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Title: ***Conserving and restoring pollination services in organic farms of Yolo and Solano Counties, Northern California***

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Introduction

Most flowering plants require pollination, the transfer of pollen grains from the male to the female reproductive parts, as a first step for successful seed set and fruit growth. Wind, water or animals can all contribute to pollination, depending on the floral anatomy and the plant breeding system. While certain plants can only reproduce via animal vectors[3], others do not require animal-mediated pollination, either because they are self-pollinated, or their pollen is transferred adequately by wind or water. Even self-fertile plants (e.g. tomatoes) or plants that are typically wind-pollinated (e.g. grapes), however, can benefit from animal vectors, because such vectors ensure pollen transport and help to effect cross-pollination, which can produce larger, better-tasting fruits with more viable seeds, and enhanced genetic diversity in seedlings (McGregor 1976).

It is generally believed that members of the bee superfamily (Apoidea) are the most important insect pollinators of most crop plants. This is because female bees are the only insects that visit flowers expressly to collect pollen as food for their larvae. They have morphological adaptations designed for collecting pollen, and they often tend to forage consistently on one species before returning to the nest to deposit their pollen load. This behavioral fidelity enhances the chance that pollen will be transported from flower to flower of the same species.

Linkage to Sustainable Agriculture

In the United States, over 100 crops are insect-pollinated (O'Grady 1987), and 15-30%[4] of the average American diet is comprised of insect-pollinated foods (McGregor 1976, O'Grady 1987, Free 1993, Buchmann and Nabhan 1996, http://www.desertmuseum.org/fp/). Thus insect pollinated crops make up an important component of dietary stability and diversity. Some of the fruits and vegetables requiring insect-mediated pollination are: almond, apple, apricot, blueberry, cantaloupe, citrus, cucumber, kiwi, peach, plum, squash, sunflower, watermelon; a far larger set of fruits and vegetables also require insect pollinators for seed production.

Many farmers rely on honey bee *(Apis mellifera)* colonies to ensure adequate pollination of crops that require insect pollination. This is particularly true in California, which makes up 40% of the rental market for honey bees. Rental fees range from $15 - $50 per colony, depending on the crop. Each year, beekeepers move about 25% of the 2.4 million U.S. colonies throughout the US for rentals--from region to region and crop to crop. Transportation of honey bees for long distances entails high costs for beekeepers. Honey production is a more important source of revenue to apiculturists than pollination rentals, making up 67% of revenues (USDA-NASS 2000). Since bees do not usually produce harvestable honey while on a crop, beekeepers may decide to reduce rentals in favor of honey-making when honey prices are high.

Bee colony availability has declined over the past 50 years due to three factors:

(1) Pesticide misuse, which is currently responsible for damages to 15,000 colonies/year[5] (Nabhan and Buchmann 1997, Allen-Wardell et al. 1998);

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[3] E.g. self infertile plants, plants with heavy or sticky pollen (e.g. cucurbits), plants with highly specialized floral morphology (e.g. alfalfa).

[4] The higher number is obtained by considering not only direct foodstuffs, but also insect-pollinated crops that contribute to livestock feed, and oil-seed crops.

[5] Losses due to pesticide misuse may have been much larger in the 1960s, and were estimated at 500,000 colonies in a single year (Levin 1984) or 10% of all colonies per year (McGregor 1976).

(2) Introduced diseases, including several mites and viruses first detected in the mid 80's, which have caused the demise of many colonies and annual losses of $160 million to beekeepers for colony upkeep and replacement;
(3) Loss of a 50 year subsidy to the honey industry in 1994, which has caused many beekeepers to quit the industry.

Overall, there are now less than half the number of colonies than operated in the 1950's, and in some regions of the United States, this reduction causes shortages of pollination services at critical times.

Africanized bees pose an imminent final threat to the bee-keeping industry. Africanized bees, introduced from Africa to Brazil in 1957, have steadily advanced northward and are now present in southern California (Ventura, San Bernardino and Kern counties). As they interbreed with European honey bees, they confer an aggressive trait which makes them difficult to manage and potentially dangerous to livestock and humans. Most apiculturists will therefore be reluctant to maintain honey bee colonies if interbreeding occurs, due to the potential liability issues, and as many as 80% of beekeepers are expected to abandon bee-keeping if Africanization becomes wide-spread (Buchmann and Nabhan 1996).

Thus the availability of honey bee colonies for pollination rentals varies depending on market and social factors, as well as environmental influences that affect the health and behavior of honey bees. Honey bees are vital to American agriculture, yet their contribution in future years remains uncertain.

We also have a valuable natural asset in many species of native bees, which also visit and pollinate selected crops. Native bee pollinators provide a free service to farmers and consumers that is not influenced by market factors; to date, though, the quantitative importance of native bees in crop pollination remains largely undocumented. In a few cases, however, native bees are known to be more effective pollinators than honey bees (e.g. the alkali bee on alfalfa, *Nomia melanderi,* and bumblebee species on watermelons and blueberries, Kevan 1977, Kevan and LaBerge 1979, Kevan et al. 1990, Stanghellini et al. 1997). Thus, in addition to the insurance that native bees provide in the event that managed honey bees fail, they may already be providing a significant and measurable value to agriculture (Kevan et al. 1990).

Native bees may also be at risk, though, from environmental change. Pesticides have taken their toll on native bee populations as they have on honey bees (Parker et al. 1987, Kevan et al. 1990, OToole 1993). Habitat loss, fragmentation and degradation are suspected agents in the decline of native bee populations and diversity (Frankie et al. 1990, Matheson et al. 1996, Allen-Wardell et al. 1998, Frankie et al. 1998). Native bees require natural habitat to provide blooming plants throughout their flight period (Tepedino et al. 1997) and nesting sites for rearing young (O'Toole and Raw 1992). As natural habitats are converted to urban or agricultural uses, the pool of available areas that can support bees is declining. Thus while natural ecosystems may be providing pollinators, and hence pollination services, for free, non-sustainable land use is potentially eroding these benefits.

