

## LETTER

# Native bees provide insurance against ongoing honey bee losses

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## Abstract

One of the values of biodiversity is that it may provide ‘biological insurance’ for services currently rendered by domesticated species or technology. We used crop pollination as a model system, and investigated whether the loss of a domesticated pollinator (the honey bee) could be compensated for by native, wild bee species. We measured pollination provided to watermelon crops at 23 farms in New Jersey and Pennsylvania, USA, and used a simulation model to separate the pollen provided by honey bees and native bees. Simulation results predict that native bees alone provide sufficient pollination at > 90% of the farms studied. Furthermore, empirical total pollen deposition at flowers was strongly, significantly correlated with native bee visitation but not with honey bee visitation. The honey bee is currently undergoing extensive die-offs because of Colony Collapse Disorder. We predict that in our region native bees will buffer potential declines in agricultural production because of honey bee losses.

## Keywords

Agro-ecosystems, biodiversity – ecosystem function, ecosystem services, pollination, pollinator decline.

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## INTRODUCTION

Ecosystems provide numerous services to humanity such as nutrient cycling, water filtration and pollination (Millenium Ecosystem Assessment 2005). One value of such services is that they could serve as biological insurance in the event that alternative human-provided methods of delivering the service fail. However, to date few studies have documented ecosystem services sufficiently to show that they could in fact fulfil this function (Kremen 2005; Kremen & Ostfeld 2005). Crop pollination has become a model system for the study of ecosystem services (Kremen *et al.* 2007). Animal-mediated pollination is required by crop plants accounting for 35% of the global food supply (Klein *et al.* 2007). In many parts of the world, crop pollination is perceived to rely on a single domesticated pollinator species, the European honey bee (*Apis mellifera*; Committee on the Status of Pollinators in North America, National Research Council 2007). In North America, where the honey bee is not native, it provides pollination services to crops worth an estimated \$14.8 billion annually (Morse & Calderone 2000). Such reliance on a single pollinator species is risky because it leaves crop pollination vulnerable to the effects of species-specific parasites and diseases. Over the past 58 years

domesticated honey bee stocks have declined by 59% in the USA, largely because of infestation by parasitic mites, in particular *Varroa destructor* (Committee on the Status of Pollinators in North America, National Research Council 2007). In 2006–2007, North American honey bees experienced an additional, unprecedented decline for unknown reasons, with 29% of bee-keepers in the USA reporting up to 75% losses (Stokstad 2007). This phenomenon is termed Colony Collapse Disorder and may be affecting other continents as well (Stokstad 2007). There are multiple hypotheses as to the cause of Colony Collapse Disorder, including pathogens, parasites, pesticides or an immune system disorder, with recent evidence pointing to a known pathogen of honey bees, Israel acute paralysis virus (IAPV) (Stokstad 2007a, b).

Although a single species of honey bee is the main domesticated pollinator, there are at least 17 000 other described bee species globally (Michener 2000) and many of these visit crops (Nabhan & Buchmann 1997; Klein *et al.* 2007). As far as it is known, non-*Apis* bees are subject to few of the same pests and diseases that cause the greatest mortality in honey bees. For example, *V. destructor* parasitizes only members of the genus *Apis* (Committee on the Status of Pollinators in North America, National Research Council

2007). Non-*Apis* crop pollinators therefore potentially provide an insurance policy against the loss of the honey bee. Wild, native bees are known to contribute to the pollination of watermelon (Kremen *et al.* 2002, 2004), coffee (Klein *et al.* 2003a,b; Ricketts 2004), canola (Morandin & Winston 2005), sunflower (Greenleaf & Kremen 2006) and many other crops (Klein *et al.* 2007). However, in previous studies that partitioned the contributions of native bees and honey bees relative to crop pollination requirements, native bees alone were insufficient to pollinate the crop at all but the least intensively managed farms (Kremen *et al.* 2002; Greenleaf & Kremen 2006). Both of these studies were carried out in California's agriculturally intensive Central Valley, where the majority of farms are intensively managed monocultures that are isolated from natural habitat, leading to species-poor and low-density native bee communities (Kremen *et al.* 2004). In other systems where there are few or no domesticated pollinators and crops rely on native bees for pollination, native bees (including native *Apis* species in some cases) can pollinate the crops fully under certain environmental conditions (e.g., when crops are near to natural habitat), but pollination is inadequate when these conditions are not met (Klein *et al.* 2003a,b; Morandin & Winston 2005). Demonstration that native bees can provide sufficient crop pollination throughout a region of intensive human land use would be a compelling example of the insurance value of biodiversity (Naeem 1998).

We studied crop pollination by honey bees and native bees in New Jersey and Pennsylvania, USA. In this region honey bees have been severely affected by *V. destructor* and *Acarapis woodi* mites since the 1990s, such that at present domesticated hives do not survive from year to year without miticide treatment and there are few feral honey bee colonies (Stanghellini & Raybold 2004). In addition, the current epidemic of Colony Collapse Disorder was first reported from Pennsylvania (Stokstad 2007). The goals of this study were to (i) estimate the pollination services by native bees relative to pollination services provided by honey bees; (ii) determine whether the pollination provided by native bees alone is sufficient to pollinate the crop fully and (iii) determine whether native bee pollination is sufficient even in landscapes with little remaining natural habitat cover.

## METHODS

### Study system

Our study system is a 90 by 60 km area of central New Jersey and east-central Pennsylvania, USA. The native ecosystem is temperate forest dominated by deciduous tree species such as oaks (*Quercus* spp.), maples (*Acer* spp.) and hickories (*Carya* spp.). Data were collected in July–August 2005 at 23 farms growing watermelon. All farms were

located at least 1 km apart, which is beyond the typical flight distance of all but the largest bees in the study (Greenleaf *et al.* 2007), and > 99% of inter-farm distances were > 2 km, making the sites spatially independent for all but a small fraction of species at a small fraction of sites. We used watermelon (*Citrullus lanatus*) as our model crop because it has high pollination requirements and requires multiple pollinator visits to obtain enough pollen to set a marketable fruit (see Table S1 in Supplementary Material). Watermelon is monoecious (has separate male and female flowers on the same plant) and depends on insect pollination to produce fruit (Delaplane & Mayer 2000). An individual flower is active for only 1 day, opening at daybreak and closing by early afternoon.

