

Wild bees enhance honey bees' pollination of hybrid sunflower

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Edited by Pamela A. Matson, Stanford University, Stanford, CA, and approved July 19, 2006 (received for review February 3, 2006)

Pollinators are required for producing 15–30% of the human food supply, and farmers rely on managed honey bees throughout the world to provide these services. Yet honey bees are not always the most efficient pollinators of all crops and are declining in various parts of the world. Crop pollination shortages are becoming increasingly common. We found that behavioral interactions between wild and honey bees increase the pollination efficiency of honey bees on hybrid sunflower up to 5-fold, effectively doubling honey bee pollination services on the average field. These indirect contributions caused by interspecific interactions between wild and honey bees were more than five times more important than the contributions wild bees make to sunflower pollination directly. Both proximity to natural habitat and crop planting practices were significantly correlated with pollination services provided directly and indirectly by wild bees. Our results suggest that conserving wild habitat at the landscape scale and altering selected farm management techniques could increase hybrid sunflower production. These findings also demonstrate the economic importance of interspecific interactions for ecosystem services and suggest that protecting wild bee populations can help buffer the human food supply from honey bee shortages.

agriculture | biodiversity | conservation | ecosystem services | *Helianthus annuus*

The honey bee (*Apis mellifera*) is the principal species used for crop pollination worldwide (1); the pollination services honey bees provided to U.S. crops were worth \$14.6 billion in 2000 (2). Although honey bees pollinate a wide variety of crops, they are often relatively ineffective pollinators on a per-visit basis (1, 3–6). Farmers obtain adequate pollination services by bringing large numbers of honey bees to crop fields. However, supplies of honey bees have declined, in part because of problems caused by parasitic mites and pesticide misuse. Since the 1970s the number of managed honey bee colonies in the U.S. decreased from >4 million to 2.41 million; declines were also reported in Europe (5, 7–14). Several documented examples show that reductions in bee abundance can cause reduced crop yields (15, 16). If crop production suffers from diminished supplies of honey bees now or in the future, then an increase in the per-visit pollination efficiency of honey bee individuals may be immensely valuable for global food production.

Non-*Apis* bees, also known as pollen bees (hereafter wild bees), are also valuable for crop pollination (17), but far less is known about their ecology and contribution to crop production. Previous studies have indicated that surrounding and in-field habitat affects the composition of wild bee communities that pollinate crops (18–25). Both the abundance and diversity of wild bee communities are associated with increased crop pollination (16, 21, 22), and in some cases wild bee diversity predicts crop production better than wild bee abundance (20). Species richness of wild bees may be important because of lack of density compensation (26), because of complementarity in which behavioral differences result in each species pollinating a different part of the flower (27), and because the most important pollinators may be most susceptible to local extinction (26).

The species composition of the bee community may also affect pollination outcomes because behavioral interactions among species may alter the pollination efficiency (defined as seeds resulting from a single pollinator visit) of some species. For example, under some conditions the foraging behavior of a given bee species could reduce both the pollinating contribution of another species and the total pollination provided (28–30). In hybrid sunflower seed production, honey bees were observed with more sunflower pollen on their bodies in fields where wild bees were more abundant (31), which suggests that the presence of wild bee individuals could enhance the pollination efficiency of honey bees in this crop system.

In this study we researched the pollination of hybrid sunflower (*Helianthus annuus*) seed production, which is an economically important industry that supports other agricultural sectors (sunflower oil and confection markets that use hybrid seeds). To grow hybrid sunflower seed, male-fertile cultivars (pollen-producing, hereafter “males”) and male-sterile cultivars (only nectar-producing, hereafter “females”) are planted in separate rows within a field. Animal-mediated pollination is essential for transferring pollen from male to female parents (1, 32). Even though honey bees are relatively inefficient sunflower pollinators on a per-visit basis (4), growers rent them for pollination services because there are no other widely available commercial alternatives. We hypothesized that variation in wild bee community composition could affect pollination efficiency of honey bees via interspecific behavioral interactions. We further hypothesized that proximity to natural habitat and farm management practices would influence bee community composition and thus alter the pollination services provided both directly and indirectly by wild bees.

