Wild bee pollinators provide the majority of crop visitation across land-use gradients in New Jersey and Pennsylvania, USA

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Summary

1. Concern about a global decline in wild pollinators has increased interest in how pollinators are affected by human land use, and how this, in turn, affects crop pollination.

2. We measured wild bee visitation to four summer vegetable crops, and investigated associations between flower visitation rates and land-use intensity at local and landscape scales. We studied 29 farms in New Jersey and Pennsylvania, USA. Over 2 years we recorded >7400 bee visits to crop flowers and identified 54 species of wild bees visiting crops.

3. Wild bees were the dominant flower visitors at three of the four crops studied; domesticated honeybees, *Apis mellifera* L., provided the remainder of visits.

4. Ordination of the two best studied crops showed that the wild bee species visiting tomato, *Solanum lycopersicum* L., were distinct from those visiting watermelon, *Citrullus lanatus* (Thunb.) Matsum. & Nakai.

5. Crop visitation by wild bees was not associated with organic farming, nor with natural habitat cover at either local or landscape scale.

6. *Synthesis and applications*. The extent of crop visitation by wild bees observed in this study is among the highest recorded. In contrast to previous studies of crop visitation by wild bees, we did not find negative effects of conventional farming or natural habitat loss. In our study system, organic and conventional farms differ little in field size, crop diversity and weedy flower diversity, unlike some systems where organic farms have smaller fields with greater crop and weed diversity. Such variables may be more important than organic vs. conventional farming practices. Second, small patches of natural habitat are dispersed throughout our entire study system, and this habitat heterogeneity may support high bee abundance even in landscapes with a low proportion of natural habitat overall. Our findings suggest that agri-environment schemes and similar programmes that work through local habitat restoration should target farms in intensively agricultural (homogeneous) landscapes to gain maximum conservation benefits.

Key-words: agroecosystems, biodiversity–ecosystem function, crop pollination, ecosystem services, forest fragmentation, landscape mosaic, organic farming

Introduction

Wild insects provide important services to agriculture, including pest control and pollination of crops (Tscharntke *et al*. 2005; Losey & Vaughan 2006). Agricultural landscapes, when managed appropriately, can in turn provide habitat for many

insect species (Tscharntke *et al*. 2005). However, insect biodiversity is threatened by increasing agricultural intensification, which includes the loss of natural and semi-natural habitats, extensive monoculture plantings, and increased pesticide and herbicide use (Krebs *et al*. 1999; Tscharntke *et al*. 2005). A better understanding of the benefits provided by insects, and of land management practices that support insect biodiversity, could provide for better cost–benefit analyses of land-use alternatives and help to make agricultural production more sustainable.

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Pollination is an important ecosystem service because crops accounting for 35% of the global plant-based food supply require animal-mediated pollination (Klein *et al.* 2007). Bees (Hymenoptera: Anthophila) are the most important crop pollinators. Most farmers rely on managed bees, primarily the honeybee, to provide crop pollination. Despite the honeybee's effectiveness as a pollinator for many crops, the risks associated with reliance on a single, managed pollinator species have become evident over the past 15 years as North American honeybee populations have declined due to the parasitic mite *Varroa destructor* Anderson & Trueman, Colony Collapse Disorder (Stokstad 2007), and other diseases (National Research Council 2006). Many wild bee species contribute to pollination of such crops as coffee (*Coffea* spp., Klein, Steffan-Dewenter & Tscharntke 2003b); watermelon (*Citrullus lanatus* (Thunb.) Matsum. & Nakai, Kremen, Williams & Thorp 2002); tomato (*Solanum lycopersicum* L., Greenleaf & Kremen 2006a); blueberry (*Vaccinium* spp., Cane 1997); sunflower (*Helianthus annuus* L., Greenleaf & Kremen 2006b); canola (*Brassica* spp., Morandin & Winston 2005), providing a supplement to honeybee pollination as well as an insurance policy against honeybee declines.