Finally, global warming constitutes an impending threat to native bee species with unknown consequences. As temperatures climb 2-4 ° in the next 50 years, some bee species may find themselves at the limits of their physiological tolerance. Certain species may adapt by moving northwards or higher in elevation, but some species may not be able to reach suitable habitat patches, particularly if habitat patches are few and far between due to habitat conversion. These species will go extinct, decreasing both the pool of potential crop pollinators and the insurance policy against crop failure. In California, the biggest impact of global climate change on native flora and fauna is likely to be through the negative synergistic effects of climate and fragmentation (Field et al. 1999).

Native bee pollinators link natural habitats with agricultural areas. Native bee populations may rely on natural habitats to provide forage and nesting resources during part of the year, and agricultural areas the rest of the year. Native bee pollinators may provide pollination services in both areas, and may in turn depend on both. Thus problems in one area could affect the other. For example, if natural areas suffer a reduction in pollination services due to declining populations of native bees, some native plants would fail to reproduce, further impoverishing natural areas already declining in species diversity and abundance due to habitat fragmentation and degradation. This in turn will diminish the abundance of forage available for bees in the following year, potentially reducing bee populations available to provide pollination services to crops.

Understanding the contributions of native bees to agriculture, and the dependence of native bees on both natural and agricultural habitat, will help us to develop plans for managing and conserving the pollination services they provide. In our two-year study on various crops in Yolo County, we have been documenting:

- the role of native bees in crop pollination
- the role of natural areas in maintaining bee abundance, diversity and pollination services
- the economic value of native bees as crop pollinators
- the role of land management practices in enhancing pollination services on farms

The rest of this report will discuss what we have learned so far, and indicate what we still need to find out in order to conserve, restore and maintain these vital services.

Methods

Visitation of native bees to watermelon

We studied the pollination of watermelon in Yolo County, California, on 11 organic and 3 conventional farm fields in 1999, and on 1 1 organic and 13 conventional farm fields in 2000. Overlap between organic farm fields in 1999 and 2000 was four fields; overlap between conventional farm fields was zero. These farms were distributed across a landscape gradient: farms at one extreme were embedded in an agricultural matrix, while farms at the other extreme were embedded in a natural area matrix (oak woodland, chapparal, and riparian habitat). We conducted four or more 10 minute samples along 50 m transacts on each farm field, counting the number of bee visitors to watermelon and identifying visitors to the lowest taxonomic level (usually genus, but to species in some cases) and by sex, whenever possible. The taxonomic groups that we could reliably discern included: *Apis mellifera, Agapostemon texanus, Peponapis pruinosa, Bombus vosneskenskii + californicus, Halictus tripartitus + ligatus, Halictus farinosus, Osmia sp., Melissodes sp., Lasioglossum (evylaeus)* sp., and *Lasioglossum (dialictus)* sp. Any individuals that could not be identified at this level were placed in a category (e.g. the category "tiny black bee" included three genera, *Ceratina, Hylaeus and Lasioglossum (dialictus)* sp.). In total, 310 observation periods of 10 minutes each were conducted over the two-year survey, and 10,223 bees were recorded. In 1999, each farm was visited once during the morning period (9:30 - 12:30) and once during the afternoon period (12:30 - 2:30), while in 2000, each farm was visited three times during the morning period (8:30 - 12:30), because this period was found to have the highest bee activity. In 2000, we also conducted observations on selected organic farms throughout the period 7:30 - 2:30, which is the entire blooming period of watermelon flowers.

In separate studies, we measured the proportion of significant to non-significant visits for each of the above taxonomic groups. A significant visit was defined as a visit in which the body of the bee contacted the floral reproductive parts; whereas in a non-significant visit, the bee took nectar from the flower without contacting the reproductive parts, and was therefore unlikely to transfer any pollen (unpublished data).

We collected voucher specimens of floral visitors to watermelon flowers and used these vouchers to determine the sex ratio of bees in each taxonomic group. This information was used to estimate the number of female bees among the observed bees whose sex could not be determined during the observation. Female bees transport and transfer higher amounts of pollen during visitation than males (unpublished data), and estimates of pollen deposition (see below) were therefore based solely on female bees.

Trapping

We trapped bees using two trapping methods in June 1999 on 20 organic farms in the Yolo County study area (including farms with and without watermelon). Pan-trapping was conducted for 24 hours using six sets of yellow, white and blue pan traps filled with a solution of soapy water, and laid out along two 50 m transects, each consisting of three sets of traps. We also used upright 1-meter PVC pipes, radius 1.5", to collect bees, which new into the pipe and then could not get out. These pipes were left open for 10 days. All specimens were pinned and sorted to genus and/or to species.

Pollen deposition

We bagged female buds of watermelon flowers the day before opening, and then presented the virgin flowers to female bees caught foraging in the watermelon field, using a caging device. Female bees were chilled briefly before being introduced into the cage, in order to allow handling of the bee. After the bee visited the flower, we then collected the stigma, treated it in 10% KOH to remove stigmatic secretions, stained it in 3% basic fuschin, and counted stained pollen grains in a squashed whole-mount of the stigma [Kearns, 1993 #1103]. This procedure allowed an estimate of the average amounts of pollen deposited by different bee species per visit to a female flower. The following taxa and individuals were tested: *Apis mellifera* (N= 14)*; Agapostemon texanus* (N= 1); *Bombus vosneskenskii* (N=9); *Lasioglossum (dialictus)* sp. (N=36); *Halictus tripartitus + ligatus* (N=31); *Melissodes* spp. (N=4); *Hylaeus* spp> (N=l), *Lasioglossum (evylaeus)* sp. (N=l). Certain taxa were rare and only some individuals behaved naturally within the cages; therefore sample sizes are low, and the pollen levels deposited can give an idea only of the average deposition rate per visit plus the range of possible deposition.