Results

Bee Visitors of Sunflower. Honey bees, which were stocked on seed-production fields at the standard rate of 1.5 hives per acre (32), were the most abundant pollinator species, comprising 72% of the 20,472 bee visits to sunflower by 33 bee species observed over 2 years (see Table 2, which is published as supporting information on the PNAS web site, for a list of bee species). We found that pollen-collecting honey bees were significantly more abundant on male flowers (median, 3.5; range, 0–20 bees per 20 m) than on female flowers (median, 0; range, 0–2 bees per 20 m) ($n = 20$; $z = -3.92$; $P < 0.001$). Conversely, nectar-collecting honey bees were more abundant on female flowers (median, 11; range, 1–55 bees per 20 m) than on male flowers (median, 5; range, 0–35 bees per 20 m) ($n = 20$; $z = -3.17$; $P = 0.002$). Wild bees were more abundant on male (median, 1; range, 0–17 bees per 20 m) than on female (median, 0; range, 0–4 bees per 20 m) flowers ($n = 20$; $z = -3.82$; $P < 0.001$).

Bee Pollination Efficiencies and Behavioral Interactions. We found high variation in bee pollination efficiencies both among species and

Conflict of interest statement: No conflicts declared.

This paper was submitted directly (Track II) to the PNAS office.

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Table 1. Pollination efficiency of wild bees visiting sunflower (seeds per visit)

Bee species	Sex	Mean	SD	n
<i>S. obliqua expurgata</i>	F	19.1	5.02	16
<i>Anthophora urbana</i> , <i>Diadasia</i> spp., <i>Melissodes</i> spp.	F	14.5	3.67	10
<i>Melissodes</i> spp.	M	5.8	0.95	38
<i>Bombus vosnesenskii</i>	F	2.0	—	1
<i>Dialictus</i> spp.	F	2.0	0.86	7
<i>Halictus ligatus</i> and <i>Halictus tripartitus</i>	F	2.0	0.72	20
<i>Peponapis pruinosa</i>	M	1.3	0.72	3
<i>H. ligatus</i> and <i>H. tripartitus</i>	M	0.5	0.35	2

Seed set after a single bee visit to a previously unvisited flower head. Not all bees could be reliably identified to genus and species in the field; therefore, some species with similar morphology are grouped. We did not assess the effects of bee community composition on wild bee pollination efficiency. F, female; M, male.

within honey bees. Pollination efficiencies of wild bee species ranged from <1 to 19 seeds per visit on average per species (Table 1). When wild bees were rare, honey bee pollination produced three seeds per single visit on average (Fig. 1), but honey bee pollination efficiency increased strongly with wild bee abundance (Fig. 1 *Left*) (adjusted $R^2 = 0.96$; $P = 0.002$; $F = 92$) and richness (Fig. 1 *Right*) (adjusted $R^2 = 0.95$; $P = 0.003$; $F = 83$), up to 15 seeds per visit on average. When considered jointly in a multiple regression, both abundance ($P = 0.025$) and species richness ($P = 0.027$) of wild bees significantly contributed to the overall model (adjusted $R^2 = 0.997$; $P = 0.002$; $F_{2,2} = 591$). All three models explained a large portion of the variation in honey bee pollination efficiency.

After interacting with a wild bee on a male flower ($n = 53$), 20% of honey bees moved to a female sunflower, whereas only 7% switched after interacting with another honey bee ($n = 64$). Thus, honey bees were nearly three times more likely to move from a male to a female sunflower after interacting with a wild bee rather than another honey bee (Fisher's exact test, $P = 0.008$). Furthermore, honey bees that had just moved from a male sunflower carried significantly more pollen on their bodies (median, 1,522 pollen grains; range, 188–6,750; $n = 12$) than did control bees that were foraging on female flowers and had not just moved from a male flower (median, 307 pollen grains; range, 178–1,190; $n = 12$) (Mann-Whitney U test: $z = 2.71$; $P < 0.01$).

Economic Impact. No field received sufficient pollination for seed set of all florets, indicating that production may often be limited by

pollination even when fields are fully stocked with honey bee colonies (Fig. 2). We found the sunflower hybrid seed production industry to be worth \$26 million in the U.S. in 2002. Thus, the upper-bound estimates of the different components of pollination service, as based on the total value of the crop (see refs. 2 and 17), are as follows: for direct pollination services provided by wild bees, \$1.9 million \pm 0.9 million (SE); for direct pollination by honey bees, \$13.8 million \pm 2.6 million; for the enhancement by wild bees of honey bees' pollination, \$10.4 million \pm 4.7 million. The lower-bound estimate for wild bee pollination services can be based on the cost of renting replacement honey bee hives (33), and the enhancement by wild bees of honey bees' pollination is worth \$431,000. For comparison, we estimated current rental fees for honey bees (honey bee direct pollination) at \$579,000.