### Data collection

At each farm, we established a 50-m transect of crop row where all data were collected; this was the maximum row length that could be standardized among farms. Transects began at the edge of the farm field to standardize edge effects. We measured pollinator visitation rate to flowers during 45-s scans of flowers at 40 equally spaced points along each transect. We observed visits to as many flowers as we could view simultaneously within an approximately one by one metre area. Visitation rate data are therefore measured as bee visits per flower per time. Honey bees were readily identified to species during observations. Few native bees are identifiable to species level in the field; we therefore identified native bees to four species groups, which were created on the basis of morphology, recognizability and pollination efficiency (i.e. per-visit pollen deposition). These groups were bumble bees (five *Bombus* species plus the morphologically similar *Xylocopa virginica*), (other) large bees (seven species), green bees (*Augochlorines* and *Agapostemon*; five species) and small bees (28 species; for names of all species, see Table S2). Most species groups were strongly dominated by one or two species, e.g. 95% of the bumble bees were *Bombus impatiens*, 83% of the other large bees were either *Melissodes bimaculata* or *Peponapis pruinosa*, 74% of the green bees were *Augochlora pura* and 71% of the small bees were species in the subgenus *Lasioglossum* (*Dialictus*). Although in principle the way in which unique entities are grouped can change and even reverse an outcome, our results were very similar when groups were assigned differently. All species referred to as 'native bees' are believed to be native to our ecoregion. Although there are several exotic and naturalized bee species in our study area, we did not observe any of them on watermelon.

We censused each transect three times per day, beginning at 8:00, 9:30 and 11:00 hours, and visited each farm on 2 days. Data were collected only on days that were sunny, partly cloudy or bright overcast, and when wind speed was

$< 2.5 \text{ m s}^{-1}$ . After collecting the flower visitation rate data, we netted bees from watermelon flowers for 30 min and used these specimens for species identification. We also measured two co-variables related to floral resource availability: the density of crop flowers in the data collection transect, and the density of weedy flowers growing between the crop rows and in the fallow field borders. The line intercept method (Kercher *et al.* 2003) was used to measure weed flowers.

Per-visit pollen deposition was measured by bagging unopened female flowers with pollinator-exclusion mesh, and then offering virgin flowers to individual bees foraging on watermelon. After a bee visited a flower, the bee was identified to species group, and the flower was removed to a protected location for *c.* 24 h to allow the pollen to adhere to the stigma. Stigmas were then removed, softened in 10% KOH, stained with 1% fuschin and prepared as microscopic slides so that the number of watermelon pollen grains on the stigma could be counted with a compound microscope (Kremen *et al.* 2002). Control flowers were left bagged until the end of the field day, and contained few pollen grains (mean = 3 grains,  $N = 40$  stigmas). 'Open-pollinated' flowers were left open to pollinator visitation and collected at the end of the field day. Because open-pollinated flowers often contained  $> 10\,000$  grains, pollen was counted on a subsample of *c.* 30% of the slide and the total number of grains was then estimated.

### Spatial analyses

We mapped the centre of each data collection transect with a Trimble GeoExplorer Global Positioning System (GPS; Trimble Navigation, Sunnyvale, CA, USA) corrected to  $\pm 10$ -m accuracy with GPS PATHFINDER OFFICE (version 2.9, Touch Vision, Cypress, CA, USA). Geographical Information Systems (GIS) land-cover data for New Jersey were provided by the New Jersey State Department of Environmental Protection, and were on the basis of aerial photographs taken in 2002 and subsequently classified to 61 land-cover types. GIS data for Pennsylvania were provided by the Delaware Valley Regional Planning Commission, and were on the basis of aerial photographs taken in 2000 and subsequently classified to 27 land-cover types. We combined all land-cover types composed of woodland, the native habitat type, into one category for analysis.

In our study system, patches of remaining woodland are irregularly shaped and often interconnected by riparian corridors or other narrow strips of vegetation. Therefore, we did not attempt to define fragment size. Rather, we analysed landscape cover as the proportion of woodland at various radii surrounding each site (see Statistical Analyses below). The proportion of habitat cover is highly correlated with other area-based indices of habitat proximity, and is

appropriate for analysing community-scale response variables such as total pollen deposition (Winfree *et al.* 2005). We used ARCGIS 9.0 (Environmental Systems Research Institute, Redlands, CA, USA) to determine the proportion of the area surrounding each farm that consisted of woodland. As a second, local-scale measure of isolation from natural habitat, we measured the linear distance from the centre of our data collection transect to the nearest  $\geq 1$ -ha patch of woodland.

### Simulation methods

We developed a Monte Carlo simulation of the pollination process to estimate pollen deposition over the lifetime of each flower while also separating the contributions of the different bee species groups. The simulation was written in Matlab R2006a (The MathWorks, Inc., 2006, Natick, MA 01760, USA). Programme input is (i) the flower visitation rate for each bee species group at each farm and (ii) the per-visit pollen deposition for each bee species group pooled across farms. In the simulation, flower visitation rates represent visits to female flowers. However, *c.* 90% of our field observations were of male flowers, because watermelon has a biased sex ratio. Therefore, we used visitation rates as measured to male flowers as programme input, but scaled these rates by 0.88 on the basis of the overall ratio of bee visits per female flower/bee visits per male flower. We combined the pollen deposition data across farms on the assumption that per-visit pollen deposition by a bee foraging within a patch of watermelon is a function of bee morphology and behaviour, i.e. species identity, rather than site (Kremen *et al.* 2002; Morris 2003; Vázquez *et al.* 2005; Greenleaf & Kremen 2006); sample sizes were insufficient to test this assumption empirically. Programme output is the distribution of the number of pollen grains deposited on a flower over its lifetime by the various groups of bees: honey bees, bumble bees, large bees, small bees, green bees and all native bees combined.

