower field, pan samples were less abundant in week one than in weeks two and three ($P = 0.02$ and 0.03 , respectively) but did not vary between weeks two and three ($P = 0.89$). Finally, we found no interaction between week and habitat for pan collections.

Similar trends were found for *Bombus* spp. abundance as for total bee abundance: hand-collected bumble bees were significantly more abundant in the sunflower field during all

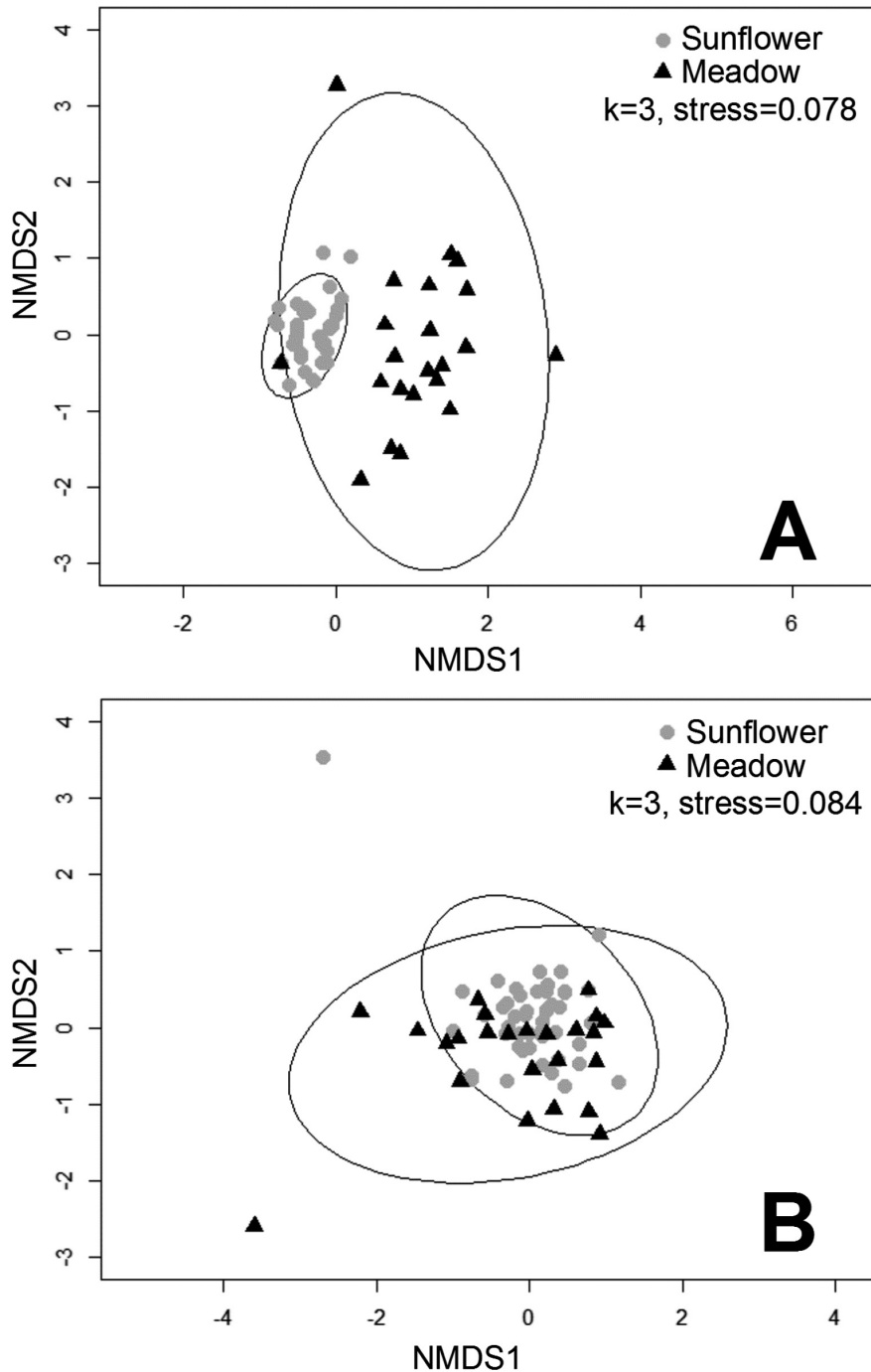


Fig. 2. NMDS analysis of bee community composition by habitat and collecting method. (A) Hand-collected bees in the sunflower field as compared to the meadow habitat. Limited overlap occurs amongst habitat types and illustrates that the pollinator communities in these habitats are distinct ($P < 0.01$). (B) Pan-trapped specimens show a more overlapping bee community between habitats than hand-collected specimens (A), although community composition between habitats was significantly different in both pan and hand-collected bees ($P < 0.01$), as determined by a PERMANOVA using distance matrixes.

sampling periods ($F_{1,264} = 126.27$, $P < 0.01$). Across weeks, hand-collected bumble bee abundance fluctuated in the sunflower field ($F_{2,264} = 3.67$, $P = 0.03$). In the meadow, hand-collected bumble bee abundance did not vary across weeks. Likewise, pan trap samples only varied by habitat and not by week, with *Bombus* spp. significantly more abundant in the sunflower field ($F_{1,264} = 12.46$, $P < 0.01$) overall.

INFLUENCE OF SUNFLOWER DENSITY: We found no correlation between hand-collected bee abundance ($P > 0.05$, $R^2 = 0.24$) or hand-collected bee diversity ($P > 0.05$, $R^2 = 0.05$) and sunflower density. Similarly, the abundance and diversity of our most frequently encountered species *Bombus impatiens* was not correlated with sunflower density ($P_{\text{hand}} = 0.15$, $R^2_{\text{hand}} = 0.01$; $P_{\text{pan}} = 0.62$, $R^2_{\text{pan}} = 0.00$).