Proximity to Natural Habitat and Farm Management Practices. The amount of direct wild bee pollination and enhanced honey bee pollination delivered to sunflower varied according to farm management practices and the proximity to natural habitat. We found a significant, positive association between the number of consecutive years that sunflowers had been planted within 3 km of a field and the amounts of both direct wild bee pollination ($R^2 = 0.33$; $F_{1,15} = 95.8$; $n = 20$; $P < 0.0001$) and enhanced pollination ($R^2 = 0.28$; $F_{1,15} = 14.8$; $n = 20$; $P < 0.01$) (Fig. 3). We also found that both direct wild bee ($R^2 = 0.17$; $F_{1,15} = 4.5$; $n = 20$; $P < 0.05$) and enhanced ($R^2 = 0.19$; $F_{1,15} = 5$; $n = 20$; $P < 0.05$) (Fig. 4) pollination

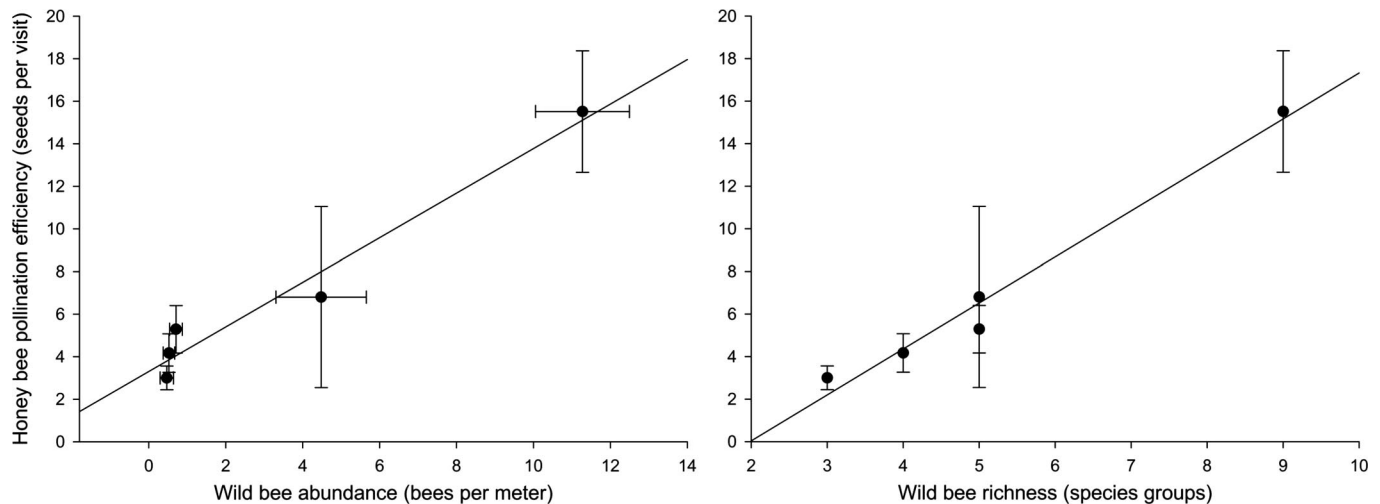


Fig. 1. Honey bee pollination efficiency is related to wild bee abundance and richness. Honey bee pollination efficiency is shown as mean seeds produced per single honey bee visit for a particular field; bars show SE. Each data point represents 20–25 honey bee visits to separate virgin female sunflowers on a single field. (*Left*) Wild bee abundance is reported as mean wild bee visits per 1 m length of a single row during 1 min in a particular field; bars show SE ($n = 4$ transects). (*Right*) Wild bee richness is reported as the number of species groups.