The simulation weights bee visitation rate per flower per day by pollen deposition in a two-step process to obtain total pollen deposition per flower and per bee group. First, it draws a mean flower visitation rate and a mean number of pollen grains deposited per visit from distributions having the empirical mean, and a variance on the basis of our measurement uncertainty. Drawing different values to represent the mean at each repetition of the simulation incorporates our uncertainty about what the true population mean might be (measurement error). Second, the mean values that were chosen in the previous step are used to create distributions from which the simulation draws the actual number of bee visits, and the actual number of pollen grains deposited per visit. Drawing from the second distribution incorporates uncertainty about how much

pollen a particular flower in the population might receive, given the population mean (process error). Including both forms of error leads to larger uncertainty about the final result and is therefore conservative.

Each run of the simulation represents one flower on 1 day (i.e. a flower lifetime) at a given farm. Because both flower visitation rates and per-visit pollen deposition varied over the course of the day, the day was divided into three equal 2.25-h time periods, with different parameter values used for each time period. Parameter values for each 2.25-h time period were on the basis of data collected within the given time period. A run of the simulation proceeds as follows. The run begins by drawing a number that represents the mean number of visits to the flower by the first bee species group in the first time period from a gamma distribution with  $a =$  bee visits per flower per time period and  $b = (\text{number of flowers observed})^{-1}$  (Winfree *et al.* 2006). The simulation then uses this mean to establish a second distribution, a Poisson with  $\lambda =$  bee visits per flower per time period, from which it then draws the actual number of visits for this bee species group in this time period. For the first time period only, the number of visits is reduced by 39% to reflect lower bee visitation rates when flowers first open, but prior to the start of our standard data collection periods. Further, the simulation draws a mean number of pollen grains deposited per visit during the first time period by the first bee species group, from a normal distribution with the empirical mean and  $SD = SD_{\text{data}}/\sqrt{N}$ . The simulation then uses this mean to establish a second distribution from which a number of pollen grains is drawn for each of the  $N$  visits. For this last distribution, we used a gamma with the same mean and variance as the measured number of grains per visit, which we found provided a good fit to the data. To account for the fact that the true distribution of pollen grains deposited per visit may not be as long-tailed as the gamma, we capped the maximum at 1300 grains per visit, which is slightly more than the maximum value observed in 271 data points. Because this cap predominantly affects bumble bees, any biases introduced are conservative with regard to our main result.

This completes the first loop through the simulation, and the total number of pollen grains deposited in the first time period by the first type of bee is recorded. The simulation then loops through the second and third time periods for the first bee species group, and then repeats the entire process for the other bee species groups. At the end of each run, the total number of pollen grains deposited on the flower by each bee species group is recorded. We ran the simulation for 1000 repetitions (runs) per farm which was sufficient to stabilize the output within 2% (i.e. multiple runs with the same input data produced output that did not differ by more than 2%).

On the basis of these 1000 values, we used the following forms of simulation output for each farm in further analyses: (i) median pollen grains deposited by native bees per flower per day and (ii) median pollen grains deposited by honey bees per flower per day. We used medians instead of mean values because the distributions were skewed in some cases. We defined 'sufficient pollination' as 50% or more of flowers on a farm receiving at least 1400 pollen grains, which is sufficient for maximal fruit set in watermelon (see Table S1).

### Statistical analyses

To assess the influence of honey bee and native bee visitation rate to flowers on pollination, we used least squares linear regression of pollen deposition on open-pollinated flowers against either honey bee or native bee flower visitation rate at the same farm on the same day. To account for the fact that we had pollen counts from multiple (4–8) flowers from each farm and these were differentially variable among farms, regressions were weighted by  $(\text{variance of mean pollen counts across flowers})^{-1}$ .

We used Moran's  $I$  to check for spatial autocorrelation among sites in total native bee visitation rate to watermelon flowers (Casgrain & Legendre 2001), and did not find significant autocorrelation at any scale (all  $P \geq 0.16$ ). To identify the most explanatory scale of analysis for surrounding land cover, we regressed total native bee visitation rate against the proportion of woodland cover surrounding study sites at radii of 0.5, 1.0, 1.5, 2.0, 2.5 and 3.0 km; these distances include typical bee flight ranges (Greenleaf *et al.* 2007) as well as larger scales to account for the possibility of population-level processes such as dispersal determining bee abundance at a site. We then compared the resulting  $r^2$  values, and used the scale with the highest  $r^2$  value (2.0 km) in subsequent analyses (Holland *et al.* 2004). We used measures of bee abundance (visitation rate to flowers or specimens collected) for the preliminary tests of spatial relationships because abundance was the variable measured across space (Kremen *et al.* 2004), whereas our ultimate variable of interest, pollen deposition, was derived from it and other data.

To assess associations between the ecosystem services delivered at a farm and the natural habitat cover near the farm, we used simple linear regressions with woodland cover at a 2 km radius and distance to the nearest woodland patch as predictor variables (these two variables were uncorrelated; Pearson's  $r = -0.28$ ), and as the outcome variable, median pollen grains deposited by native bees per flower per day estimated by the simulation. Several co-variables including crop flower abundance, weedy flower abundance, farm management (whether organic or conventional), weather variables and surrounding cover by other

habitat types were considered in earlier multiple regression models but dropped from final analyses as unexplanatory variables. Analyses were performed in JMP (JMP version 7.0, SAS Institute, Cary, NC, USA).

