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# Native Solitary Bees Provide Economically Significant Pollination Services to Confection Sunflowers (*Helianthus annuus* L.) (Asterales: Asteraceae) Grown Across the Northern Great Plains

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## Abstract

The benefits of insect pollination to crop yields depend on genetic and environmental factors including plant self-fertility, pollinator visitation rates, and pollinator efficacy. While many crops benefit from insect pollination, such variation in pollinator benefits across both plant cultivars and growing regions is not well documented. In this study, across three states in the northern Great Plains, United States, from 2016 to 2017, we evaluated the pollinator-mediated yield increases for 10 varieties of confection sunflowers, *Helianthus annuus* L. (Asterales: Asteraceae), a plant that is naturally pollinator-dependent but was bred for self-fertility. We additionally measured pollinator visitation rates and compared per-visit seed set across pollinator taxa in order to determine the most efficacious sunflower pollinators. Across all locations and hybrids, insect pollination increased sunflower yields by 45%, which is a regional economic value of over $40 million and a national value of over $56 million. There was, however, some variation in the extent of pollinator benefits across locations and plant genotypes, and such variation was significantly related to pollinator visitation rates, further highlighting the value of pollinators for confection sunflowers. Female *Andrena helianthi* Robertson (Hymenoptera: Andrenidae) and *Melissodes* spp. (Hymenoptera: Apidae) were the most common and effective pollinators, while other bees including managed honey bees (Hymenoptera: Halictidae), *Apis mellifera* L. (Hymenoptera: Apidae), small-bodied sweat bees (Hymenoptera: Halictidae), bumble bees *Bombus* spp. (Hymenoptera: Apidae), and male bees were either infrequent or less effective on a per-visit basis. Our results illustrate that wild bees, in particular the sunflower specialists *A. helianthi* and *Melissodes* spp., provide significant economic benefits to confection sunflower production.

**Key words:** honey bee, sunflower bee, crop pollination, pollinator efficacy, sunflower yields

Insect pollinators are an important component of crop production worldwide, with approximately 70% of the world's leading crops benefiting from insect-mediated pollination (Klein et al. 2007). For some crops, however, little to no information exists regarding the value of insect pollinators, while for other crops, information is restricted to a few cultivars or growing regions (Delaplane and Mayer 2000, Klein et al. 2007, Garibaldi et al. 2013, Bartomeus et al. 2014). Plant pollination requirements will depend on plant self-compatibility and rates of self-pollination, which are influenced by the plant's genotype but can also be affected by environmental conditions including temperature, soil fertility, and humidity (Herrero and Johnson 1980, Sarracino and Vorsa 1991, DeGrandi-Hoffman and Chambers 2006, Astiz and Hernandez 2013, Ramírez and Davenport 2013, Mallinger and Prasifka 2017a). The benefits of insect-mediated pollination to crop yields will furthermore depend not only on the crop's pollination requirements, but on the abundance and diversity of pollinators, their visitation frequency to the crop, and their efficacy as pollinators (Rader et al. 2012, Garibaldi et al. 2013, Rogers et al. 2014, Mallinger and Gratton 2015, Martins et al. 2015). Identifying the most important pollinators for individual crops can inform crop management practices to conserve or enhance populations of effective pollinators.

Sunflowers, *Helianthus annuus* L. (Asterales: Asteraceae), are native to North America but grown globally for oil (i.e., oilseed sunflowers) as well as for fresh eating and baking (i.e., confection sunflowers). Within sunflowers, different production systems determine the role of insect pollinators; insects are essential for the production of hybrid seed, in which pollen must be transferred from male-fertile to male-sterile varieties, while the subsequent growing of oilseed or confection hybrids is less dependent on insect pollinators due to relatively high rates of plant self-fertility (Fick and Miller 1997, Greenleaf and Kremen 2006, Sun et al. 2012). Despite such self-fertility, yields for both oilseed and confection sunflowers have increased with insect-mediated pollination (Dag et al. 2002, DeGrandi-Hoffman and Chambers 2006, Nderitu et al. 2008, Chambo et al. 2011). However, recent research has also shown that the benefits of insect pollination vary across confection sunflower hybrids, or varieties, likely due to variation in both selfing rates and in their relative attractiveness to pollinators (Mallinger and Prasifka 2017a).

In addition to variation across plant genotypes, pollinator benefits may also vary across the sunflower growing region. Sunflower production in the United States is concentrated in the northern Great Plains but includes a large range in latitude from northern North Dakota (approximately 48°N) through southern Texas (approximately 26°N). Across this gradient, the relative contribution of insects to sunflower pollination may change with variation in insect community composition or with changing abiotic conditions. For instance, temperatures outside of a relatively narrow range (21–25°C) during sunflower bloom reduced sunflower pollen production (Astiz and Hernandez 2013), and high temperatures appeared to result in lower rates of self-pollination, thereby enhancing the benefit of insect pollinators (Degrandi-Hoffman and Chambers 2006). Given the differences in climate across the large sunflower growing region in North America, the benefits of insect-mediated pollination may vary with both changing abiotic factors, including temperature and humidity, as well as with changing pollinator communities. Such variation in pollination across space, however, has not been previously documented for sunflowers.