Concern about a global decline in pollinators (Buchmann & Nabhan 1996; Kearns, Inouye & Waser 1998; Biesmeijer *et al.* 2006), in combination with the recognition that few large-scale data sets on pollinator populations exist (Ghazoul 2005), has led to increased interest in how wild pollinators are affected by human activity. Most previous studies suggest that bees, the main pollinator taxon in most ecosystems (Axelrod 1960), are sensitive to the loss of natural and seminatural habitats (Kremen & Chaplin-Kramer 2007). For example, bee abundance and/or species richness decreases with increasing isolation from natural habitats in such ecosystems as subtropical dry forest (Aizen & Feinsinger 1994), chaparral (Kremen, Williams & Thorp 2002), tropical moist forest (Klein, Steffan-Dewenter & Tscharntke 2003a, 2003b; Ricketts 2004) and subtropical premontane forest (Chacoff & Aizen 2006). However, in some situations wild bees are more abundant and/or species-rich in human-disturbed areas (Eltz *et al.* 2002; Klein *et al.* 2002; Westphal, Steffan-Dewenter & Tscharntke 2003; Winfree, Griswold & Kremen 2007a).

In this study we investigated wild bees visiting flowers of summer vegetable crops in a temperate deciduous forest ecosystem. We focused on three questions: (1) To what extent are crops visited by wild, predominantly native bees compared with managed honeybees? (2) Are different crops visited by different wild bee species? (3) Is the frequency of wild bee visits to crops associated with land-use intensity at the local and/or landscape scales? We defined local land use as farm management (conventional farming vs. the less intensive organic strategy) and distance to the nearest patch of natural habitat, and landscape-scale land use as the proportion of natural habitat (woodland) remaining at various radii (0·5–3 km) around each farm. We expected that crops with different floral structures would be visited by different wild bee species, which are known to have species-specific floral preferences (Wcislo & Cane 1996), and that visitation by wild bees would be positively associated with both organic farming and the extent of natural habitat near the farm. Our outcome variable is frequency of bee visits to crop flowers, which is a proxy for the pollination services delivered (Vázquez, Morris & Jordano 2005).

Materials and Methods

STUDY SYSTEM AND DESIGN

Our study system was a 90 × 60-km area of central New Jersey and eastern Pennsylvania, USA, where the native habitat is temperate deciduous forest. In 2004 we studied 22 farms, of which six were no-spray (growers do not spray either pesticides or herbicides) or US Department of Agriculture certified organic, and 16 were conventional. In 2005 we used 16 of the previously selected farms and added seven new farms to make a total of 23, of which seven were no-spray or organic and 16 were conventional. Not all crops were grown at each farm, so sample sizes varied by crop (Table 1). The study was designed to minimize spatial autocorrelation and colinearity between local- and landscape-scale variables in several ways. Farms of a given management type (organic or conventional) and landscape setting (wooded or not) were interspersed throughout the study area (Fig. 1), and farms were selected so that these local- and landscape-scale variables were uncorrelated. Farms were also

Table 1. The six data sets analysed, with the radius (scale) used in analyses of landscape cover, and the range of variation in the proportion of woodland at that scale

Crop	Year	Number of farms	Radius with highest r^2 (m)	Range of variation in proportion of woodland (%)
Watermelon	2005	23	2000	8–60
Wood-nesting (7 species)			1000	5–53
Eusocial (22 species)			3000*	10–64
Solitary (18 species)			1000	5–53
Tomato	2005	13	500	3–38
Watermelon	2004	12	2000	8–59
Tomato	2004	17	500	3–42
Muskmelon	2004	14	1000	5–51
Pepper	2004	22	500	3–59