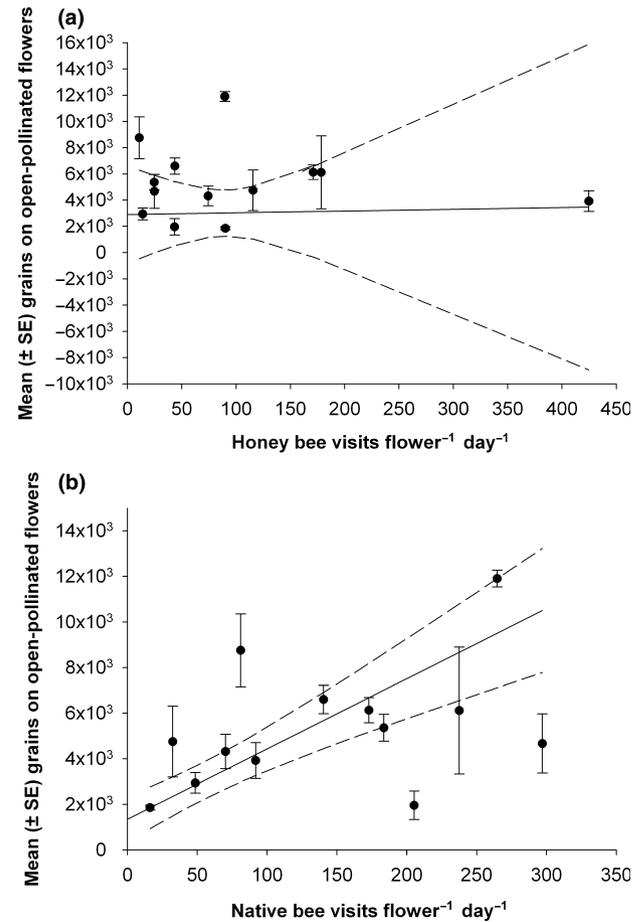
## RESULTS

We found 46 species of native, wild bees visiting watermelon flowers (see Table S2). We observed 15 888 watermelon flowers to which we recorded a total of 6187 bee visits, and obtained 271 records of per-visit pollen deposition. We counted day-long pollen deposition on 74 open-pollinated flowers from a subset of 13 of the 23 farms.

Empirical measures of day-long pollen deposition on open-pollinated flowers showed that watermelon flowers receive more than sufficient pollination at all farms (Fig. 1). Honey bee visitation rate at a farm was unrelated to day-long pollen deposition ( $r^2 = 0.00$ , d.f. = 12,  $P = 0.94$ ; Fig. 1a). Even at farms with very few honey bees, flowers received ample pollination. In contrast, native bee visitation rate was strongly, positively related to pollen deposition at open-pollinated flowers ( $r^2 = 0.79$ , d.f. = 12,  $P < 0.001$ ; Fig. 1b).

Simulation results, which we used to investigate the contributions of the different types of bees in more detail, were broadly consistent with the data from open-pollinated flowers. Per-visit pollen deposition by honey bees was intermediate among the native bee species groups (Fig. 2; bumble bees > other large bees > honey bees > green bees > small bees,  $X^2 = 15.5$ ,  $P = 0.004$ , Wilcoxon test). We report elsewhere that honey bees contributed significantly fewer total visits than did all native bees combined (paired  $t$ -test with d.f. = 22,  $t = -2.45$ ,  $P = 0.02$ ; Winfree *et al.*, 2008, in press). When visitation rate and per-visit pollination were combined using a simulation, the results indicated that across the entire study, native bees were responsible for 62% ( $\pm 5\%$ ) of the pollen grains deposited on female watermelon flowers. Native bees alone deposited enough pollen to pollinate the watermelon crop fully at 91% of farms, and honey bees did so at 78% of farms (Fig. 3). When pollination by all types of bees is combined, all farms received more than enough pollen for full fruit set ( $\geq 1400$  watermelon pollen grains; Fig. 3). In fact, most farms could be pollinated fully by only one native bee species group, e.g. bumble bees (six species) or small bees (27 species; Fig. 4).

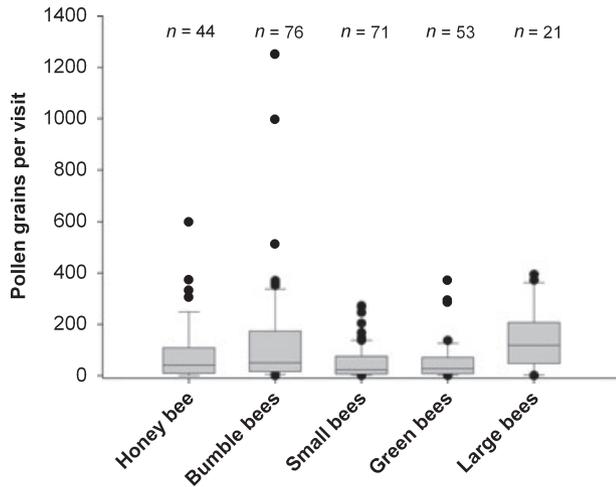
We made additional comparisons between the counts of pollen grains on open-pollinated flowers and the simulation results. The simulation result for a given farm was a good predictor of pollen counts on open-pollinated flowers at that farm ( $r^2 = 0.67$ ; d.f. = 12,  $P = 0.0006$ ; regressions were weighted by [variance of mean pollen counts across flowers] $^{-1}$ ). However, the regression slope was 0.39, suggesting that only a fraction of the pollen grains deposited



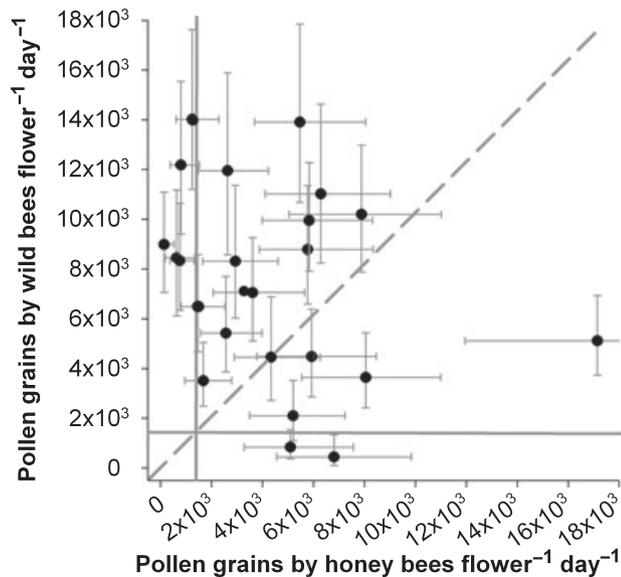
**Figure 1** Inverse variance weighted linear regressions of day-long pollen deposition on open-pollinated watermelon flowers as a function of bee visitation rate. Points show the mean ( $\pm$  SE) pollen grains per flower. Dashed lines are 95% CI for the regressions. (a) There is no relationship between honey bee visitation rate and pollen deposition. (b) Native bee visitation rate is positively related to pollen deposition.