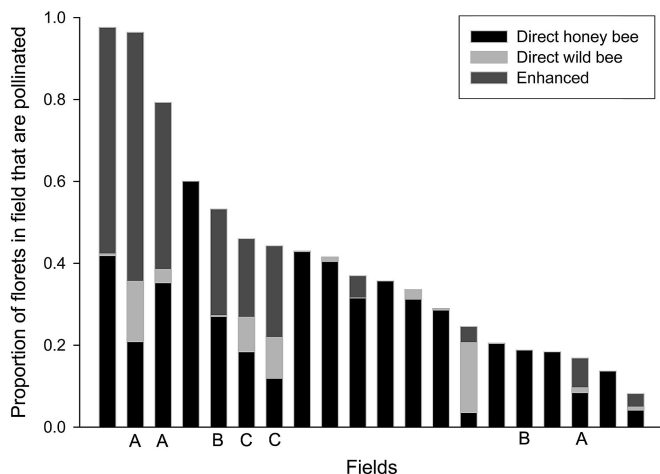


Fig. 2. Pollination services measured in hybrid sunflower fields. Each histogram is a field. Fields are rank-ordered according to total pollination provided. Fields whose wild bees were present only on male flowers would show contributions from enhanced pollination but not direct wild bee pollination. Fields that had a large number of wild bees but extremely low numbers of honey bees, despite stocking rates varying little between fields, show little contribution from enhanced pollination. Three fields, designated A, B, and C, were each sampled in multiple years.

increased with increasing proximity to natural habitat. In a multiple regression using both sunflower continuity and proximity to natural habitat as independent variables and direct wild bee pollination as the dependent variable, we found that the overall model was significant ($R^2 = 0.36$; $F_{2,15} = 89$; $n = 20$; $P < 0.0001$) and that only sunflower continuity contributed significantly to the model ($P < 0.05$). In a similar multiple regression but with enhanced pollination as the dependent variable, we found that the overall model was significant ($R^2 = 0.33$; $F_{2,15} = 165$; $n = 20$; $P < 0.0001$) but that neither independent variable was significant ($P > 0.05$). Nuisance variables (year and time of year) did not significantly explain variation in either direct wild bee pollination or enhanced pollination ($P > 0.05$).

Discussion

Wild bees indirectly provide pollination services to hybrid sunflower seed production by increasing the per-visit effectiveness of honey bees. Although our data are specific to sunflower hybrid seed production, it is likely that wild bees enhance honey bee pollination efficiency for other crops via similar mechanisms. Individual honey bee foragers specialize on pollen or nectar during foraging trips (34), and previous studies of hybrid seed production in other crops have shown that pollen-specializing honey bees rarely visit male-sterile flowers (e.g., cotton and onion, summarized in ref. 1). Bee movement between male and female flowers is also critical in crops having separate male and female flowers, such as melons, pumpkins, and kiwis, and in plants with strong self-incompatibility mechanisms, such as apples, almonds, and sweet cherries (1, 35, 36). Because honey bees are the principal pollinator used in food production around the world and also have declined globally in recent decades (5, 7–14), any factors that can either enhance their efficiency and/or provide partial replacement for the services they provide (21) reduce our dependence on honey bees and increase food security (37).

Honey bees' relative inefficiency on sunflower when native bees are rare may result from individual honey bee workers specializing in collecting either nectar or pollen on each trip (34). If pollen-collecting and nectar-collecting honey bees specialize on male and female flowers, respectively, then they may rarely move between male and female sunflowers, providing relatively little pollination.