The role of insects in crop pollination will be determined not only by their visitation frequency to the crop plant, but by their efficacy on a per-visit basis. The per-visit efficacy of pollinators has been found to vary both within and across species, including between managed bees and wild bees, as well as among different species of wild bees in crops such as apples, blueberries, pumpkins, and oilseed rape (Free 1960, Vicens and Bosch 2000, Javorek et al. 2002, Sampson et al. 2004, Artz and Nault 2011, Woodcock et al. 2013, Park et al. 2015). Factors that influence per-visit efficacy typically include the size and morphology of the pollinator, with large-bodied pollinators generally able to carry and deposit more pollen on a per-visit basis (Willmer and Finlayson 2014). Additionally, the foraging behavior of a pollinator can vary across individuals within the same or different species; pollinators that make direct contact with anthers and stigmas are generally more efficient than those that do not make direct contact with plant reproductive parts (i.e., nectar robbers or sideworkers) (Free 1960, Javorek et al. 2002, Artz and Nault 2011, Park et al. 2015, Sapir et al. 2017). Finally, the sex of the pollinator can influence its efficacy due to both morphology and behavior, with female bees generally more efficacious on a per-visit basis, though males can contribute significantly to pollination when abundant (Cane et al. 2011). While previous studies have established that numerous species of wild bees along with managed honey bees, *Apis mellifera* L. (Hymenoptera: Apidae), visit sunflowers throughout their growing region, no study has examined the per-visit efficacy of these pollinators for confection sunflower production within the Great Plains (Hurd et al. 1980; Parker 1981; Minckley et al. 1994; Mallinger and Prasifka 2017a,b). Examining the relative contributions of different managed and wild bee species can help to identify potential alternative managed pollinators, or target crop pollination strategies to the most effective species.

Land-use change in the Great Plains has reduced natural habitat for pollinators (Wright and Wimberly 2013, Johnston 2015, Otto et al. 2018) creating a disparity between pollinator demand and supply (Koh et al. 2016). Nationally, 1.5–2 million acres of sunflowers have been planted in recent years, the vast majority (over 95%) within the Great Plains states (https://quickstats.nass.usda.gov/, accessed on 10 September 2018). In addition to sunflowers, other oilseed crops that benefit from insect-mediated pollination, including canola, are grown in this region (Morandin and Winston 2005, Lindström et al. 2015). Establishing the benefit of pollinators for sunflower production may therefore motivate efforts to increase pollinator resources within the landscape, including for both managed and wild bees, with potential spillover effects in other crop production systems (Allsopp et al. 2008, Gallai et al. 2009). The goals of this study were therefore to 1) evaluate the overall benefit of insect pollination for yields of modern confection sunflowers grown in the northern Great Plains, 2) evaluate the consistency of these benefits across the growing region as well as across different plant genotypes, 3) quantify the economic impact of pollinators for confection sunflower production, and 4) compare the pollination contribution of different floral visitors to confection sunflowers, including managed bees and wild bees.

## Methods

### Benefit of Pollinators for Confection Sunflower Yields

In 2016 and 2017, across three states, we planted 10 confection hybrids that previously showed variable pollinator benefits in North Dakota, and also represented the commercial varieties available for growers in the United States including four hybrids from CHS Inc. (Royal Hybrid [RH] 1121, RH 1130EX, RH 843, and RH 841) (Inver Grove Heights, MN), two hybrids from Nuseed (5009, Jaguar II) (Breckenridge, MN), and four hybrids from SunOpta-Dahlgren (9530, 9579, 9589, 9592) (Edina, MN) (Mallinger and Prasifka 2017a). In Casselton, ND (46.88°N, 97.43°W), on 18 May 2016 and 19 May 2017, and in Scottsbluff, NE (41.89°N, −103.68°W), on 17 June 2016 and 15 June 2017, each hybrid was planted in a pair of adjacent 20-ft rows at a density of 20 seeds per row, and this design was replicated across two blocks with hybrid order randomized within each block. In Volga, SD (44.3°N, −96.92°W), on 15 June 2016, this same planting design was used across three blocks while on 19 June 2017, this planting design was used across two blocks in identical fashion to the plantings in North Dakota and Nebraska. All plots were planted on research station property in landscapes highly dominated by intensively managed field crops. Overall management was similar to that in commercial confection sunflower fields. Research plots were treated with herbicides prior to planting, and planted seeds were coated with insecticidal and fungicidal seed treatments, though no pesticides were applied to the plots after planting. In both years, honey bees were placed at the plots in Casselton, ND, at a density of 4 hives per acre, while hives were not deployed in Nebraska or South Dakota to mimic typical commercial confection sunflower fields that do not utilize managed pollinators.

For each hybrid, one of the paired rows was assigned to receive pollinator benefits ('open' treatment) and the other to be excluded from pollinators ('closed' treatment), and we randomly chose up to 10 heads within each row for each treatment. As poor germination reduced sample sizes below 10 heads per row in some cases, we only included hybrids with at least five heads per treatment per location per year for our analyses. This resulted in excluding two hybrids planted in 2016 in Nebraska (RH 1130 EX and RH 843) and one hybrid planted in 2017 in South Dakota (9589). As each research location contained multiple hybrids planted in close proximity to one another, our estimates of pollinator benefits include potential self-pollination, within-hybrid cross-pollination, and between-hybrid cross-pollination, and may thus be higher than pollinator benefits received within a large, single-hybrid commercial field. However, our results indicate the degree to which confection sunflower yields may be limited by a lack of pollination including between-hybrid cross-pollination.

Flower heads in the closed treatment were bagged immediately pre-bloom with insect exclusion mesh (Delnet bags, DelStar Technologies, Middletown, DE) that prevents even the smallest pollinators from visiting. Flower heads in the open treatment were unbagged during bloom to receive pollinator visits but were bagged immediately post-bloom to equalize conditions across treatments and to prevent seed predation. While bagging during the bloom period could have potential effects on seed set apart from pollination (i.e., through affecting light, temperature, or humidity), previous results showed that sunflower seed set did not differ between open and bagged sunflowers that were hand-pollinated daily (Mallinger and Prasifka 2017a). When seeds were mature, approximately 5–6 wk after bloom, flower heads were harvested and kept in individual mesh bags while they were dried at a temperature between 32 and 38°C. When fully dried, each flower head was individually processed using a mechanically assisted thresher attached to a vacuum system, which separates filled achenes ('seeds') from empty hulls produced by unsuccessful pollination. For each flower head, we recorded the total mass of filled achenes ('seed mass') as this is the best indicator of yield. We additionally calculated flower head size by measuring the head diameter across the outermost whorl of florets.