actually stick on open-pollinated stigmas. Ninety-five per cent of 74 open-pollinated stigmas received sufficient pollination, when compared to 100% predicted by the simulation. Median pollen deposition on open-pollinated flowers was 4785 grains per flower, when compared to a median of 11 250 predicted by the simulation. The maximum pollen deposition on open-pollinated flowers was 13 547 grains, when compared to a maximum of 18 042 predicted by the simulation.

There were no detectable associations between either local- or landscape-scale measures of natural habitat cover and the median number of pollen grains deposited per flower per day by native bees (for distance to the nearest woodland fragment,  $r^2 = 0.01$ ; d.f. = 22;  $P = 0.59$ ; for proportion woodland cover in the landscape,  $r^2 = 0.00$ ; d.f. = 22,  $P = 0.86$ ; Fig. 5).



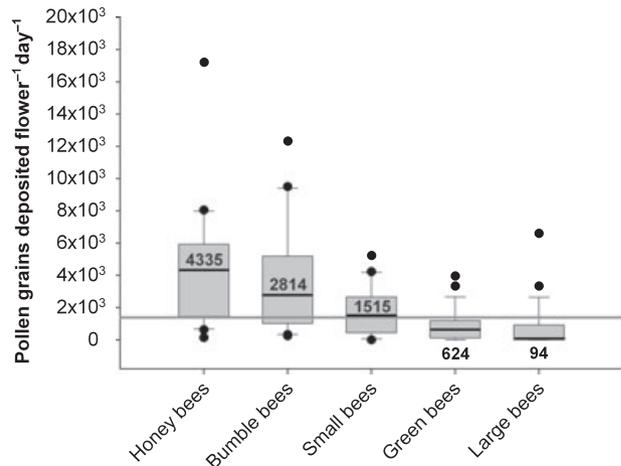
**Figure 2** Number of pollen grains deposited per visit by each of the bee species groups. Central lines represent medians, boxes represent the interquartile range and whiskers represent 10%/90% quantiles. For full pollination (> 1400 grains), roughly 10–60 visits are necessary.



**Figure 3** Simulation estimates for median ( $\pm$  10%/90% quantiles) pollen grains per flower per day delivered by honey bees vs. native bees. Each data point represents a farm. Points above the dashed line received most of their pollination from native bees. Pollination is sufficient when the median flower receives > 1400 pollen grains, as indicated by the grey shaded lines. Native bees alone provide sufficient pollination at 91% of farms (points above the horizontal grey line), and honey bees at 78% of farms (points to the right of the vertical grey line). Total pollination is more than adequate at all farms.

**DISCUSSION**

Both empirical and simulation results showed that native bees are the most important crop pollinators in this system,

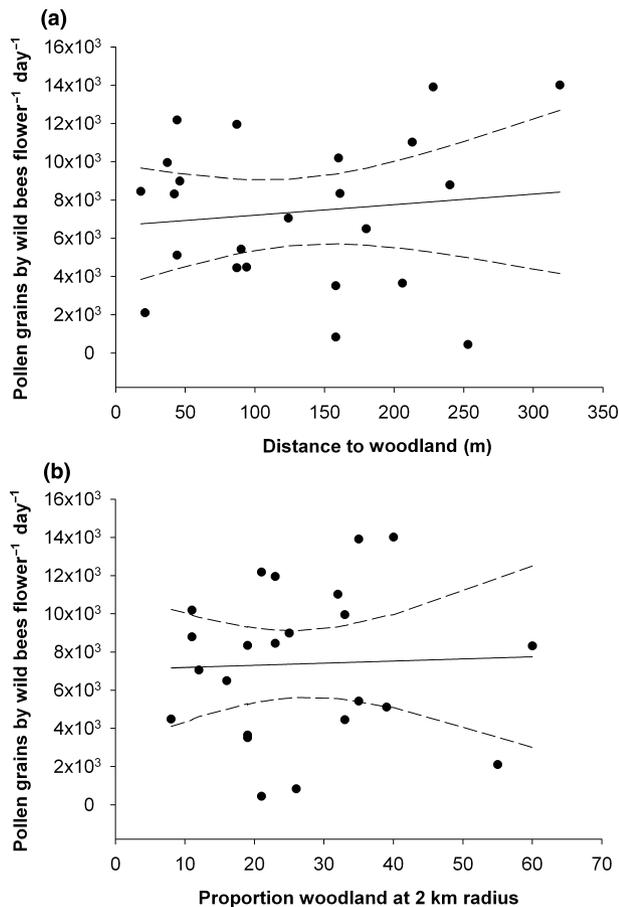


**Figure 4** Simulation estimates for median number of pollen grains deposited per flower per day by each of the bee species groups. Black lines and numbers represent medians, boxes represent the interquartile range and whiskers represent 10%/90% quantiles. When the median flower receives 1400 pollen grains, as indicated by the grey shaded line, pollination is sufficient. Bumble bees alone pollinate the crop fully at 70% of farms, small bees alone at 57% of farms and green bees alone at 22% of farms.

and that native bees alone are sufficient to pollinate the watermelon crop fully at the great majority of farms. This is a compelling example of the insurance value of biodiversity: a diverse community (46 species) of native bees could largely compensate for the loss of services provided by a domesticated pollinator.