Pollination service contribution

For any bee species, the pollination services (PS) contributed by the bee are equal to its foraging rate (number of visits per flower per day) x average pollen deposition/visit x proportion of significant visits. All of these rates will differ with the sex of the bee. Although male bees also transport small amounts of pollen, we limited the estimates of pollination services to female bees, which transport much larger quantities of pollen. "Insignificant visits" by females may also transfer tiny amounts of pollen (unpublished data), but we ignored these contributions. Thus the estimates of pollination services will be on the conservative side.

The female daily foraging rate was calculated for each taxonomic unit from the data from the organic farms, which included sampling over the entire bloom period of the flower (7:30 - 2:30). To calculate this rate, we assigned each 10 minute sample to a half hour interval, calculated the average number of female visits per taxonomic unit during that half hour interval, and then summed over all the half-hour intervals and multiplied by three. We made a similar calculation for visitation from bees of undetermined sex, and then weighted these visits by the species-specific proportion of female visits determined from voucher specimens. Rates were standardized to per flower rates by dividing by the average floral density across all sample sites. Once the daily female foraging rate was calculated per taxonomic unit, the pollination services contributed by that taxonomic unit was calculated by multiplying times the average pollen deposition per species for females, and the proportion of significant visits from females. When we had no pollen deposition data for a given taxonomic unit, we estimated likely deposition by considering the average pollen deposition from similarly sized bees. Size classes (large, medium, small or tiny) were previously assigned based on inter-tegular widths [unpublished data).

Results

The Role of Native Bees in Crop Pollination

We surveyed the native pollinators visiting strawberries, tomatoes, squash, eggplant, watermelon and muskmelon on several or more organic farms for each crop. Twenty-six or more species[6] of native bees in 19 genera were found to visit these crops (see Appendix 1). While some crops were visited by only a few species, others were visited by most of them. Interestingly, there seemed to be little specialization by bees on particular crops. A few species visited all of the crops (e.g. *Halictus tripartitus).* A few crop species (watermelon, strawberry) received visits from most of the 19 genera of crop-visiting bees. Thus a complex of native bees in this region appears to be well-adapted to the agro-ecosystem and readily visits a variety of agricultural crops.

We studied pollination services in five crops: tomato, eggplant, strawberry, muskmelon and watermelon. The percentage of visits from native bees, out of all visits by bees (e.g. native plus introduced honey bees), varies from crop to crop, and from farm to farm within crops (Table 1). Since native bees often make up a large proportion of the flower visitors to these crops, they are thus potentially important pollinators. In addition, they may provide "insurance" in the event that honey bee populations decline due to disease or management problems.[7]

Although bees may visit crop flowers frequently, visitation alone does not ensure pollination. For this reason, we carried out several different studies to assess how effective different bee species are as pollinators. We restricted these studies to watermelon, a plant that has separate male and female flowers, large, sticky pollen, and requires animal vectors for pollination.

In the first set of studies, we observed the behavior of bees on watermelon flowers, to determine whether they are likely to transfer pollen from male to female flowers, and how much pollen they carry. From these studies, we found that all of the bee species we observed (11 out of 18 potential species) visited flowers in a manner consistent with transfer of pollen from male to female flowers. Different bee species carried different amounts of pollen, and individuals within a species also varied greatly. Individual bees may carry from 0 to 4000 grains of pollen. For comparison, watermelon flowers require 500 to 1000 pollen grains for adequate fertilization and fruit development (Adlerz 1962).

Next, we studied how much pollen is characteristically deposited onto the female stigma of watermelon flowers by the visit of a single bee from different species. As expected from the large variation in pollen loads, these pollen deposition results were also highly variable, both within and between species (10 out of 18 potential species were studied). In general, the minimum and maximum estimates of pollen deposition were consistent with the levels of pollen that bees carry, although they were lower (0-571 grains deposited in a single visit).[8]

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[6] Not all bees have yet been identified to species. Here we assume that each genus for which identifications remain to be made contributes only one as yet unidentified species to the pool of crop visitors. Therefore, the figures presented represent a minimum number of species, because some of the genera with unidentified species will contribute more than one species (e.g. *Lasioglossum (Evylaeus)* consists of six morphospecies in our area, R. Thorp, unpublished data).

[7] E.g. reduced management due to hybridization with Africanized "killer" bees

[8] It is not surprising that pollen transport would be greater than pollen delivery. Female bees are adapted for collecting pollen to transport to their nests. These adaptations prevent the removal of the entire pollen load that the bee is carrying.

Using this information, we next calculated the total contribution of each species to watermelon pollination. While some bees deliver a large number of pollen grains on each visit, their visits are relatively infrequent. Thus it is important to consider both total visitation frequency, estimated over an entire day, and pollen delivery, in assessing the total contribution.

Table 2a shows the total estimated amounts of pollen deposited on average by native bees and by honey bees on the organic farms in our study. These estimates were based on two factors: the average visitation frequencies of different bee species over the course of the day, and the average pollen deposited by different bee species per visit. We combined data from separate studies in 1999 and 2000 across 11 farms in each year.[9] Thus these average estimates include the range of both inter-annual and inter-site variation. Table 2a also shows what percent of watermelon pollination native bees or honey bees each potentially contribute, relative to the total amount of pollen necessary to fully pollinate a watermelon (1000 grains). Finally, the table shows the percent of pollination provided by native bees out of the entire pollination provided by native + honey bees.