## Bee Visitation Rates

To measure bee visitation rates, we conducted walking counts in all hybrids during bloom in all three states, North Dakota, Nebraska, and South Dakota. Each walking count consisted of two consecutive 1-min walks through each pair of 20-ft rows per hybrid per block (subsequently referred to as a 'plot'). During this count, observers recorded all bees foraging on the sunflower head to the following morpho groups: honey bees, bumble bees (*Bombus* spp.), green metallic sweat bees (Hymenoptera: Halictidae), large other bees (>8 mm in length), and small other bees (4–8 mm in length). Non-bee pollinators visiting sunflowers were previously observed in very low frequencies and were thus not included in this study. Bees that were not on the sunflower disc (area containing floral rewards and plant reproductive parts) but rather on the petals, leaves, or other parts of the plant were not counted. During the second 1-min pass through the paired rows, observers counted all bees present on the sunflower disc regardless of whether they were counted during the first pass or were 'new' visitors, and total visits per plot were summed across the two consecutive walks. Observers additionally recorded the total number of open flower heads in bloom per plot in order to calculate the number of bee visits per flower head per plot.

In 2016, these counts were made 3 times per hybrid in South Dakota and Nebraska, and 4–7 times per hybrid in North Dakota, varying across hybrids with the length of their bloom period. In 2017, each hybrid was again observed 3 times during bloom in South Dakota, and 6–10 times during bloom in North Dakota and in Nebraska. For analyses, visitation rates were averaged across these observation periods. After observations, on each of 3 d during bloom coinciding with early, mid, and late bloom, observers spent 30 min/d collecting all non-honey bees foraging on the sunflower head. The primary goal was to collect as many unique specimens as possible from each morpho group used in observations in order to determine the community composition of these morpho groups. As such, honey bees were not collected as they were included at the species level in observation periods. Bees were then processed in the lab and were identified to species using reference collections, Discover Life (Ascher and Pickering 2018), and confirmation by an expert taxonomist (J. Gibbs).

## Per-Visit Efficacy

The effectiveness of pollinators is a product of their visitation frequency to the plant and their per-visit efficacy, which can be measured as the amount of pollen deposited, or the seed or fruit set resulting from a single visit (Ne'eman et al. 2010). In this case, we measured per-visit efficacy as seed set resulting from a single visit as this variable is most directly related to yield. In Casselton, ND, in 2016–2017, we planted a block consisting of ten 20-ft rows of the cytoplasmic male-sterile (CMS) sunflower inbred CMS HA 467 at a density of 25 seeds per row. This and other CMS lines are pollenless and cannot produce seed without animal-mediated pollination and are thus ideal for evaluating the contribution of individual pollinator visits to seed set (Parker 1981). This particular male-sterile sunflower variety was chosen due to its previously demonstrated attractiveness to pollinators (Mallinger and Prasifka 2017b).

Prior to bloom, we bagged all male-sterile developing sunflower heads with cloth bags that prevent even wind pollination. During bloom, we removed bags individually and waited for a single insect pollinator to visit the unbagged head. Once a pollinator landed, we recorded the type of visitor to bee morpho group (honey bee, bumble bee, large other, small other, green metallic sweat bee), sex (male or female), or to genus and species if possible. We aimed for relatively equal visits across bee morpho groups, sex, and taxa by disrupting certain common bees from visiting while waiting for a visit from a less common bee group. We timed the length of each bee visit, allowing the bee to forage undisturbed for up to 5 min; the few visitors that remained on the flower head after 5 min were gently removed from the flower head. We additionally allowed a subset of flower heads to be visited by two or three bees consecutively (including bees from the morpho groups 'large other' and 'small other') so that we could compare the pollination services provided by a single bee to those provided by multiple visits. After a sunflower head was visited by a bee(s), it was immediately covered again with a cloth bag until harvest. Finally, we reserved some flower heads to remain closed (bagged) for the entirety of the season to serve as a control group. Flower heads were harvested, dried, and seed mass per flower head was determined according to the previously described protocols.

## Statistical Analyses

To assess the effects of insect pollination on confection sunflower yields, we ran a linear model with seed mass per flower head (sqrt-transformed) as the response variable ($n$ = 2,027, flower heads treated as individual data points), and with treatment (open vs closed), location (Nebraska, North Dakota, or South Dakota), hybrid ($n$ = 10), and year (2016, 2017) as factors, and with flower head area ($m^2$) as a covariate (function 'lm', R v. 3.2). We additionally included a three-way interaction between treatment, year, and location, as well as two-way interactions between treatment and year, treatment and location, and treatment and hybrid, in order to assess variation in pollinator benefits across environments, years, and plant genotypes. We conducted post hoc treatment comparisons with a Holm's *P*-value adjustment for each set of post hoc comparisons across locations or hybrids (function 'lsmeans', R v. 3.2.2). We did not include three-way interactions with hybrid (treatment by hybrid by year, or treatment by hybrid by location), or the full four-way interaction (treatment by hybrid by location by year) as sample sizes per hybrid per location and/or per year were too small to analyze statistically. Results, including estimates and SEs, were back-transformed for presentation by squaring all values.