This study is the first documented example of wild, native pollinators providing sufficient crop pollination even in areas of intensive human land use. Previous studies have found that native bees contribute to crop pollination at farms near natural habitat, but not in more intensively used areas (Kremen *et al.* 2002, 2004; Klein *et al.* 2003a,b, 2007; Ricketts 2004; Chacoff & Aizen 2006), where growers would need to use domesticated honey bees for pollination purposes. No such studies have previously been carried out in the Eastern USA, which is the region currently most affected by Colony Collapse Disorder. In a previous analysis of bee visitation to multiple vegetable crops in this region (Winfree *et al.* 2008, in press), we found that native bees are abundant on multiple crops. However, this study did not include any measures of actual pollination. Here, we propose two untested hypotheses that could potentially explain why our findings differ from previous work.

First, native bees may be more likely to use human-altered habitats in temperate forested ecosystems such as the one we studied, when compared to the tropical, subtropical and chaparral ecosystems studied by most other workers. Although temperate woodlands can offer abundant floral resources at certain times of year (mainly early spring), they



**Figure 5** Single linear regressions ( $\pm$  95% CI) showing the lack of relationship between native bee pollination and land use. Each point represents one farm. Simulation estimates for median pollen grains per flower per day delivered to watermelon by all native bee species combined, and (a) distance to nearest woodland fragment ( $r^2 = 0.01$ , d.f. = 22,  $P = 0.59$ ) and (b) proportion woodland cover in the surrounding landscape at a 2 km radius ( $r^2 = 0.00$ , d.f. = 22,  $P = 0.86$ ).

provide few flowers once the tree canopy closes. Klemm (1996) proposed that many bees native to central Europe originally relied on natural disturbances such as flood plains, and are now dependent on human-disturbed habitats. In another central European study, Steffan-Dewenter *et al.* (2002) defined suitable bee habitat as including semi-natural areas such as fallow agriculture, gardens and grasslands, but not native woodlands. In southern New Jersey, native bee abundance and species richness is greater in agricultural and suburban areas than in native woodlands (Winfrey *et al.* 2007). Furthermore, in our system, disturbed habitats (including the farms themselves) offer floral resources in seasons when bloom is scarce in native woodlands. This complementarity in floral phenology between natural and human-dominated areas may allow such landscapes to support many bees (Kremen *et al.* 2007).

A second and not mutually exclusive possibility is that high dispersion of natural habitat patches throughout our study system might support high biodiversity even where the overall proportion of natural habitat is low. Even though natural habitat cover at a 2 km radius falls as low as 8%, none of our data collection transects was more than 0.3 km from a patch of natural habitat, which is within the foraging range of all bee species in our study system (Greenleaf *et al.* 2007). In addition, our entire study system meets a published definition of 'heterogeneous agricultural landscapes' as those containing  $\geq 20\%$  non-crop habitat (Tscharntke *et al.* 2005). Such heterogeneity is a key factor promoting biodiversity in agricultural landscapes (Tscharntke *et al.* 2005; Rundlöf & Smith 2006). In contrast, previous studies of crop pollination by native bees report maximum distances of 0.9–6 km from the nearest natural habitat patch (Kremen *et al.* 2002; Klein *et al.* 2003a,b; Ricketts 2004; Chacoff & Aizen 2006). Both the floral phenology and the landscape heterogeneity hypotheses merit further study as possible mechanisms behind the provision of this ecosystem service.

Although our simulation results were broadly consistent with pollen counts from open-pollinated flowers in that both showed more than sufficient pollination at all farms studied and a larger role of native bees in pollination, the simulation predicted greater cumulative pollen deposition than that observed on open-pollinated flowers, and explained only 67% of the variance. We expect the variability and the lower values found for the open-pollinated flowers are due to reduced adhesion of additional pollen on stigmas already loaded with pollen, possibly combined with pollen removal from saturated stigmas during subsequent visits by bees. Although our study was not designed to document this process, detailed studies of another cucurbit species found that stigmas were saturated with pollen within 2 h of anthesis (pollen release), and stigmas harvested at the end of the day actually had less pollen than those harvested earlier (Winsor *et al.* 2000). In contrast, our simulation adds up per-visit pollen deposition values estimated from single-visit measurements to a virgin stigma over the course of the day, without accounting for reduced adhesion on already-pollinated stigmas.

An alternative explanation for why our simulation results exceed pollen counts on open-pollinated flowers is that bees stay on a flower for longer, and therefore deposit more pollen, on the virgin flowers used in single-visit experiments because nectar has accumulated on these flowers (Thomson 1986). Although we did not perform the experiments necessary to rule out this possibility, we believe it is unlikely to be an important explanation, because in this data set the duration of a bee's visit to a flower is unrelated to the amount of pollen deposited.

The simulation results are important because they permit separating the contributions of different pollinator taxa. In this way, we can assess the potential of each taxon to pollinate the watermelon crop fully should other taxa be eliminated (i.e. the insurance value of the various taxa). Which bee taxa actually pollinate a given flower by contributing the first 1400 grains of pollen that result in fruit production is yet another question, but not one which addresses the insurance value provided by multiple taxa. Our findings lead to predictions about the likely effects of Colony Collapse Disorder on agricultural production in our study region. If the agent(s) causing Colony Collapse Disorder do not affect native bees, as is suggested by ongoing studies finding no reduction in native bee abundance in two regions affected by Colony Collapse Disorder (R. Winfree and C. Kremen, unpublished data), then crop production in our study region should be buffered against pollination failure. Even if the agent(s) causing Colony Collapse Disorder in honey bees did affect native solitary and social bees, the large number of species involved in crop pollination in this region may still serve to buffer the impact, as long as species respond to the agent differentially (Elmqvist *et al.* 2003). At a minimum, our findings predict that crop production in this region of the USA will withstand the effects of Colony Collapse Disorder better than other regions such as California's Central Valley, where intensification of agriculture is linked to declining richness and abundance of native bee species (Larsen *et al.* 2005). More generally, our findings provide ground for cautious optimism about the sustainability of crop pollination in certain human-dominated ecosystems.