Between honey bees and native bees, all organic farms received more than adequate pollination (>> 100% of requirement). Our estimates suggest that native bees alone on average could deliver more than enough pollen to pollinate a watermelon fully (111% of requirements). This effect was due to the cumulative service provided by the community of native bees, rather than by a single bee species.

Visitation rates vary across farms, and this depends in part on the environment in which the farm is situated (see below). Visitation rates will affect pollen deposition, so we therefore compared farms in three situations: organic farms embedded in a landscape of natural areas; organic farms embedded in an agricultural matrix, and conventional farms. Since we did not have data over the entire day for each of these situations, but only for the morning period, we used the morning period data (9AM - 12:30PM) to estimate the relative amounts of pollen deposited in each situation. From that, we could then estimate the total amounts of pollen deposition in the different farm environments by scaling against the full-day sample. On organic farms far from wildlands or on conventional farms, native bees were less abundant, and we estimated that native bees alone would provide on average only 24 and 12%.of required pollination, respectively. Honey bees would be required to make up the lack. Most of the farmers in these situations did indeed rent honey bee colonies.

Honey bees were abundant throughout Yolo County, however, whether farmers rented bees or not. In cases where farmers did not rent honey bees, there may have been colonies nearby, or feral colonies may have established. Only honey bees were sufficiently abundant as a species to provide a complete pollination service on their own. Between the combined contributions of honey bees (managed and feral) and native bees, then, all farms in Yolo County, regardless of their situation, appear to receive a substantial excess of pollination at this time.

The role of natural areas in maintaining bee abundance, diversity &pollination services

We sampled relative abundance of bees on 20 farm sites, 4 riparian sites, 4 chaparral sites and 3 native plant hedgerows using pan-traps and PVC traps. We found that most of the species occurring in natural areas also can be found on farms (Appendix 1). Chaparral sites had the highest relative abundance, with on average 3 to 9 times more bees collected per site (Table 3). However, chaparral sites had significantly lower diversity (here defined as species inventoried per specimens collected), whether considered on a site by site basis, or collectively. Nineteen species were inventoried in chaparral sites from 3,120 specimens, while the same number of species were inventoried in riparian habitats from only 354

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[9] Overlap between years in farm fields was four fields.

specimens. Farms and hedgerow sites displayed intermediate abundance and diversity. While the average number of species per specimen showed significant changes with habitat type, the average species richness (number of species) observed at any individual site did not differ significantly with habitat type.

Thus, riparian habitats, while relatively diverse, were low in abundance, whereas chaparral habitats were high in abundance of relatively few bee species. These same species that were numerous in the chaparral habitat also appear to be some of the most important visitors to watermelon on farms in terms of their pollen contribution (e.g, *Halictus, Melissodes).* Thus both natural habitat types have the potential to contribute to maintaining bee diversity, abundance and pollination services on farms, since most of the bee visitors to crops observed in this study have also been found in one or both natural habitat types[10].

Hedgerow samples did not differ from farm samples in abundance or species richness, and bees censused at hedgerows were also found in the farm samples (Appendix 1). Thus the hedgerows do not appear to be changing the abundance, richness or composition of bees on farms, although further work needs to be conducted.

Visitation rates to a given crop varied widely between farms. Might this be due to the varying environment around each farm, and the proportion of natural areas in close proximity to the farm? We tested this in detail using the results from studying visitation to watermelon across 14 farms[11].These farms had been selected to vary in the proportion of nearby natural areas. Some, located in the Sacramento Valley, were surrounded by agriculture (chiefly conventional) and were far from natural areas. Others, located along the Cache Creek and Putah Creek drainages, were adjacent or near to extensive natural areas. For watermelon, we found that the proportion of wildlands (chaparral plus woodland plus grassland) in a 1.5 km radius around the farm field did have a significant positive correlation with the visitation rates by native bees, but only in combination with another variable, average temperature. Together, these two variables explained 44% of the variation between farms, at a significance level of 0.02. We next tested each type of habitat separately with average temperature as a co-variate, and found that the area of grasslands bore no correlation to native bee abundance (r^2adj = 0.07, p = 0.67), whereas chaparral was marginal (r^2adj = 0.29, p = 0.06) and woodland bore a strong correlation (r^2adj 0.64, p = 0.001). Grasslands in the Yolo County area are used for grazing and largely consist of non-native grasses and weeds. Thus the presence of natural areas, particularly woodlands but perhaps also chaparral, in the environment around the farm may enhance pollination services. Further work is needed to determine threshold effects:

- How much area is required?
- How close do these habitats need to be to the farm and how may they be dispersed?
- Which habitats are most important for the most important pollinator species, and what aspects of these habitats (floral resources, nesting resources) are important?
- How do bee species move between habitat areas and farms?

In a subsequent analysis using a larger sample of conventional farms (organic plus conventional), we found that the management type of the farm had an additional effect to the wildlands effect.

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[10] Nine species of crop visitor have not yet been inventoried in wildlands. Of these nine species, six are not likely to be important pollinators of crops or native plants. Some are parasitic and do not collect pollen *(Triepeolus sp., Nomada* sp.), some ingest pollen rather than carrying it on their body *(Hylaeus* sp.), and some are introduced species specializing on introduced weeds *(Megachile apicalis* specializing on star thistle). The other three species are bumblebees *(B. sonorus and B. vosnesenskii) and Halictusfarinosus;* while they are known to occur in the wildlands, such larger-bodied insects are less likely to be trapped in the pan traps, and were rare in this pan-trap sample.