Since we found significant variation in pollinator benefits across hybrids and locations (significant treatment by location and treatment by hybrid effects), we analyzed whether such variation was due to differences in pollinator visitation rates. We calculated pollinator benefits for each hybrid per location and year as the adjusted seed mass within open flower heads minus the adjusted seed mass within closed flower heads ($n$ = 57, three hybrids excluded due to small sample sizes as previously described). Adjusted seed masses were calculated as the average seed mass divided by the average flower area, averaged across all flower heads per hybrid per location per year. We next calculated average bee visitation rates as the average number of bees per blooming flower per 2-min period, averaged across all observation periods per hybrid per location and per year. Then, using a linear model, we related the average measured pollinator benefit per hybrid per location and per year (adjusted seed mass open – adjusted seed mass closed) to the average bee visitation rate per hybrid per location and per year (function 'lm', R v. 3.2.2).

To evaluate variation in bee visitation rates to confection sunflowers, we used a linear model with average bee visitation rates per plot per location and per year, averaged across observation periods, as the response variable ($n$ = 120), and hybrid, year, and location as explanatory variables, and including interactions between hybrid and year, and between location and year (function 'lm', R v. 3.2.2). Again, we included two-way interactions, but not the interaction between hybrid, year, and location, as sample sizes were too small to evaluate this three-way interaction. We then conducted post hoc treatment comparisons across locations or hybrids with a Holm's *P*-value adjustment for each set of post hoc comparisons (function 'lsmeans', R v. 3.2.2).

We next determined the per-visit efficacy of different pollinator morpho groups by comparing seed mass per flower head across flower heads that received no visits ($n$ = 37) with those that received single visits by the bee groups 'small other' ($n$ = 27), 'large other male' ($n$ = 46), and 'large other female' ($n$ = 47), and with those that received multiple (2 or 3) bee visits ($n$ = 17). For flower heads receiving multiple (2–3) visits, these included various combinations of large other and small other bees, combined into one category as we did not have enough visits of each possible combination. We ran a linear model with seed mass per flower head (sqrt-transformed) as the response variable, and bee group as a fixed factor (none, large other M, large other F, small other, multiple) (function 'lsmeans', R v. 3.2.2) and with a Holm's *P*-value adjustment for each set of post hoc comparisons across groups. We did not have enough single visits by bumble bees, honey bees, or green metallic sweat bees to compare with the other observed groups. We next ran a comparison across taxa that could be identified to genus or species in the field, including female *Andrena helianthi* ($n$ = 11), female *Melissodes* spp. ($n$ = 9), and male *Melissodes* spp. (Hymenoptera: Apidae) ($n$ = 17) using a similar linear model with post hoc comparisons across taxa.

In order to evaluate whether differences in per-visit efficacy were due to time spent per floral visit, we first compared differences in total time spent on flowers across bee morpho groups (large other male, large other female, small other bee) and across bee taxa (female *A. helianthi*, female *Melissodes* spp., male *Melissodes* spp.) using two different linear models with time spent per visit as the response variable and bee group or taxa as the explanatory variable, and included post hoc comparisons across groups/taxa as described above. We additionally examined whether the time spent on a flower influenced seed mass using a linear model with seed mass (sqrt-transformed) as the response variable ($n$ = 185) and total time spent per flower visit as the explanatory variable (function 'lm', R v. 3.2.2). For presentation, all estimated means and SEs were back-transformed by squaring values.

## Results

### Pollinator-Mediated Yield Increases

Overall seed mass was significantly higher by 45% on open flower heads (estimated mean ± SE: 84.2 ± 1.7 g) compared to closed flower heads (58.1 ± 0.99 g) ($F_{1,1764}$ = 262.17, $P$ < 0.001), and there were significant interactions between treatment and hybrid ($F_{9,1764}$ = 4.55, $P$ < 0.001), and between treatment, year, and location ($F_{2,1764}$ = 25.55, $P$ < 0.001). Pollinator-mediated yield increases were significant for 9 out of 10 hybrids, with only RH 841 showing no significant yield increase. However, the range in yield increases for the nine significant hybrids was between 22 and 73% (Fig. 1). Likewise, treatment effects were significant in all locations in both years, but the range in yield increases per location was between 18 and 213% (Fig. 2A and B). In 2016, yield increases were lowest in North Dakota (18%) followed by South Dakota (48%), with the highest yield increases in Nebraska (213%), while in 2017, yield increases were relatively similar across all three states (North Dakota: 29%, Nebraska: 28%, South Dakota: 31%) (Fig. 2A and B). Average pollinator-mediated yield increases per hybrid per location and per year were significantly, positively related to average bee visitation rates per hybrid per location per year ($F_{1,55}$ = 6.52, $P$ = 0.01; Fig. 3).

### Bee Visitation Rates

Due to differences in planting dates, the bloom period varied across locations and years from late July through mid-September, with bloom occurring earlier in North Dakota than in Nebraska and South Dakota (Suppl Table 1 [online only]). Weather conditions during bloom also varied across locations and years, with cooler daily temperatures in South Dakota during bloom and more extreme high and low temperatures in Nebraska during bloom (Supp Table 1 [online only]).

Bee visitation rates were significantly different across locations ($F_{2,96}$ = 23.92, $P$ < 0.001), with a significant location by year interaction ($F_{2,96}$ = 21.77, $P$ < 0.001). In 2016, visitation rates were highest in Nebraska (0.47 ± 0.033 bee visits per sunflower head per 2-min observation period), followed by North Dakota (0.24 ± 0.033), and lowest in South Dakota (0.07 ± 0.033), while in 2017, visits were higher in North Dakota (0.33 ± 0.033) than in both Nebraska (0.18 ± 0.033) and South Dakota (0.16 ± 0.033). Visitation rates were also significantly different across hybrids ($F_{9,96}$ = 8.79, $P$ = 0.002), with no significant hybrid by year interactions ($F_{9,96}$ = 0.85, $P$ = 0.57). In both years, trends were similar with hybrid 9592 having the highest bee visitation rates, followed by hybrid RH 1121, though few to no pairwise comparisons were significant in either year (Supp Table 2 [online only]).