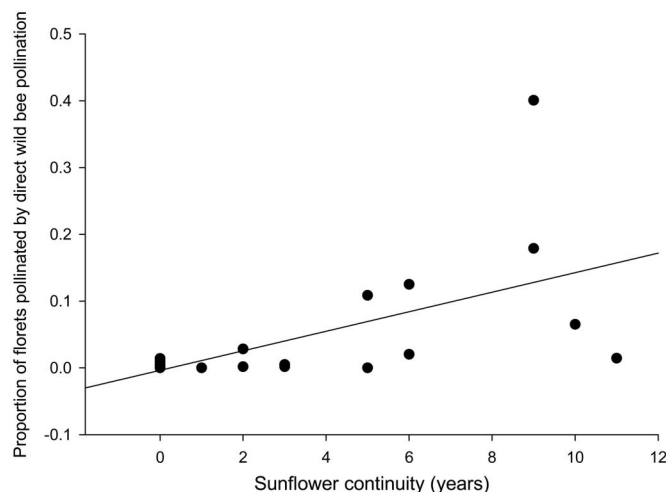
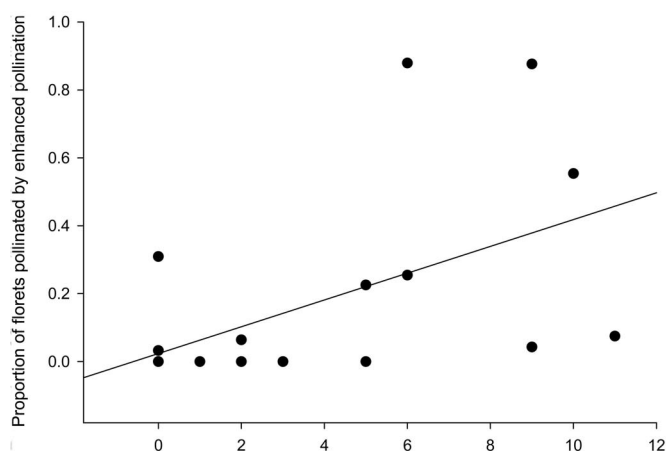


Fig. 3. Pollination services increased with interannual spatial continuity of sunflowers. Each point represents one field.

Wild bees may contribute more pollination services through enhancement than through direct pollination because wild bees concentrate on male rather than female flowers. Bees visiting only male flowers make no direct contribution to pollination but do contribute through enhanced pollination.

We documented a mechanism whereby wild bees increase the pollination efficiency of honey bees: interspecific behavioral interactions that increase the frequency of honey bee transfers from male to female plants. We observed interspecific interactions that included female wild bees with pollen loads flying into other bees. We also noticed wild male bees, which may have been searching for mates (30, 38), alighting on foraging conspecific and heterospecific female bees. When male bees landed on another bee (often a honey bee), the accosted bee generally flew away immediately. Those interactions may also alter wild bee movement.

A second mechanism, whereby wild bees could enhance the pollination efficiency of honey bees, may operate simultaneously. Honey bees are known to obtain pollen from female sunflowers (39). Because female sunflowers do not produce pollen, it must have been deposited there by wild bees or honey bees that were previously foraging on male sunflowers. Sunflower pollen clumps together, and pollen may often be deposited on female flowers in "piles." It is possible that honey bees that never forage on male flowers can nevertheless contribute to pollination by spreading this highly clumped pollen across many florets (39). This mechanism complements the interspecific interactions mechanism that we documented. When honey bees are forced to move from male to

tioning System (Trimble, Sunnyvale, CA) corrected to ± 1 m accuracy by using local base station data in Pathfinder version 2.11. We used ArcView 3.2 and a classified Landsat satellite image of the region taken in 1999 (accuracy in distinguishing natural from agricultural land classes = 96%; see ref. 24) to calculate the percent of natural habitat (riparian, chaparral, oak woodland, and mixed-oak woodland) surrounding each farm within a radius of 3,000 m. We chose the radius of 3,000 m because it represents the maximum foraging distance for *Svastra obliqua*, the largest common bee visitor in our sample (53).

We determined the interannual spatial continuity of sunflowers for each field. We measured this sunflower continuity as the number of consecutive years that sunflowers had been planted within 3 km of a field (based on maximum bee foraging range for the pollinator community) (53). Continuity data were obtained from maps kept by hybrid sunflower seed companies.

We determined bee pollination efficiencies by counting the number of seeds produced from one pollinator visit (54). Before any florets had opened, we placed a mesh bag (Delnet) over a female sunflower head to exclude pollinators. We chose only female sunflowers that were located 1.5–2.5 m from the nearest male sunflower (i.e., one female row was located between the focal female sunflower and the male rows) because the amount of pollen on honey bees foraging on female flowers declines with distance from the nearest male flower (J. Skinner, personal communication). After florets had opened, we removed the bag and watched constantly for a bee to land. When one bee landed, we allowed it to carry out normal activity while preventing other insects from visiting. If we disturbed the focal bee or if other insects accidentally touched florets, we abandoned that flower. After the focal bee left, we replaced the bag to exclude pollinators and seed predators. When the seeds matured, we counted the fertile seeds in each sunflower head.