BEE COMMUNITY COMPOSITION BY HABITAT: NMDS spatial analysis illustrated that hand-collected bee communities were distinct among our two habitats (Fig. 2A). Further PERMANOVA tests using distance matrixes supported this conclusion and indicated that highly significant differences existed between bee community compositions in each habitat ($P < 0.01$). NMDS analysis of the pan-trapped bee communities showed more overlapping and less distinct communities (Fig. 2B), but PERMANOVA results still confirmed that the pollinator communities foraging in sunflower and meadow habitats were significantly different ($P < 0.01$).

Discussion

SUNFLOWERS AS A POLLINATOR RESOURCE: As predicted, the sunflower habitat was frequented by a high abundance of foraging bees. Bee diversity, however, was not significantly different in the sunflower field than in a nearby meadow. Summed, these results imply that sunflowers are beneficial for wild bees and could be used to bolster foraging resources in agroecosystems. However, our study's short duration and restricted field locations limit its generality. More data would have to be collected across time and space in order to establish fully how sunflower plantings affect wild bees in agroecosystems. We must also caution that despite these positive results, sunflower plantings will work best as a conservation tool when complemented by additional habitats. As shown by our NMDS (Fig. 2) and PERMANOVA tests, a difference in bee community composition exists between meadow and sunflower habitats. Thus, sunflowers could support a select number of bee species with sufficient food resources but should not be planted to the exclusion of other habitats.

Moreover, since mass-flowering crops only bloom for a short duration, it is important to manage agricultural landscapes for floral resources that bloom at different times during the growing season. Such a landscape mosaic could be created through management of semi-natural habitats like grasslands (Holzschuh *et al.*, 2013; Diekötter *et al.*, 2014), native wildflower plantings (Isaacs *et al.*, 2009), or multiple mass-flowering crops that bloom at separate times (Bennett and Isaacs, 2014; Riedinger *et al.*, 2014). With additional high quality habitats incorporated within and surrounding agricultural fields, both pollinator communities and pollination services will benefit (Kennedy *et al.*, 2013; Korpela *et al.*, 2013; Blaauw and Isaacs, 2014; Holland *et al.*, 2015).