Across all locations, years, and hybrids, large other bees were the most common visitors ($n$ = 2,574 visits) followed by small other bees ($n$ = 475) and bumble bees ($n$ = 184 visits), with few visits made

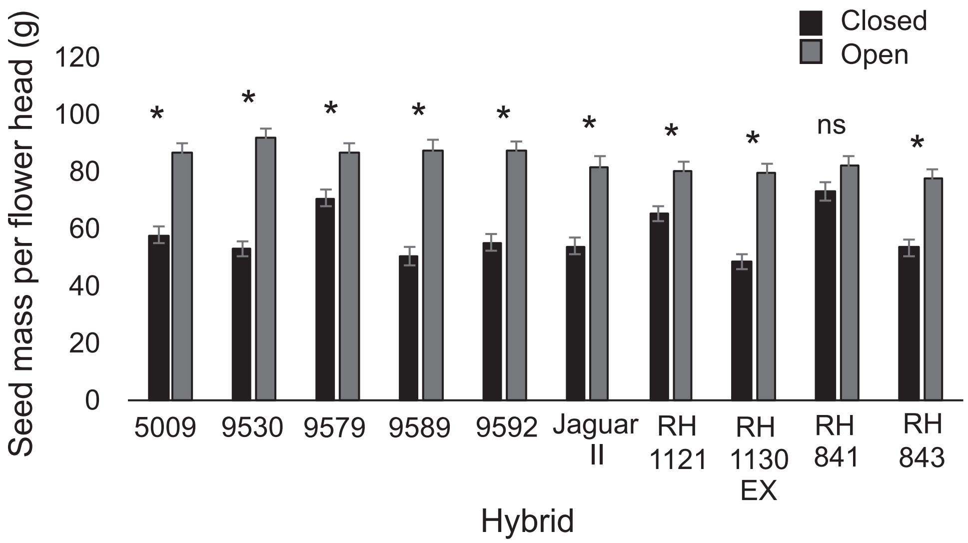


**Fig. 1.** Average seed mass per flower head (mean ± SE) of 10 different confection sunflower hybrids grown from 2016 to 2017 under two treatments: open to insect pollinators during bloom ('open') and closed to pollinators during bloom ('closed'). Estimated model fits and SEs are from a linear model including the interaction between treatment and hybrid, as well as between treatment, location, and year, and including flower head size ($m^2$) as a covariate. Seed mass was sqrt-transformed for analyses, but back-transformed for presentation by squaring all values. The * symbol indicates significant treatment differences at $P < 0.05$ for each hybrid as assessed with post hoc comparisons and a Holm's $P$-value adjustment.

by honey bees ($n$ = 17) and green metallic sweat bees ($n$ = 7 visits). The primary bee species comprising the 'large other' bee morpho group included *Melissodes trinodis* Robertson (Hymenoptera: Apidae), *M. agilis* Cresson (Hymenoptera: Apidae), *Svastra obliqua* (Say) (Hymenoptera: Apidae), and *A. helianthi*, all of which were found in all three states and are considered specialists of sunflowers and related plants (Supp Table 3 [online only]). The primary species comprising the 'small other' bee morpho group included the apparent sunflower specialists *Dufourea marginata* (Cresson) (Hymenoptera: Halictidae), found in three states, and *Pseudopanurgus simulans* (Swenk and Cockerell) (Hymenoptera: Andrenidae), found in both North Dakota and South Dakota (Supp Table 3 [online only]). Seven species of bumble bees were collected from sunflowers across the three states, with *Bombus ternarius* Say (Hymenoptera: Apidae) the most commonly collected in North Dakota, and *Bombus griseocolis* (De Geer) (Hymenoptera: Apidae) the most commonly collected in South Dakota and Nebraska (Supp Table 3 [online only]).

## Per-Visit Efficacy

Per-visit efficacy was significantly different across bee groups ($F_{4,168}$ = 30.86, $P$ < 0.001). Female 'large other' bees were the most effective visitors, setting nearly 3 g of seed per visit on average, and were significantly more effective than 'small other' bees and male 'large other' bees, both of which set less than 1 g of seed on average (Fig. 4A). However, a visit by any type of bee, including male bees, small-bodied bees, and large-bodied bees, produced significantly more seed than no visits (Fig. 4A). Additionally, a single visit by a female 'large other' bee was as effective as multiple (2 or 3) bee visits (Fig. 4A). Within the large bee group, per-visit efficacy was significantly different across taxa ($F_{2,34}$ = 13.0, $P$ < 0.001) with female *A. helianthi* the most effective pollinators, followed by female *Melissodes* spp., and with male *Melissodes* spp. least effective (Fig. 4B). The total length of the bee visit was significantly, positively related to seed mass resulting from that visit ($F_{1,145}$ = 42.55, $P$ < 0.001), and was significantly different across groups ($F_{3,133}$ = 15.88, $P$ < 0.001) and individual taxa ($F_{2,34}$ = 13.73, $P$ < 0.001) (Table 1a and b). Female bees spent significantly more time per visit than male bees, and female *A. helianthi* spent significantly more time per visit than both male and female *Melissodes* spp. (Table 1a and b).