[11] Data from 1999.

Conventional farms using heavy pesticides had significantly reduced bee visitation (p = 0.03), although conventional farms using none or mild pesiticides (e.g. Bt) were not significantly different in visitation rate from the organic farms (p=0.15).

The economic value of native bees as crop pollinators.

Many farmers rent honey bee colonies to provide pollination services for their crops. If native bees are providing some of these services "for free," what is the value of this service to farmers? Determining the value of an "ecosystem services" such as pollination is difficult, since such values fall outside of the normal marketplace, and do not respond to supply and demand. Yet such calculations can be made.

Previous researchers have examined the economic value of honey bees for crop pollination. Estimates have ranged from $8.7 billion - $34.8 billion annually in the United States (in 1999 dollars), depending on the assumptions used (Levin 1984, O'Grady 1987, Southwick Jr. and Southwick 1989, Robinson et al. 1989a, Robinson et al. 1989b, Southwick and Southwick Jr 1992). In general, the more conservative estimates (Robinson et al. 1989a, Robinson et al. 1989b, Southwick, 1992), appear more realistic. No formal attempt has been made to value the services provided by native bees.

Here we use our field data on watermelon pollination to estimate the value of native bees to farmers in Yolo County under three different scenarios:

- **replacement:** how much would it cost farmers to replace native bee services by renting more honey bee colonies
- **loss:** how much would farmers lose if native bee services could not be replaced
- **insurance:** how much would native bees be worth if honey bees were lost altogether

Similar valuations could be made for other crop types. Each scenario requires different assumptions that are specified at the beginning of the section.

Replacement

In this calculation, we assume that farmers rent bee colonies because they obtain a marginal value from each bee that is greater than zero. In other words, they only rent as many bees as they need, and at a price that allows each bee visitor, whether a honey bee or a native, to confer added value to the farmer. We assume that no bees are in excess, and that therefore, colony rentals make up the difference between the services provided by freely available bees, and what the crop needs. We ask the question, what would the shortfall in pollination be if farmers were suddenly to lose pollination services from native bees?

Under this logic, organic and conventional farms would differ greatly in the value attributed to native bees, and these values would also vary based on farms' proximity to wildlands. This is because native bees made up a higher proportion of the visits to organic farms, and an even higher proportion of the visits to organic farms near wildlands (Table 4). Thus, their replacement value[12] would be highest on organic farms near wildlands, where they make up a large proportion of flower visitors and contribute between 12 and 97% of the pollination requirements of watermelon, depending on the farm envirom-nent. Indeed, few organic farmers in our study rented bees, and thus they relied heavily both on native bees, and on honey bees that

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[12] Values were calculated as the percentage of the cost for renting a honey bee colony as a replacement. Typically, watermelon growers require one to two colonies per acre at $15 - $20 per colony for full pollination. Thus, if native bees made up 12% of the required pollination, as it did on conventional farms, their replacement value would equal 12% x $30 per acre.

were freely available (either from nearby rental colonies, or from feral colonies.) In contrast, all conventional farmers in our study rented honey bees.

Loss

How much would farmers lose if native bees were suddenly lost from the system? Given that honey bees appear to be super-abundant and provide more than ample pollination for watermelon (Table 2a), one is tempted to say that farmers would lose nothing if native bees were lost from the system. If we assume, however, that all bees are visiting flowers randomly according to their relative abundance, then, prior to saturation with pollen, native bees will be contributing pollen alongside of honey bees in proportion both to their abundance and their pollination efficiency.[13] Thus we can calculate what would be lost if native bees were no longer there by considering the proportion of total pollination effected that is attributable to native bees out of all bees (Table 2b). To calculate the value, we use the following equation, based on Robinson (1989):

$$V_{nb} = D*P*V_n$$

where V_{nb} = the annual value of the crop that is attributable to native bees
D = the dependency of the crop on insect pollinators
P = the proportion of total pollination caused by native bees
V_n = net value of the crop

Watermelons are almost exclusively insect-pollinated (McGregor 1976, Free 1993, Stanghellini et al. 1997, unpublished data) therefore we set D at 99%. Net values of the crop were obtained based on the watermelon seed market, because the price variations on the fresh market vary tremendously from farm to farm and season to season. In contrast, prices for the seed market vary less because they are fixed by contract. Net values were estimated at $200 $500 per acre (Adelman 2000, Rominger 2000). The proportion of total pollination due to native bees depends largely on the frequency of the different bee species in the system. This in turn appears to vary with the management type (organic or conventional) and the farm environment (high or low level of wildlands in the vicinity of the farm) (Table 2b). We therefore calculated the value of native bees for three situations: organic farms with high wildlands; organic farms with low wildlands, and conventional farms with low wildlands, using the appropriate P value (from Table 2b) for each situation. These values, presented in Table 5, are quite similar to the replacement values estimated in Table 4.

Insurance

Next we ask a slightly different question - what would the value of native bees become if honey bees were suddenly lost from the system, for example, due to the spread of the Africanized bee and the loss of the honey bee rental industry. If this were to happen, there would most likely be a large decline in yield. In particular, those farms which rely heavily on honey bee pollination would most likely have to abandon farming crops such as melon that require insect pollination. Consequently the price of honey bee-pollinated commodities would rise, impacting consumer's willingness to pay for these commodities. Consequently, the loss to consumer surplus resulting from the honey bee decline would equal the value of the service. Native bees could fully replace honey bees on some farms, see Table 2b. In this case, the value of the service they would provide would equal the value of the consumer surplus that would otherwise have been lost due to honey bee decline (Southwick and Southwick Jr 1992, Adelman 2000).