BOMBUS SPECIES ABUNDANCE: Our study found sunflowers were highly attractive to *Bombus* species. In particular, the common eastern bumble bee, *B. impatiens*, was very abundant throughout the duration of our study and comprised 81.5% of all specimens. This large collection of *B. impatiens* partially drove our significant results of (1) higher bee abundance within the sunflower field and (2) different bee community composition among our study sites; *B. impatiens* had a mean abundance of 31 bees in each sunflower plot whereas mean abundance in the meadow was less than 1 *B. impatiens* per plot. Such a

high abundance is not surprising considering *B. impatiens* is both a common species in the study region and is managed as a commercial greenhouse pollinator where escapes from greenhouses are not uncommon (Whittington and Winston, 2004; Velthuis and van Doorn, 2006; Ratti and Colla, 2010).

However, even when *B. impatiens* was excluded from our analyses, other species in the *Bombus* genus were still much more abundant in the sunflower fields than in the meadow. Mean *Bombus* spp. abundance in the meadow was 1 bumble bee per 10 m² whereas mean *Bombus* spp. abundance in the sunflower field was 21 bumble bees per 10 m². Only one specimen of *B. grisecolis* and nineteen specimens of *B. impatiens* were collected in the old field meadow while five species, *Bombus bimaculatus* Cresson ($n=1$), *Bombus fervidus* (Fabricius) ($n=7$), *B. grisecolis* ($n=10$), *B. impatiens* ($n=1868$), and *Bombus perplexus* Cresson ($n=6$), were found in the sunflower field. Differences in *Bombus* spp. abundance within these two habitats could be influenced by floral density differences between the meadow and sunflower field or the bee's floral preferences based on tongue length. Yet, our data and past records indicate *Bombus* spp. forage on sunflowers despite variance in tongue length (Hurd *et al.*, 1980; Colla *et al.*, 2011; Koch *et al.*, 2012), and this suggests sunflowers are generally attractive to bumble bees.

In light of bumble bee decline (Goulson *et al.*, 2008; Potts *et al.*, 2010), our observations that *Bombus* spp. frequently forage on sunflowers are relevant to bumble bee conservation. Meta-analyses have hypothesized that the most significant driver of bumble bee decline is likely loss of foraging and nesting resources from land use changes, habitat loss (Goulson *et al.*, 2008; Ricketts *et al.*, 2008; Brown and Paxton, 2009), or large-scale agricultural intensification (Goulson, 2003; Grixti *et al.*, 2009; Ollerton *et al.*, 2014). Thus, efforts which address these drivers, such as providing foraging sunflower habitats in agroecosystems, may be important for bumble bee conservation.

Conclusions

Our study provides insight into patch-scale mass flowering crops as a unique pollinator conservation method, especially for bumble bee populations. Despite some limitations, our results indicate that high abundances of select pollinator communities forage on sunflowers. Thus, we recommend further investigation into the compelling relationship between patch-scale sunflower plantings and pollinator conservation. Sunflowers represent a promising management tool for farmers and researchers interested in creating bee friendly landscapes.

Acknowledgements

Bee species verification and identification were conducted, in part, by Leo R. Donovall of the Pennsylvania Department of Agriculture's Entomology Program and by Dr. David Biddinger of the Pennsylvania State University's Fruit Research Extension Center. All sunflowers were planted by Lynn Wingert. For invaluable field and laboratory assistance, we thank K. Ellis, I. Gallo, M. Kammerer, L. Miller, L. Putney, A. Ritz, E. Shirey, and K. Wholaver. For comments, suggestions, and support, we thank members of the Ag-Urban Landscape Ecology Lab. Support for this work, in part, was provided by NSF CAREER DEB Ecosystem Studies Program (CAREER 1253197), and NSF and USFS ULTRA-Ex Program (NSF 0948985). Additional funding and resources were provided by the Department of Biological Sciences and the Sustainability Office at Messiah College, and Pennsylvania State University's Fruit Research Extension Center.