## Discussion

While bees are essential for providing pollination services to sunflower seed production systems (DeGrandi-Hoffman and Watkins 2000, Greenleaf and Kremen 2006, Martin and Farina 2016), their benefit to oilseed and confection sunflowers is less evident due to the relatively high rates of self-pollination in these plants. Indeed, we found that confection sunflowers can set substantial amounts of seed without any insect pollination. However, we also found that insect pollination increased yields by 45% across the Great Plains. Based on this yield increase, we estimate the value of insect pollinators for confection sunflower production at $40.8 million within the Great Plains, and $56.7 million nationwide (https://quickstats.nass.usda.gov/, accessed on 13 February 2018). We additionally found that while pollinators significantly increased yields for most hybrids and all locations evaluated, there was variation in pollinator benefits due to differences in pollinator visitation rates. Thus, the actual value of pollinators within a given commercial field will vary, and could be higher or lower than what we estimated across our study sites. Finally, despite the presence of honey bees in or near field sites, native wild bees provided the vast majority of floral visits across all states, and female large-bodied bees, in particular *A. helianthi* and *Melissodes* spp., were the most effective pollinators on a per-visit basis. Our study highlights the economic importance of pollinators for achieving maximum confection sunflower yields, particularly native wild bees including the sunflower specialists *A. helianthi* and *Melissodes* spp.

By expanding the geographical scope of the study across the northern Great Plains, we found increased evidence for the role of insect pollinators in confection sunflower production. Similar to the results from a previous study in North Dakota (Mallinger and Prasifka 2017a), our results in this study show an overall benefit of insect pollination for confection sunflower yields. Furthermore, for sunflowers grown in North Dakota, we found a nearly identical pollinator-mediated yield increase (25%) to that previously found

(26%; Mallinger and Prasifka 2017a), suggesting that insect benefits are remarkably consistent within a site over time. However, while only 5 of 15 hybrids previously showed significant pollinator benefits (Mallinger and Prasifka 2017a), in this study, 9 of 10 hybrids, including those previously studied, showed significant benefits when combined across locations. Pollinator benefits were overall higher in South Dakota and Nebraska than in North Dakota, particularly in 2016, thus contributing to the more significant responses among hybrids observed in this study. But, despite their significance, pollinator-mediated yield increases still varied from 22 to 73%, similar to what was previously documented (Mallinger and Prasifka 2017a). Thus, by expanding the study's geographic range, we found that the majority of hybrids benefited from insect pollination, though there was still substantial variation in the extent of these benefits.

The benefit of insect pollinators for crop yields can be determined by pollinator attributes, including their visitation frequency and efficacy, as well as by plant pollination requirements, including self-compatibility and self-pollination rates. Indeed, in this study, we found that pollinator benefits varied significantly with bee visitation rates. Variation in visitation rates is in turn likely due to a combination of factors including plant genotype, environment, and their interaction. For example, variation in floral traits, including the amount and composition of nectar and pollen rewards, floral volatile emissions, or corolla depth, may contribute to variation in pollinator visitation rates across plant genotypes (Silva and Dean 2000, Roldan-Serrano and Guerra-Sanz 2005, Ceuppens et al. 2015, Mallinger and Prasifka 2017b, Portlas et al. 2018). In particular, hybrid 9592 has consistently shown higher attractiveness to pollinators across years and locations, suggesting that it possesses attractive floral traits (Mallinger and Prasifka 2017a). Additionally, differences in environmental conditions, specifically flowering time and corresponding weather patterns, may have affected pollinator visitation rates across locations. Pollinator visitation rates were generally higher in North Dakota than in South Dakota, likely in part because the earlier planting dates in North Dakota led to warmer weather favorable to pollinator activity during the bloom period, though other factors such as surrounding landscape may have influenced bee visitation rates as well. Therefore, growers may be able to increase pollination and yields by planting relatively early and selecting hybrids with known attractiveness to bees. Alternatively, if planting later in the season, growers may consider hybrids with higher self-pollination rates and lower dependency on bees.

Our results also suggest that plant genotype and environment interact to affect plant self-pollination rates, with consequences for pollinator benefits. In particular, hybrid RH 841 has consistently displayed high selfing rates (i.e., relatively high seed set in closed bags) and insignificant pollinator-mediated yield increases across locations and years, suggesting that this trait is influenced by plant genotype (Mallinger and Prasifka 2017a). Floral traits such as floret length, pollen quantity and agglutination, stigma orientation, or the timing of maturity for male and female reproductive parts can affect selfing rates to influence the value of pollinators (Segala et al. 1980, George et al. 1982, Griffiths and Erickson 1983, Sun et al. 2012). Weather during bloom can additionally affect self-pollination rates and