We measured honey bee pollination efficiency on five fields that varied in wild bee community composition (see below) on 20–25 sunflower heads in each field. For wild bees, we measured the pollination efficiency of individual species opportunistically on four fields. Because sample sizes for wild bee pollination efficiencies were small, we averaged the data across all fields. Some wild bee species could not be reliably distinguished on the wing; therefore, morphologically similar species were grouped (Table 2).

To assess bee community composition on the five fields where honey bee pollination efficiency was being measured, we simultaneously conducted standardized, hourly surveys of sunflower visitors. We then used the same standardized survey technique to assess bee visitation rates of different bee groups (e.g., bee species groups; pollen or nectar-collecting honey bees) to sunflower in additional fields. We walked 20-m transects at 10 m/min, recording all bee visits. Four transects were established along female rows and four transects were established along male rows in each field, beginning 5 m from the edge of the field to standardize for any edge effects (21). We categorized honey bees with pollen in the corbiculae as pollen-collecting bees and bees without pollen in the corbiculae as nectar-collecting bees, rather than noting whether bees were actively foraging for nectar or pollen, because bees that forage primarily for pollen on sunflower also may collect small amounts of nectar (unpublished observations). Wild bees were sexed and identified to the lowest taxonomic level possible. Some bees could be identified to the species level whereas other, morphologically similar bees were classified into species groups (Table 2). To verify identities of wild bees, voucher samples were collected and identified by Robbin Thorp (University of California, Davis), and deposited at the Bohart Museum of Entomology (University of California, Davis). Bee richness is reported as the number of species groups.

We tested our hypothesis that interactions between wild and honey bees increase the probability that honey bees move between male and female sunflower rows. We located honey bees that were

foraging alone on male flowers and waited until the focal bee interacted with either a honey bee or a wild bee (one bee joining the other bee on the same flower head). After the interaction, we followed the focal honey bee to determine whether it would remain on male flowers or transfer to a female flower within the next four transfers between flower heads. If we lost track of the focal honey bee when it flew off the initial flower and before it landed on another flower head, we discarded it from the data set. We used Fisher's exact test to determine whether honey bees were significantly more likely to move from a male flower to a female flower after interacting with a wild bee rather than with another honey bee (55).

If increased male-to-female flower movement is to enhance honey bee pollination efficiency, honey bees should be carrying more pollen when they arrive on a female from a male rather than from another female flower. To test this hypothesis, we collected honey bees from female flowers under two conditions, distinguishing between bees that had just transferred from a male to a female flower and bees that had been on female flowers for at least 10 min (controls). We then compared the amounts of pollen on the bodies of the two groups of bees (excluding pollen in the corbiculae, which is largely unavailable for pollination) (39).

Calculations. We estimated the number of seeds produced per unit area in each field. The total pollination service that is delivered to a field comes from three sources: direct pollination from wild bees, direct pollination from honey bees (the amount of pollen honey bees would deliver if wild bees were not present), and enhanced pollination (the increase in honey bee pollination caused by behavioral interactions with wild bees). We assumed that sufficient pollen and pollinators were available for florets to be pollinated within a 5-h window each day, based on daily bee activity patterns and observations of the eventual depletion of pollen from a field. A floret typically remained open for 1 day (unpublished data) (1, 48).

For a particular field, the direct pollination provided by each wild bee species group was calculated by multiplying the observed number of visits to female flowers per unit area during 1 min by that group's pollination efficiency and by 300 min (5 hours) of active pollination time. We summed these amounts to estimate direct pollination provided to that field per unit area and time by the entire wild bee community (22, 56).

Similarly, direct pollination provided to a field by honey bees was calculated by multiplying observed honey bee visits to female flowers in that field per unit area during 1 min by the efficiency that we found for honey bees foraging in fields with the lowest observed levels of wild bee abundance and species richness, and multiplying by 300 min of active pollination time. Thus, direct honey bee pollination was the amount of pollination that the honey bees would have provided if they had not interacted with wild bees.