Literature Cited

- Albrecht, M., B. Schmid, Y. Hautier, and C. B. Müller. 2012. Diverse pollinator communities enhance plant reproductive success. *Proceedings of the Royal Society B: Biological Sciences* 279: 4845–4852.
- Ash, M., 2015. Oil crops yearbook, OCS-2015. U. S. Department of Agriculture (USDA), Economic Research Service (ERS). Available from <http://www.ers.usda.gov/data-products/oil-crops-yearbook.aspx> (Last accessed: November 2015).
- Beismejer, J. C., S. P. M. Roberts, M. Reemer, M. Edwards, T. Peeters, A. P. Schaffers, S. G. Potts, R. Kleukers, C. D. Thomas, J. Settele, and W. E. Kunin. 2006. Parallel declines in pollinators and insect-pollinated plants in Britain and the Netherlands. *Science* 313: 351–354.
- Bennett, A. B., and R. Isaacs. 2014. Landscape composition influences pollinators and pollination services in perennial biofuel plantings. *Agriculture, Ecosystems and Environment* 193: 1–8.
- Berglund, D. R. 2007. Sunflower production. Extension Publication A-1331 (EB-25 Revised). *North Dakota State University*. 117 pp.
- Blaauw, B. R., and R. Isaacs. 2014. Flower plantings increase wild bee abundance and the pollination services provided to a pollination-dependent crop. *Journal of Applied Ecology* 51: 890–898.
- Bommarco, R., O. Lundin, H. G. Smith, and M. Rundlof. 2012. Drastic historic shifts in bumble-bee community composition in Sweden. *Proceedings of the Royal Society B: Biological Sciences* 279: 309–315.
- Brown, M. J. F., and R. J. Paxton. 2009. The conservation of bees: A global perspective. *Apidologie* 40: 410–416.
- Colla, S. R., and L. Packer. 2008. Evidence for decline in eastern North American bumblebees (Hymenoptera: Apidae), with special focus on *Bombus affinis* Cresson. *Biodiversity and Conservation* 17: 1379–1391.
- Colla, S., L. Richardson, P. Williams, S. Colla, L. Richardson, and P. Williams. 2011. Guide to bumble bees of the eastern United States. *The Xerces Society for Invertebrate Conservation*. 104 pp.
- Degrandi-Hoffman, G., and M. Chambers. 2006. Effects of honey bee (Hymenoptera: Apidae) foraging on seed set in self-fertile sunflowers (*Helianthus annuus* L.). *Environmental Entomology* 35: 1103–1108.
- Diekötter, T., F. Peter, B. Jauker, V. Wolters, and F. Jauker. 2014. Mass-flowering crops increase richness of cavity-nesting bees and wasps in modern agro-ecosystems. *Global Change Biology: Bioenergy* 6: 219–226.
- Dirzo, R., H. S. Young, M. Galetti, G. Ceballos, N. J. B. Isaac, and B. Collen. 2014. Defaunation in the Anthropocene. *Science* 345: 401–406.