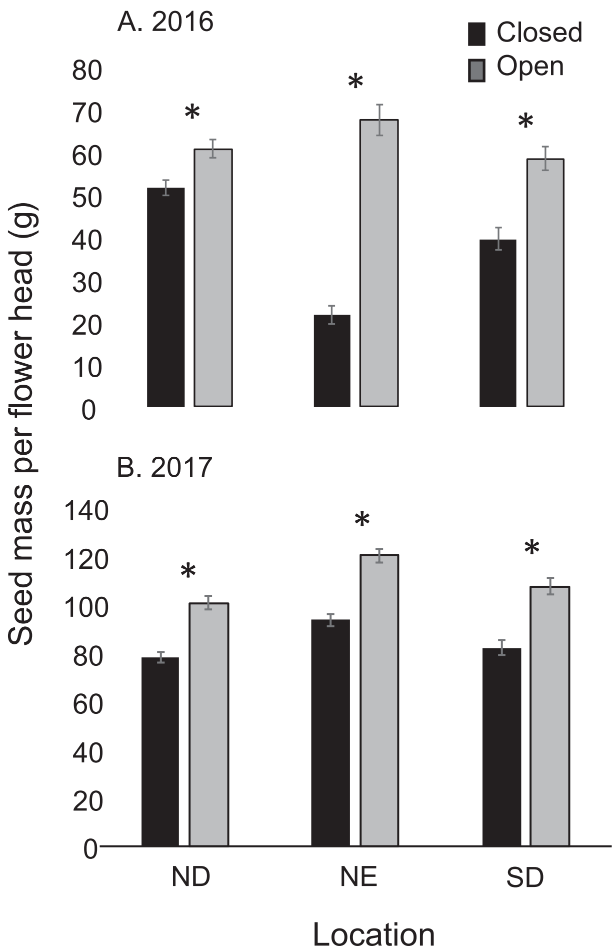


**Fig. 2.** Average seed mass per flower head (mean ± SE) of confection sunflower hybrids grown in three locations (North Dakota, Nebraska, and South Dakota) and under two treatments: open to insect pollinators during bloom ('open') and closed to pollinators during bloom ('closed') in (A) 2016 and (B) 2017. Estimated model fits and SEs are from a linear model including the interaction between treatment, location and year, as well as between treatment and hybrid, and including flower head size ($m^2$) as a covariate. Seed mass was sqrt-transformed for analyses, but back-transformed for presentation by squaring all values. The * symbol indicates significant treatment differences at $P < 0.05$ for each location as assessed with post hoc comparisons and a Holm's $P$-value adjustment.

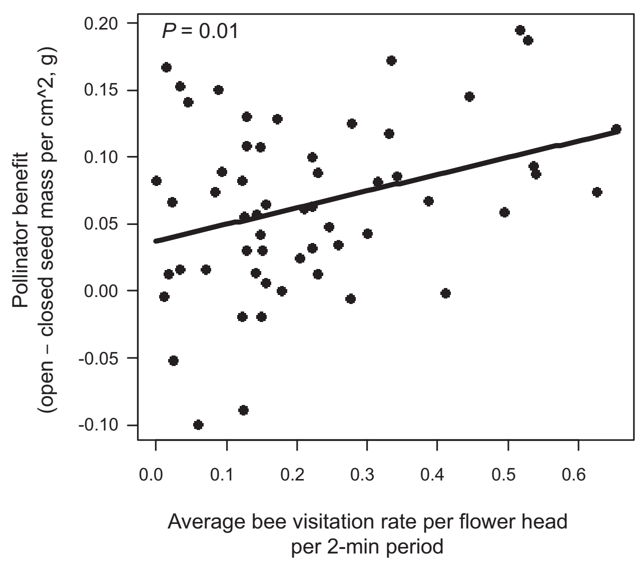


**Fig. 3.** The relationship between the measured pollinator-mediated yield increases for each hybrid in each location and in each year, measured as the difference between the average seed mass on open flower heads per $cm^2$ and the average seed mass on closed flower heads per $cm^2$, and average bee visitation rates (bee visits per flower head per 2-min period, averaged across all observation periods).

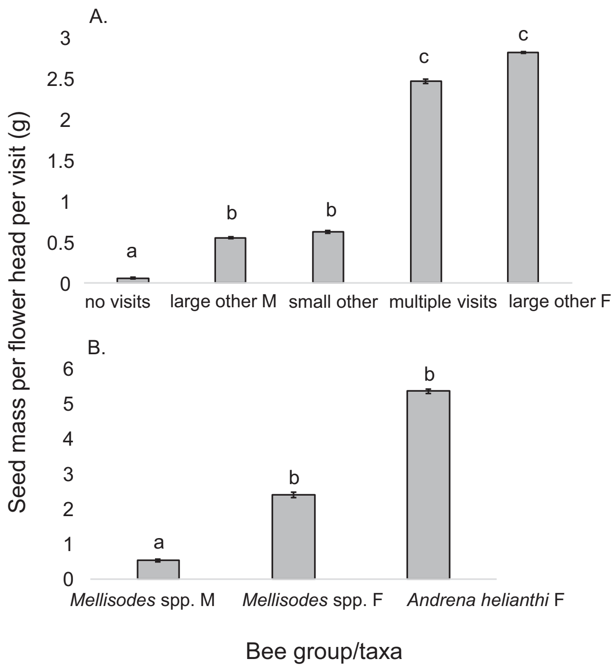


**Fig. 4.** Average (mean ± SE) seed mass resulting from (A) single visits by different bee morpho groups to male-sterile sunflower heads, including large solitary females ('large other F'), large solitary males ('large other M'), and small-bodied bees ('small other') and seed mass resulting from no bee visits and visits by multiple (2–3) bees, and (B) the seed mass resulting from single visits by individual bee taxa including female *Andrena helianthi*, female *Mellisodes* spp., and male *Melissodes* spp. Different letters indicate significant differences across morpho groups or taxa as determined with post hoc comparisons and a Holm's *P*-value correction.

may have contributed to the variation in pollinator benefits found across locations. For example, in 2016, low average temperatures and extreme high and low temperatures during the bloom period in Nebraska may have reduced plant selfing rates, in turn increasing the relative value of insect pollinators (De-Grandi Hoffman and Chambers 2006, Astiz and Hernandez 2013). Finally, soil fertility may have affected the relative value of insect pollinators, as differences in fertility across or within fields can affect seed set potential, thereby constraining pollinator-mediated yield increases (Tamburini et al. 2016, 2017). Such intraspecific variation in the pollination requirements of crops suggests that studies should be done with numerous cultivars under varying growing conditions.

Despite a relatively high honey bee stocking density at one of our locations, and the presence of honey bees in the landscape at all sites, honey bees were very infrequent sunflower visitors. While some previous studies have found that honey bees are the most common visitors to oilseed and confection sunflowers, the majority of these studies were conducted outside of North America, and thus outside of sunflower's native range, and none were conducted within the Great Plains (Krause and Wilson 1981, Farkas 1983, Dag et al. 2002, De-Grandi Hoffman and Chambers 2006, Pisanty et al. 2014, Hevia et al 2016, Rasheed et al. 2015). In North America, numerous species of native wild bees visit sunflowers, including many specialists such as the frequent visitors in our study, *A. helianthi* and *Melissodes* spp. (Hurd et al. 1983). These specialist bees generally show a strong attraction to, and preference for, sunflowers including cultivated sunflowers. In contrast, honey bees have shown limited attraction to cultivated sunflowers in other studies done in North and South America, instead preferring to visit flora surrounding the crop field (Andrada et al. 2004; Mallinger et al. 2017a,b). Thus, our results in combination with these previous findings suggest that renting honey bees in the Great Plains may not have a significant impact on crop yields due to their relatively low visitation rates, though this may vary across contexts and with hive density.