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[13] Both honey bees and native bees visit flowers between 8 AM and 2 PM, so there is no timing difference that would cause one group or the other to complete all of the pollination before the other group arrived.

We calculate this value again using our data on watermelon pollination, and considering the impact on the watermelon seed market. This market specifically would affect farmers, because it would determine the price of watermelon seed, an important and expensive input that will determine their net profit.

Southwick and Southwick (1992) estimated a 40% crop loss in the event of complete failure of honey bees. Using data obtained for prices and yields for watermelon seed production in Yolo County, Adelman (2000) calculated that seed prices would increase by \$2.55/pound. Societal losses would include the loss to consumers still purchasing watermelon seed (\$495 per acre) and the loss to people no longer purchasing watermelon seed (\$153 per acre), for a total societal loss of \$612 per acre. If native bees could replace honey bee services, they would then be worth this amount to society.

Data presented in Table 2b suggest that native bees could replace honey bee services in some farms and situations, but that they would not replace them everywhere. Therefore, there would still be a net loss in consumer surplus, and hence, the current actual value of native bees would be somewhat less than this estimate. This suggests the need for promoting land management practices that would enhance native bee populations across the entire agricultural landscape and maintain their insurance value in the event of a honey bee failure.

Extrapolating valuation of pollination services to other crops

While we lack detailed information on pollen delivery by native bees for other cropping systems, our preliminary results show that the proportion of native bee visitors to selected other crops (e.g. strawberry) can be far higher than for watermelon. Other crops also have different net values per acre than watermelon. We have thus made preliminary estimates of values in other crops, based on the average proportions of native bee visitation (from Table 1) and estimates of net profits. Values varied between \$30 and \$344 per acre, depending on the crop (Table 6). These values reflect the amounts per acre that the farmer might lose if native bees were suddenly lost. One caveat is that visitation does not translate directly into pollination, but this estimate assumes that pollination service value is directly proportional to visitation, regardless of the species.

The role of land management practices in enhancing pollination services on farms

A variety of land management practices appear to enhance bee abundance, diversity and pollination services on farms. The use of pesticides has been shown to diminish bee abundance and negatively affect pollination services in certain cases (e.g. blueberries, Kevan 1977, Kevan et al. 1979). This year, we compared visitation rates on 11 organic farms and 11 conventional farms *(results forthcoming).* On conventional farms, reducing the use of pesticides (particularly those most toxic to bees) or careful application of pesticides would assist in maintaining populations of native bees. For example, use of ground-rig sprayers allows greater control of spray applications that does aerial spraying, and nighttime pesticide applications would reduce harm to female bees since they remain in their nests at night. Tillage, weeding and irrigation practices that destroy bee nests or disrupt nesting activities could also be modified to favor bee populations on farms. For example, farmers should avoid flood irrigation since it destroys the nests of ground-nesting bees. Also farmers can promote bee visitation to crops by using irrigation sprinklers only at night, when bees do not fly. Farmers can promote the nesting of ground-nesting bees (which include many of the most important pollinators in our study) by practicing no-till agriculture, scraping areas of fields to provide bare soil for nest sites, and/or plowing shallowly so as not to destroy brood cells in nests below the surface.

Providing blooming resources in the off-season of the crop requiring pollination is an important mechanism for ensuring that bee populations are abundant when they are needed for crop pollination. Farmers can provide floral resources by:

- planting of hedgerows, containing diverse plant species with sequential, overlapping bloom periods (Long et al. 1998);
- allowing cover crops such as vetch and clover to bloom before plowing them under;
- leaving weedy borders on field margins and maintaining fallow fields unmowed;
- planting rows of bee-attractive plants such as lavender and thyme.

Finally, a larger-scale land management practice would protect areas of natural habitat along rivers and in upland areas near farms, to provide habitat for source populations of pollinators. Such large-scale conservation efforts could be reinforced through smaller scale restoration activities (e.g. native plantings in hedgerows and tailwater ponds, see Pickett and Bugg 1998) that would provide stepping-stone habitats for pollinators between the larger natural areas.

Further research is required in several areas. With respect to blooming plants, we need to know how to manage other sources of bloom on a farm in order to maintain bee populations on the farm without creating too much competition between the blooming plants for the pollination services. It might be possible, for example, to plant an attractive resource such as lavender during an off time, and then to harvest the lavender when the crop requiring pollination is flowering, thereby obliging the bees to find a new resource. Further research is also needed to determine the nesting resources that bees require, and how these might be enhanced on farms. We also need to understand how bees use resources in both natural areas and farmlands, how they move between these resources, and what plants should be planted in what spatial distributions to maintain pollination services where they are needed.

Conclusions

This work is still in progress, and much remains to be discovered, both in the analysis of existing data and the collection of new information. To date we have demonstrated that:

- A diverse assemblage of native bees visits a variety of field crops,
- These native bees also occur in nearby natural areas,
- The environment around the farm (proportion of wildlands in the vicinity of the farm) appears to influence positively the bee abundance on farms (see also Banaszak 1992).
- Native bee communities can fully pollinate selected crops when they occur in sufficiently high numbers on farms.

Further analysis will examine the impact of farm management type (organic versus conventional) on bee abundance and pollination services.

We have also quantified the values provided by native bees through pollination, using a variety of scenarios. Native bees provide a measurable service - of highest value when they are abundant on a given farm and make up a large proportion of the visitors to crop flowers. No single species of native bee stands out as sufficient by itself: instead it is the entire community of native bees that provides this pollination service. When valued for their insurance against the risk of failure of honey bees, the value of native bees is evidently much larger. Such a scenario is not altogether unlikely. If honey bees were to fail altogether, through a combination of disease and the introduction of Africanized bees, then native bees would have to take up the slack. This work strongly suggests that native bees could take up the slack, but only on farms where conditions are right. It furthermore suggests that conditions would not be right on most farms (e.g conventional farms removed from natural habitats). It therefore seems clear that the majority of farms would be at risk from honey bee failure, and that as a society, we are overly reliant on honey bees as the major source of crop pollination.