- Gallai, N., J. M. Salles, J. Settele, and B. E. Vaissière. 2009. Economic valuation of the vulnerability of world agriculture confronted with pollinator decline. *Ecological Economics* 68: 810–821.
- Garibaldi, L. A., L. G. Carvalheiro, S. D. Leonhardt, M. A. Aizen, B. R. Blaauw, R. Isaacs, M. Kuhlmann, D. Kleijn, A. M. Klein, C. Kremen, L. Morandin, J. Scheper, and R. Winfree. 2014. From research to action: Practices to enhance crop yield through wild pollinators. *Frontiers in Ecology and the Environment* 12: 439–447.
- 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, I. Bartomeus, F. Benjamin, V. Boreux, D. Cariveau, N. P. Chacoff, J. H. Dudenhöffer, B. M. Freitas, J. Ghazoul, S. Greenleaf, J. Hipólito, A. Holzschuh, B. Howlett, R. Isaacs, S. K. Javorek, C. M. Kennedy, K. M. Krewenka, S. Krishnan, Y. Mandelik, M. M. Mayfield, I. Motzke, T. Munyuli, B. A. Nault, M. Otieno, J. Petersen, G. Pisanty, S. G. Potts, R. Rader, T. H. Ricketts, M. Rundlöf, C. L. Seymour, C. Schüepp, H. Szentgyörgyi, H. Taki, T. Tschamtkke, C. H. Vergara, B. F. Viana, T. C. Wanger, C. Westphal, N. Williams, and A. M. Klein. 2013. Wild pollinators enhance fruit set of crops regardless of honey bee abundance. *Science* 339: 1608–1611.
- Goulson, D. 2003. Conserving wild bees for crop pollination. *Food, Agriculture & Environment* 1: 142–144.
- Goulson, D., G. C. Lye, and B. Darvill. 2008. Decline and conservation of bumble bees. *Annual Review of Entomology* 53: 191–208.
- Grixti, J. C., L. T. Wong, S. A. Cameron, and C. Favret. 2009. Decline of bumble bees (*Bombus*) in the North American Midwest. *Biological Conservation* 142: 75–84.
- Holland, J. M., B. M. Smith, J. Storkey, P. J. W. Lutman, and N. J. Aebischer. 2015. Managing habitats on English farmland for insect pollinator conservation. *Biological Conservation* 182: 215–222.
- Holzschuh, A., C. F. Dormann, T. Tscharntke, and I. Steffan-Dewenter. 2013. Mass-flowering crops enhance wild bee abundance. *Oecologia* 172: 477–484.
- Hurd Jr., P. D., W. E. LaBerge, and E. G. Linsley. 1980. Principal sunflower bees of North America with emphasis on the southwestern United States (Hymenoptera: Apoidea). *Smithsonian Contributions to Zoology* 310: 1–168.
- Isaacs, R., J. Tuell, A. Fiedler, M. Gardiner, and D. Landis. 2009. Maximizing arthropod-mediated ecosystem services in agricultural landscapes: The role of native plants. *Frontiers in Ecology and the Environment* 7: 196–203.
- 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, L. G. Carvalheiro, N. P. Chacoff, S. A. Cunningham, B. N. Danforth, J. H.