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## REFERENCES

- Casgrain, P. & Legendre, P. (2001). *The R Package for Multivariate and Spatial Analysis*, version 4.0.. Department of Biological Sciences, University of Montreal, Montreal, Canada.
- Chacoff, N.P. & Aizen, M.A. (2006). Edge effects on flower-visiting insects in grapefruit plantations bordering premontane subtropical forest. *J. Appl. Ecol.*, 43, 18–27.
- Committee on the Status of Pollinators in North America, National Research Council (2007). *Status of Pollinators in North America*. The National Academies Press, Washington, DC.
- Delaplane, K.S. & Mayer, D.F. (2000). *Crop Pollination by Bees*. CABI Publishing, New York, NY.
- Elmqvist, T., Folke, C., Nyström, M., Peterson, G., Bengtsson, J., Walker, B. *et al.* (2003). Response diversity, ecosystem change, and resilience. *Front. Ecol. Environ.*, 1, 488–494.
- Greenleaf, S.S. & Kremen, C. (2006). Wild bees enhance honey bees' pollination of hybrid sunflower. *Proc. Natl Acad. Sci. U.S.A.*, 103, 13890–13895.
- Greenleaf, S.S., Williams, N., Winfree, R. & Kremen, C. (2007). Bee foraging ranges and their relationship to body size. *Oecologia*, 153, 589–596.
- Holland, J.D., Bert, D.G. & Fahrig, L. (2004). Determining the spatial scale of species' response to habitat. *Bioscience*, 54, 227–233.
- Kercher, S.M., Frieswyk, C.B. & Zedler, J.B. (2003). Effects of sampling teams and estimation methods on the assessment of plant cover. *J. Veg. Sci.*, 14, 899–906.
- Klein, A.M., Steffan-Dewenter, I. & Tscharntke, T. (2003a). Fruit set of highland coffee increases with the diversity of pollinating bees. *Proc. R. Soc. Lond. Ser. B Biol. Sci.*, 270, 955–961.
- Klein, A.M., Steffan-Dewenter, I. & Tscharntke, T. (2003b). Pollination of *Coffea canephora* in relation to local and regional agroforestry management. *J. Appl. Ecol.*, 40, 837–845.
- Klein, A.M., Vaissière, B.E., Cane, J.H., Steffan-Dewenter, I., Cunningham, S.A., Kremen, C. *et al.* (2007). Importance of pollinators in changing landscapes for world crops. *Proc. R. Soc. Lond. Ser. B*, 274, 303–313.
- Klemm, M. (1996). Man-made bee habitats in the anthropogenous landscape of central Europe: substitutes for threatened or destroyed riverine habitats? In: *The Conservation of Bees* (eds Matheson, A., Buchmann, S.L., O'Toole, C., Westrich, P. & Williams, I.H.). Academic Press, London, UK, pp. 17–34.
- Kremen, C. (2005). Managing ecosystem services: what do we need to know? *Ecol. Lett.*, 8, 468–479.
- Kremen, C. & Ostfeld, R.S. (2005). A call to ecologists: measuring, analyzing, and managing ecosystem services. *Front. Ecol. Evol.*, 3, 540–548.
- Kremen, C., Williams, N.M. & Thorp, R.W. (2002). Crop pollination from native bees at risk from agricultural intensification. *Proc. Natl Acad. Sci. U.S.A.*, 99, 16812–16816.
- Kremen, C., Williams, N.M., Bugg, R.L., Fay, J.P. & Thorp, R.W. (2004). The area requirements of an ecosystem service: crop pollination by native bee communities in California. *Ecol. Lett.*, 7, 1109–1119.
- Kremen, C., Williams, N.M., Aizen, M.A., Gemmill-Herren, B., Leubhn, G., Minckley, R. *et al.* (2007). Pollination and other ecosystem services produced by mobile organisms: a conceptual framework for the effects of land use change. *Ecol. Lett.*, 10, 299–314.
- Larsen, T.H., Williams, N.W. & Kremen, C. (2005). Extinction order and altered community structure rapidly disrupt ecosystem functioning. *Ecol. Lett.*, 8, 538–547.
- Michener, C. (2000). *The Bees of the World*. Johns Hopkins University Press, Baltimore and London.
- Millennium Ecosystem Assessment (2005). *Ecosystems and Human Well-being: Synthesis*. Island Press, Washington, DC.