Further work is required in order to determine the exact conditions that would favor the restoration and maintenance of native bee pollination services on farms that do not currently enjoy them. In order for farmers to rely entirely on native bees, such services would have to be dependable from season to season, year to year, and farm to farm. It is doubtful that pollination services from a community of native bees could be managed so exactly, and thus, a combination of managed honey bees and restoration for native bees would probably be the best strategy. In addition, selected species of native bees are already managed for crop pollination, and many others have the potential to be managed pollinators (Kevan 1990).

As described above, restoring and maintaining native bee pollination services could combine conservation of natural areas, restoration of native plants in hedgerows, maintaining sources of bloom on farm fields along crop borders, in fallow fields and cover crops. Such activities might also promote the establishment and maintenance of feral colonies of honey bees. Thus natural and restored areas might have pollination service value, not only due to native bees, but also due to feral honey bees.

Conservation, restoration and other practices favoring bees may have added benefits beyond those attributable to pollination services. Conservation of natural areas maintains open spaces for recreation, protects plant and animal biodiversity, prevents erosion, provides local climate control, and maintains watershed integrity. Restoration of hedgerows provides windbreaks, shades drainage ditches, prevents erosion, provides habitat for farmland biodiversity, and is aesthetically appealing. Properly constructed, such hedgerows can also foster populations of beneficial insects - not only pollinating insects, but also predators of pest insects. Similarly, cover crops can provide a variety of benefits, including prevention of flooding, reduction of soil erosion, and nitrogen fixation and conservation. Farms can thus help to maintain biodiversity and ecosystem services while themselves benefiting from such services.

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Table 1. Percent of native bees out of total bee visits (natives + honey bees) to different crops in farms in Yolo and Solano counties.[14]

	Watermelon	Muskmelon	Strawberry	Eggplant	Tomato
Number of farms	14	14	4	5	6
Range	4% - 92%	0% - 42%	87%-100%	33%-100%	97-100%
Average ± S.E.	**34 ± 4**	**8 ± 2**	**96 ± 1**	**74 ± 8**	**99 ± 0.004**

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[14] Data from 1999 study.

Table 2a. Pollen deposition (per watermelon flower per day) across 11 organic farms in 1999 and 11 organic farms in 2000 (total of 18 separate fields).

	Average value
Total native bee pollen contribution (number of pollen grains)	1116
Honey bee pollen contribution (number of pollen grains)	5407
Percent of required pollen provided by native bees[15]	111%
Percent of required pollen provided by honey bees	540%
Percent of total pollination effected by native bees out of all bees	17%

Table 2b. Influence of farm environment on pollen deposition. Estimates were based on bee visitation between the restricted hours of 9AM and 12:30PM in order to have an equal sample effort between farm types; therefore these values do not represent the entire amount of pollen that would be deposited per flower per day. We then scaled these values to a full day sample by dividing by the proportion of pollination effected in the 9-12:30 period compared to the full day (using the organic farms in the natural area matrix, for which we had sufficient full day data). Organic farms in natural area matrix ($N_{1999} = 6$, $N_{2000} = 6$, overlap = 3); organic farms in agricultural matrix ($N_{1999} = 5$, $N_{2000} = 4$, overlap = 1); conventional farms ($N_{1999} = 3$, $N_{2000} = 10$, overlap = 0).

Farm environment	Organic in natural area matrix	Organic in agricultural agricultural	Conventional
Number of farms	12	9	13
Total native bee contribution (number of pollen	666	169	85
Total honey bee contribution (number of pollen grains, 9 - 12:30)	3571	2833	2726
Total native bee contribution, full day	952	-	-
Percent of required pollen provided by native bees in 9 - 12:30 sample	66%	17%	9%
Percent provided by native bees relative to full day sample	70%	-	-
Estimated percent provided in a full day	97%	24%	12%
Percent of total pollination effected by native bees	16%	6%	3%

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[15] Watermelons require 500 to 1000 grains for fruit maturation. We assumed that they required 1000 grains to calculate the percent of required pollen provided by native versus honey bees.

Table 3. Comparisons between sites for bee community relative abundance, species richness, and diversity. Data are presented collectively for each habitat type, and as averages over habitat types. ANOVA were performed to test for significance on species richness, log abundance and diversity (the latter using Kruskal-Wallis non-parametric test); the same letter indicates that means do not differ significantly for a given test.

	Sites	Overall abun-dance	Overall species richness (number of species[16]	Overall diversity (species/ specimen	Average abun-dance	S.D.	Average diversity (species/ specimen	S.D.	Average species richness (number of species)	S.D.
Chaparral	4	3120	19	0.006	780^{a}	390	0.016	0.009	10.25	2.06
Farm	20	4463	32	0.007	223^{b}	114	0.054	0.025	9.75	1.91
Hedgerow	3	633	13	0.021	211^{bc}	220	0.067	0.058	7.76	2.31
Riparian	4	354	19	0.054	88.5^{c}	31.6	0.	0.035	9	1.82
Significance of statistical test					0.0001		0.003		0.3 n.s.	

Table 4. Replacement value of native bees for watermelon pollination. The values are the cost of replacing the free service provided by native bees with additional honey bee rentals, and the calculation assumes that each visit by a bee, whether native or managed, is of value to the farmers (i.e., there are no surplus bees).