- Dudenhöffer, E. Elle, H. R. Gaines, L. A. Garibaldi, C. Gratton, A. Holzschuh, R. Isaacs, S. K. Javorek, S. Jha, A. M. Klein, K. Krewenka, Y. Mandelik, M. M. Mayfield, L. Morandin, L. A. Neame, M. Otieno, M. Park, S. G. Potts, M. Rundlöf, A. Saez, I. Steffan-Dewenter, H. Taki, B. F. Viana, C. Westphal, J. K. Wilson, S. S. Greenleaf, C. Kremen. 2013. A global quantitative synthesis of local and landscape effects on wild bee pollinators in agroecosystems. *Ecology Letters* 16: 584–599.
- Koch, J., J. Strange, and P. Williams. 2012. Bumble bees of the western United States. *The Xerces Society for Invertebrate Conservation*. 144 pp.
- Korpela, E. L., T. Hyvönen, S. Lindgren, and M. Kuussaari. 2013. Can pollination services, species diversity and conservation be simultaneously promoted by sown wildflower strips on farmland? *Agriculture, Ecosystems and Environment* 179: 18–24.
- Kremen, C., N. M. Williams, and R. W. Thorp. 2002. Crop pollination from native bees at risk from agricultural intensification. *Proceedings of the National Academy of Sciences of the U.S.A.* 99: 16812–16816.
- Lautenbach, S., R. Seppelt, J. Liebscher, and C. F. Dormann. 2012. Spatial and temporal trends of global pollination benefit. *PLoS One* 7: e35954.
- LeBuhn, G., T. Roulston, V. Tepedino, T. Griswold, J. Cane, N. Williams, R. Minckley, F. Parker, C. Kremen, S. Droege, S. Buchmann, and O. Messenger. 2003. A standardized method for monitoring bee populations: The bee inventory (BI) plot. Available from <http://online.sfsu.edu/beeplot/pdfs/Bee%20Plot%202003.pdf> (Last accessed: November 2015).
- Minckley, R. L., W. T. Wcislo, D. Yanega, and S. L. Buchmann. 1994. Behavior and phenology of a specialist bee (*Dieunomia*) and sunflower (*Helianthus*) pollen availability. *Ecology* 75: 1406–1419.
- Minitab. 2014. Minitab 17 statistical software. Minitab Inc., State College, Pennsylvania.
- Neff, J. L., and B. B. Simpson. 1990. The roles of phenology and reward structure in the pollination biology of wild sunflower (*Helianthus annuus* L., Asteraceae). *Israel Journal of Botany* 39: 197–216.
- Oksanen, J., F. G. Blanchet, R. Kindt, P. Legendre, P. R. Minchin, R. B. O'Hara, G. L. Simpson, P. Solymos, M. H. H. Stevens, and H. Wagner. 2013. vegan: Community ecology package. R package version 2.0-10. Available from <http://CRAN.R-project.org/package=vegan> (Last accessed: November 2015).
- Ollerton, J., H. Erenler, M. Edwards, and R. Crockett. 2014. Extinctions of aculeate pollinators in Britain and the role of large-scale agricultural changes. *Science* 346: 1360–1362.
- Parker, F. D., 1981. How efficient are bees in pollinating sunflowers? *Journal of the Kansas Entomological Society* 54: 61–67.
- 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 in Ecology and Evolution* 25: 345–353.
- Ratti, C. M., and S. R. Colla. 2010. Discussion of the presence of an eastern bumble bee species (*Bombus impatiens* Cresson) in western Canada. *The Pan-Pacific Entomologist* 86: 29–31.
- 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, L. A. Morandin, A. Ochieng, and B. F. Viana. 2008. Landscape effects on crop pollination services: Are there general patterns? *Ecology Letters* 11: 499–515.
- Riedinger, V., M. Renner, M. Rundlöf, I. Steffan-Dewenter, and A. Holzschuh. 2014. Early mass-flowering crops mitigate pollinator dilution in late-flowering crops. *Landscape Ecology* 29: 425–435.
- SAS Institute Inc., 2013. Version 9.4 of the SAS System for Microsoft Windows. SAS Institute Inc., Cary, North Carolina.
- 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. *Environmental Entomology* 37: 707–718.
- Vaughan, M., and M. Skinner. 2008. Using Farm Bill programs for pollinator conservation. USDA Technical Note. *United States Department of Agriculture*. 12 pp.
- Velthuis, H. H. W., and A. van Doorn. 2006. A century of advances in bumblebee domestication and the economic and environmental aspects of its commercialization for pollination. *Apidologie* 37: 421–451.
- Westphal, C., I. Steffan-Dewenter, and T. Tscharntke. 2003. Mass flowering crops enhance pollinator densities at a landscape scale. *Ecology Letters* 6: 961–965.
- Westphal, C., I. Steffan-Dewenter, and T. Tscharntke. 2009. Mass flowering oilseed rape improves early colony growth but not sexual reproduction of bumblebees. *Journal of Applied Ecology* 46: 187–193.
- Whittington, R., and M. L. Winston. 2004. Comparison and examination of *Bombus occidentalis* and *Bombus impatiens* (Hymenoptera: Apidae) in tomato greenhouses. *Journal of Economic Entomology* 97: 1384–1389.
- Williams, G. R., D. R. Tarpay, D. VanEngelsdorp, M. P. Chauzat, D. L. Cox-Foster, K. S. Delaplane, P. Neumann, J. S. Pettis, R. E. L. Rogers, and D. Shutler. 2010. Colony collapse disorder in context. *BioEssays* 32: 845–846.
- Winfree, R., and C. Kremen. 2009. Are ecosystem services stabilized by differences among species? A test using crop pollination. *Proceedings of the Royal Society B: Biological Sciences* 276: 229–237.