- Morandin, L.A. & Winston, M.L. (2005). Wild bee abundance and seed production in conventional, organic, and genetically modified canola. *Ecol. Appl.*, 15, 871–881.
- Morris, W. (2003). Which mutualists are most essential? In: *The Importance of Species: Perspectives on Expendability and Triage* (eds Karieva, P. & Levin, S.). Princeton University Press, Princeton, NJ, pp. 260–280.
- Morse, R.A. & Calderone, N.W. (2000). The value of honey bees as pollinators of U.S. crops in 2000. *Bee Cult.*, 128, 1–14.
- Nabhan, G.P. & Buchmann, S.L. (1997). Services provided by pollinators. In: *Nature's Services: Societal Dependence on Natural Ecosystems* (ed. Daily, G.C.). Island Press, Washington, DC, pp. 133–150.
- Naeem, S. (1998). Species redundancy and ecosystem reliability. *Conserv. Biol.*, 12, 39–45.
- Ricketts, T.H. (2004). Tropical forest fragments enhance pollinator activity in nearby coffee crops. *Conserv. Biol.*, 18, 1262–1271.
- Rundlöf, M. & Smith, H.G. (2006). The effect of organic farming on butterfly diversity depends on landscape context. *J. Appl. Ecol.*, 43, 1121–1127.
- Stanghellini, M. & Raybold, P. (2004). *Crop Profile for Honey Bees in New Jersey*. Rutgers University, New Brunswick, NJ, p. 29.
- Steffan-Dewenter, I., Münzenberg, U., Bürger, C., Thies, C. & Tscharntke, T. (2002). Scale-dependent effects of landscape context on three pollinator guilds. *Ecology*, 83, 1421–1432.
- Stokstad, E. (2007a). The case of the empty hives. *Science*, 316, 970–972.
- Stokstad, E. (2007b). Puzzling decline of U. S. bees linked to virus from Australia. *Science*, 317, 1304–1305.
- Thomson, J.D. (1986). Pollen transport and deposition by bumble bees in *Erythronium*: influences of floral nectar and bee grooming. *J. Ecol.*, 74, 329–341.
- Tscharntke, T., Klein, A.M., Kruess, A., Steffan-Dewenter, I. & Thies, C. (2005). Landscape perspectives on agricultural intensification and biodiversity – ecosystem service management. *Ecol. Lett.*, 8, 857–874.
- Vázquez, D.P., Morris, W.F. & Jordano, P. (2005). Interaction frequency as a surrogate for the total effect of animal mutualists on plants. *Ecol. Lett.*, 8, 1088–1094.
- Winfree, R., Dushoff, J., Crone, E., Schultz, C.B., Williams, N. & Kremen, C. (2005). Testing simple indices of habitat proximity. *Am. Nat.*, 165, 707–717.
- Winfree, R., Dushoff, J., Robinson, S.K. & Bengali, D. (2006). A Monte Carlo model for estimating the productivity of a generalist brood parasite across multiple host species. *Evol. Ecol. Res.*, 8, 213–236.
- Winfree, R., Griswold, T. & Kremen, C. (2007). Effect of human disturbance on bee communities in a forested ecosystem. *Conserv. Biol.*, 21, 213–223.
- Winfree, R., Williams, N.M., Gaines, H., Ascher, J. & Kremen, C. (2008, in press). Wild pollinators provide the majority of crop visitation across land use gradients in New Jersey and Pennsylvania. *J. Appl. Ecol.*
- Winsor, J.A., Peretz, S. & Stephenson, A.G. (2000). Pollen competition in a natural population of *Cucurbita foetidissima* (Cucurbitaceae). *Am. J. Bot.*, 87, 527–532.

### SUPPLEMENTARY MATERIAL

The following supplementary material is available for this article:

**Table S1** Pollination requirements for watermelon, estimated from the published literature.

**Table S2** Bee species recorded in the study.

This material is available as part of the online article from: <http://www.blackwell-synergy.com/doi/full/10.1111/j.1461-0248.2007.01110.x>.

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Supplementary Material Table S1: Pollination requirements for watermelon, estimated from data in the published literature.

Table S1: Pollination requirements for watermelon, estimated from data in the published literature. We used the mean across the two bee species (1400 grains per flower) as the pollination requirement for watermelon in our study. Only 50% of open-pollinated flowers set fruit even where open-pollinated flowers receive ample pollination (Stanghellini et al. 1997). Our measure of sufficient pollination is therefore that the median flower receives >1400 pollen grains.

Bee species	Number of bee visits needed for asymptotic seed set <sup>1</sup>	Number of pollen grains deposited per bee visit <sup>2</sup>	Estimated grains per flower for asymptotic seed set
<i>Bombus impatiens</i>	12	152	1819
<i>Apis mellifera</i>	18	55	995

<sup>1</sup>(Stanghellini et al. 1998)

<sup>2</sup> Mean of 960 samples (Stanghellini et al. 2002)

## References

- Stanghellini M.S., Ambrose J.T. & Schultheis J.R. (1997) The effects of honey bee and bumble bee pollination on fruit set and abortion of cucumber and watermelon. *American Bee Journal*, 137, 386-391
- Stanghellini M.S., Ambrose J.T. & Schultheis J.R. (1998) Seed production in watermelon: a comparison between two commercially available pollinators. *HortScience*, 33, 28-30
- Stanghellini M.S., Ambrose J.T. & Schultheis J.R. (2002) Honey bees and bumble bees on field-grown cucumber and watermelon. *Journal of Apicultural Research*, 41, 27-34

Supplementary Material Table S2: Bee species recorded in the study.

Table S2: The bee species included in each species group used in recording flower visitation rates. Field workers' error rate in assigning pinned specimens to species groups was <1%.

Bee species group	Included bee species
Bumble bees	<i>Bombus bimaculatus</i> , <i>Bombus fervidus</i> , <i>Bombus impatiens</i> , <i>Bombus perplexus</i> , <i>Bombus vagans</i> , <i>Xylocopa virginica</i>
Green bees	<i>Agapostemon sericeus</i> , <i>Agapostemon virescens</i> , <i>Augochlora pura</i> , <i>Augochlorella aurata</i> , <i>Augochloropsis metallica</i>
Large bees	<i>Halictus rubicundus</i> , <i>Lasioglossum coriaceum</i> , <i>Megachile brevis</i> , <i>Megachile mendica</i> , <i>Melissodes bimaculata</i> , <i>Peponapis pruinosa</i> , <i>Ptilothrix bombiformis</i>
Small bees	<i>Calliopsis andreniformis</i> , <i>Ceratina calcarata</i> or <i>dupla</i> <sup>1</sup> , <i>Ceratina strenua</i> , <i>Halictus confusus</i> , <i>Halictus ligatus</i> , <i>Hylaeus affinis</i> , <i>Hylaeus mesillae</i> , <i>Hylaeus modestus</i> , <i>Lasioglossum admirandum</i> , <i>Lasioglossum albipenne</i> , <i>Lasioglossum black sp. A</i> , <i>Lasioglossum bruneri</i> , <i>Lasioglossum cattellae</i> , <i>Lasioglossum cressoni</i> , <i>Lasioglossum illinoense</i> , <i>Lasioglossum imitatum</i> , <i>Lasioglossum laevissimum</i> , <i>Lasioglossum nymphaearum</i> , <i>Lasioglossum oblongum</i> , <i>Lasioglossum pectinatum</i> , <i>Lasioglossum pilosum</i> , <i>Lasioglossum platyparium</i> , <i>Lasioglossum rohweri</i> , <i>Lasioglossum tegulare</i> , <i>Lasioglossum</i>

*truncatum, Lasioglossum versatum, Lasioglossum zephyrum*

<sup>1</sup>Females of these two species could not be separated.