Using data on both visitation frequency and per-visit efficacy, our study is the first to evaluate the relative importance of different pollinator taxa for confection sunflowers in the Great Plains. While we found that a relatively diverse community of bees visited sunflowers, female *A. helianthi* and *Melissodes* spp. were the most common and effective pollinators, similar to results found in sunflower hybrid seed production systems in the western United States (Parker 1981). Compared to *A. helianthi* and *Melissodes* spp., other taxa were less significant due to infrequent visits to sunflowers or lower per-visit efficacy. For example, bumble bees were infrequent visitors, though they can be effective sunflower pollinators when present (Aslan and Yavuksuz 2010), while small-bodied bees (e.g., sweat bees) and male *Melissodes* spp. were common but less effective on a per-visit basis. In general, female bees and large-bodied bees had greater per-visit efficacy than male bees and small-bodied bees, respectively, likely because they carry and deposit greater quantities of pollen (Javorek et al. 2002, Cane et al. 2011, Willmer and Finlayson 2014). Furthermore, in our study, visitation length increased per-visit efficacy and varied across bee groups; *A. helianthi* in particular had longer visits resulting in greater seed set, while other bees including male and small-bodied bees had shorter flower visits. Though all bees showed some degree of pollination efficacy, transferring enough pollen in a single visit to set more seed than in control sunflowers, our study suggests that specialist pollinators including *A. helianthi* and *Melissodes* spp. are the most effective and economically significant.

While a full comparison of pollinator importance would combine visitation rates and per-visit efficacy for all bees, we were only able to measure per-visit efficacy for those bees that made relatively frequent visits. We therefore were not able to calculate the per-visit efficacy of infrequent bumble bees or honey bees. However, given the low percentage of visits made by honey bees (0.6%) and bumble bees (7%), it is unlikely that their contribution to sunflower pollination would exceed that of the more frequent visitors especially given that honey bee per-visit efficacy was relatively low when studied on sunflowers in the western United States (Parker 1981). Additionally, though the most direct measure of a pollinator's value would combine both visitation frequency and per-visit seed set to

**Table 1.** Average total length of visit (seconds), mean ± SE, of different bee morpho groups (a) and taxa (b) to male-sterile inbred sunflower heads in North Dakota in 2016–2017

| | Length of visit (seconds) |
|---|---|
| a. Bee group | |
| Large other male | 116.6 ± 18.5a |
| Small other | 175.1 ± 24.1ab |
| Large other female | 184.4 ± 18.3b |
| Multiple (2–3) visits | 362.2 ± 30.4c |
| b. Bee taxa | |
| *Melissodes* spp. male | 112.3 ± 30.2a |
| *Melissodes* spp. female | 114.9 ± 22.0a |
| *Andrena helianthi* female | 285.0 ± 27.4b |

Letters indicate significant differences across the groups or taxa as determined with post hoc comparisons and a Holm's *P*-value correction for multiple comparisons.

the same plants, in this study we combined visitation rates to male-fertile hybrid confection sunflowers with per-visit efficacy measured on inbred male-sterile sunflowers. Due to the relatively high rates of selfing found in hybrid confection sunflowers, as shown herein, a single bee visit would not likely result in discernible increases in seed set while male-sterile plants allow single-visit seed set to be measured. Per-visit seed set as measured herein may thus be conservative, as it only measures contributions via cross-pollination, while pollinators in commercial sunflower fields may enhance seed set by increasing self-pollen deposition across florets on the same sunflower head (Chamer et al. 2015). Furthermore, we acknowledge that some pollinator foraging behaviors may differ between male-fertile and male-sterile sunflowers, such as the time spent foraging per sunflower head. However, other factors that can influence a bee's per-visit efficacy such as bee body size, sex, and morphology are expected to produce similar results across these sunflower types. Therefore, through a combination of measurements on different plants, including pollinator-mediated yield increases, visitation frequency, and per-visit efficacy, we obtained best estimates for the relative contributions of different pollinator taxa to confection sunflower pollination.

Our study illustrates that maximum sunflower yields are pollinator-dependent across the growing region, and, given the positive relationship between bee visitation rates and pollinator benefits, that increasing numbers of pollinators could improve yields. Furthermore, the regional estimated potential value of insect pollinators for confection sunflower production, over $40 million, along with our finding that native wild bees provide the vast majority of this pollination, suggests that pollination services may motivate bee conservation efforts in the Great Plains. Confection sunflowers are only a small proportion of cultivated sunflowers grown in North America, with the majority of sunflower production in oilseeds. If native wild bees provide similar levels of pollination services to oilseed sunflowers, their estimated potential value for combined sunflower production nationwide would be approximately $231 million. Future research evaluating the benefits of insect pollination to oilseed hybrids, as well as to both oilseeds and confections within large commercial fields, could help to refine pollination service estimates. By emphasizing the value of pollinators in the Great Plains, our study may motivate the conservation or restoration of habitats that support both managed and wild bees, including grasslands, which have recently been converted to corn and soybean (Wright and Wimberly 2013, Otto et al. 2018). Furthermore, management to enhance bee populations within or around sunflower fields could significantly increase sunflower yields as well as yields of other pollinator-dependent crops within the region.

## Supplementary Data

Supplementary data are available at *Journal of Economic Entomology* online.

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