To calculate the enhanced pollination from honey bees due to interactions with wild bees, we multiplied the observed number of honey bee visits to female flowers on each field by the honey bee's estimated pollination efficiency on that field. The estimated honey bee pollination efficiency for each field was extrapolated from the multiple regression of honey bee pollination efficiency on wild bee abundance and richness (Fig. 1). In order not to extrapolate beyond our data, the minimum average observed honey bee efficiency value was used for the cases ($n = 10$) when wild bee abundance or species richness actually observed in a field was lower than those used in developing the multiple regression. This is a conservative approach to avoid overestimating enhanced pollination. Enhanced pollination, due to the interaction between wild and honey bees, was then calculated by subtracting direct honey bee pollination from total estimated honey bee pollination.

Next we calculated the proportion of available florets that were pollinated in each field by direct wild bee pollination, by direct honey bee pollination, by enhanced pollination, and by the sum of all three pollination sources. We observed four rings of florets

opening per sunflower head each day, which is consistent with the literature (1). We estimated the number of florets open per head per day by multiplying the mean number of florets per ring (unpublished data) by four rings. For each pollination source, we divided the number of seeds set per unit area by the estimated total number of florets available to be pollinated per unit area. We assumed that bees visited florets at random and therefore calculated the proportion that would be pollinated by using a Poisson distribution (57), with the equation $x = 1 - e^{-m}$, where the proportion of florets pollinated is x and the seeds per unit area divided by available florets is m .

We calculated the proportion of pollination that came from each of the three pollination sources across all fields in our study. To estimate the economic value of each of these three pollination sources, we multiplied the proportion provided by each of the three sources by the total value of the hybrid seed production industry. We estimated the annual economic value of the sunflower hybrid seed industry by multiplying U.S. sunflower oil and confection acreage (58) by the purchase cost of the seed used for planting, which was estimated at \$12 per acre (L. Kleingartner, personal communication). As a proportion of the total value of the sunflower crop, these calculations represent an upper-bound estimate of the value of pollinators, equivalent to the value of the crop weighted according to its dependence on these different sources of pollination (1, 46, 47).

We also calculated a lower-bound estimate of the value of pollination services based on the cost of renting honey bees (33). We calculated the value of direct pollination by wild bees and by wild bees enhancing honey bees as the cost of obtaining that pollination by renting additional honey bees. To compare against the pollination that is done directly by commercial honey bees, we multiplied acres of hybrid sunflower seed planted by the typical, local cost to rent honey bees (1.5 hives per acre at \$19 per hive) (32).

Statistical Analyses. We used data from our bee community surveys to investigate the distribution of nectar-collecting honey bees, pollen-collecting honey bees, and wild bees on sunflower fields. For each of these three categories, we used a Wilcoxon matched-pairs test to determine whether a significant difference existed in abundance on female vs. male sunflowers (55).

We conducted regressions to determine whether proximity to natural habitat and crop-planting practices explained variation in either direct wild bee pollination or enhanced pollination. Independent variables measured for each field were proportion of natural habitat within foraging range of the largest bee species observed (*S. obliqua*) and interannual spatial continuity of sunflowers. Nuisance-independent variables were year and time of year (Julian days). We regressed each dependent variable on each nuisance variable and independent variable of interest. We also conducted two multiple regressions, one for each dependent variable, with both proportion of natural habitat and interannual spatial continuity of sunflowers as independent variables.

We thank three anonymous reviewers, G. Daily, G. De-Grandi-Hoffmann, J. Gould, H. Horn, J. Skinner, S. Smith, V. Tepedino, R. Thorp, N. Waser, N. Williams, and R. Winfree for comments on the manuscript; R. Thorp for identifying bees; K. Archangelski, S. Bellan, E. Bernier, R. Bugg, C. del Rosario, S. Elliott, K. Froelich, C. Hahn, J. Kim, S. Lao, D. Lowry, N. Nicola, C. Otto, L. Reimer, B. Smith, J. Smith, S. Smith, Y. Tauschek, and T. Tsukamoto for assisting in data collection; C. Hjerpe, S. Shane, T. Pellegrino, A. Walker, and K. Crerar for providing logistical support; Eureka Seeds, Pioneer Hi Bred Seed Company, and Yolo County and Solano County farmers for providing field access; and the Entomology Department and Harry H. Laidlaw, Jr., Honey Bee Research Facility of the University of California (Davis) for laboratory support. This work was supported by an Environmental Protection Agency Science to Achieve Results predoctoral fellowship (to S.S.G.) and a McDonnell Foundation 21st Century Research Award (to C.K.).

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