Management type	Matrix surrounding farm	Average % of native bee visits	Average contribution to watermelon pollination requirements (from Table 2b)	Value ($/acre)	Sufficiency of native bees?
ORG	Natural area	37.20%	97.00%	38.8	Yes
ORG	Agricultural	23.10%	24.00%	7.2	no
CNV	Agricultural	17.60%	12.00%	3.6	no

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[16] Specimens within selected genera have not yet been identified to species or morphospecies. Thus species richness here actually combines generic and specific richness.

Table 5. The value of native bees for watermelon pollination calculated if native bees were lost from they system under three scenarios: organic farms with high levels of natural areas around them; organic farms with low levels of natural areas around them; and conventional farms. High and low values for each scenario reflect the high and low bounds of net value per acre.

Management type	Matrix surrounding farm	Percent pollination effected by native bees (P) from Table 2b	Net value of crop per acre (V_n)	Value of native bees (\$/acre) (V_{NB})
ORG	Natural area	15.70%	200	31.09
		15.70%	500	77.72
ORG	Agricultural	5.60%	200	11.09
		5.60%	500	27.72
CNV	Agricultural	3.02%	200	5.98
		3.02%	200	14.95

Table 6. Values of native bee pollination for three other crops.

Crop	Net Value (V_n)	Dependency on insects (D)	Average % visitation by native bees (P) from Table 1.	Value of native bees (\$/acre) (V_{NB})
Cantaloupe	\$413	90%[17]	8%	\$30
Eggplant	\$180	70%[18]	74%	\$93
Strawberry	\$551	65%[19]	96%	\$344

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[17] D value from estimates in O'Grady, 1987

[18] D value from estimate in Robinson et al 1989

[19] D value from estimate in McGregor 1976

Appendix 1. Bee visitors to crops and their occurrence in different habitats. Parasitic bees (e.g. bees that do not collect pollen themselves but that lay their eggs in other bees nests) are indicated by an asterisk.

			Pan and PVC trap specimens				Vouchered observations								
Habitat or Crop type (Number of sites)			Riparian	Chap-arral	Farm	Hedge-row	Waterm elon	Musk melon	Squash	Cuc-umber	Egg-plant	Tom ato	Straw berry	Sun-flower	Number of visited crops
			4	4	20	3	34	14	1	2	8	10	6	1	
Family	Genus	(Subgenus) species			x										0
Andrenidae*	Calliopsis	sp.	x												0
Anthophoridae	Anthophora	urbana					x					x			2
Anthophoridae	Apis	mellifera	x	x	x	x	x	x	x	x	x	x	x	x	8
Anthophoridae	Bombus	californicus	x		x	x	x	x		x	x	x	x		6
Anthophoridae	Bombus	sonorus			x			x			x				2
Anthophoridae	Bombus	sp.			x										0
Anthophoridae	Bombus	vosnesenskii			x		x	x				x		x	4
Anthophoridae	Ceratina	sp.	x	x	x		x								1
Anthophoridae	Diadasia	sp.	x	x	x	x	x							x (*ana-vada*)	2
Anthophoridae*	Epeolus	sp.			x										0
Anthophoridae	Melissodes	sp.	x	x	x	x	x	x					x	x	4
Anthophoridae*	Nomada	sp.			x		x								1
Anthophoridae	Peponapis	pruinosa	x		x		x	x	x	x					4
Anthophoridae	Svastra	obliqua	x		x									x	1
Anthophoridae	Svastra	sp.	x												0
Anthophoridae*	Triepeolus	sp.		x	x		x						x		2
Anthophoridae	Xylocopa	sp.		x	x										0
Colletidae	Colletes	sp.													0
Colletidae	Hylaeus	sp.	x		x		x								1
Halictidae	Agapostemon	texanus	x	x	x	x	x	x		x	x	x	x		6
Halictidae	Halictus	sp.			x										0
Halictidae	Halictus	farinosus		x	x								x		1
Halictidae	Halictus	ligatus	x		x	x	x	x					x	x	4
Halictidae	Halictus	tripartitus	x	x	x	x	x	x	x	x	x	x	x		7

			Pan and PVC trap specimens				Vouchered observations								
Habitat or Crop type (Number of sites)			Riparian	Chap-arral	Farm	Hedge-row	Watermelon	Musk melon	Squash	Cuc-umber	Egg-plant	Tomato	Straw berry	Sun-flower	Number of visited crops
Halictidae	Lasioglossum	(Dialictus) sp.	x	x	x	x	x	x		x	x	x	x		6
Halictidae	Lasioglossum	(Evylaeus) sp.	x	x	x	x	x	x		x	x	x	x		6
Halictidae	Lasioglossum	sp.		x	x		x								1
Halictidae	Lasioglossum	titusi			x		x	x					x		3
Halictidae*	Sphecodes	sp.	x		x		x						x		2
Megachilidae	Ashmeadiella	sp.	x	x	x	x	x						x		2
Megachilidae*	Coelioxys	sp.													0
Megachilidae	Dianthidium	sp.		x											0
Megachilidae	Hoplitis	sp.		x											0
Megachilidae	Megachile	sp.			x										0
Megachilidae	Megachile	apicalis		x	x								x		1
Megachilidae	Megachile	sp.	x	x	x	x	x	x							2
Megachilidae	Megachile	fidelis			x										0
Megachilidae	Osmia	sp.	x	x	x	x	x								1
Megachilidae*	Stelis	sp.				x									0
Melittidae	Hesperapis	sp.		x											0
Minimum number of species			19	19	32	13	22	13	3	7	7	8	14	6	41
Minimum number of genera															29
Minimum number of non-parasitic species at crops															23
Minimum number of non-parasitic genera at crops															15