Separate analyses were done for particular species groups in the 2005 watermelon data set.
*Because 3000 m was the largest radius we examined, we cannot be sure that eusocial bees did not have a true maximum at a larger radius.
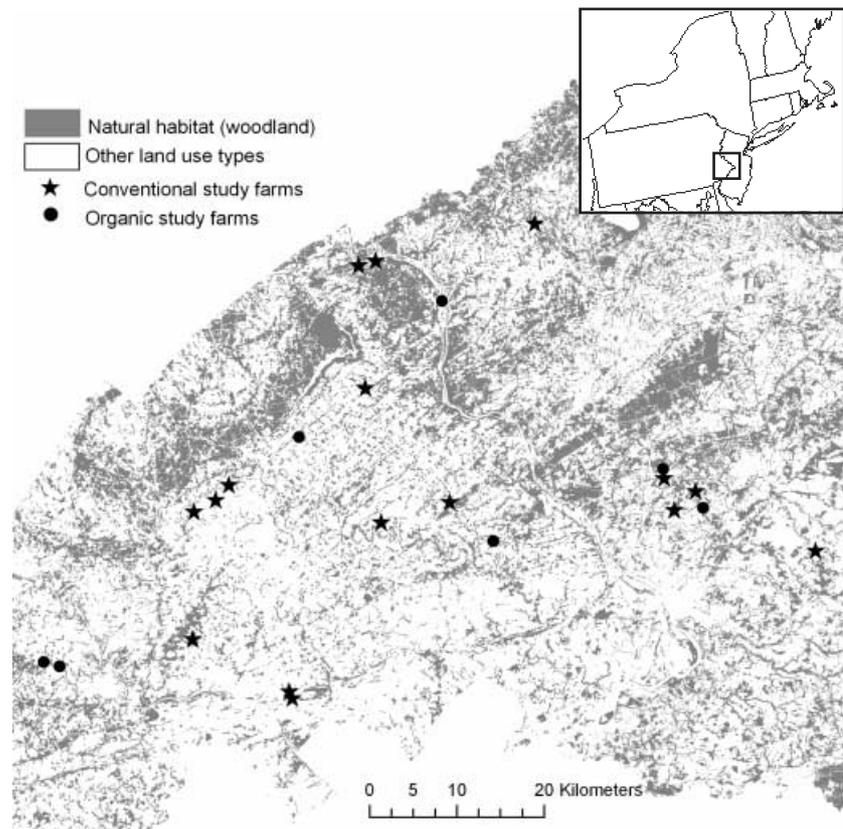
Fig. 1. Map of the study area with natural woodland habitat shaded grey and the study farms used in 2005 indicated.

at least 1 km apart, which is beyond the typical foraging movement distance of all but the largest bees in the study (Greenleaf *et al.* 2007).

In 2004 we surveyed pollinator visitation to four crops: tomato, bell pepper (*Capsicum annuum* L.), muskmelon (*Cucumis melo* L.) and watermelon. In 2005, we focused on two crops, cherry tomatoes (including plum and grape varieties; hereafter cherry tomato) and watermelon, and collected more detailed data on each. Tomato and pepper can self-pollinate without insect vectors; however, fruit number and quality increase with bee pollination (Delaplane & Mayer 2000; Greenleaf & Kremen 2006a). Tomato flowers do not produce nectar, and the anthers require sonication for full release of pollen. Sonication behaviour is performed by many wild bees, but not by honeybees; we therefore expected tomato to be visited predominantly by wild bees. Pepper produces nectar and pollen that does not require sonication, but is relatively unattractive to bees (Delaplane & Mayer 2000). Watermelon and muskmelon require insect vectors to produce fruit because they have unisexual flowers (watermelon) or functionally unisexual flowers (muskmelon; Delaplane & Mayer 2000). Flowers produce abundant nectar (females) and easily accessible pollen as well as nectar (males), and are attractive to bees. Flowers are active for only one day, opening at daybreak and closing by early afternoon. We therefore collected our data in the morning.

Of the farmers in our study, 64% use hived honeybees for crop pollination. Feral honeybees were virtually eliminated in our study region during the 1990s by *Varroa* mites and other problems (Paul Raybold, New Jersey State Apiarist, personal communication). Therefore most honeybees recorded in our study would have been managed. We define 'wild bees' as either native to our study area, or non-native but unmanaged. The latter category accounted for only two species and 0·002% of specimens collected.

DATA COLLECTION

Our data collection protocol in 2004 was a simplified version of that used in 2005, so we first describe the latter. We established a 50-m transect of crop row where all data were collected, with transects beginning at the edge of the farm field in order to standardize edge effects. We measured pollinator visitation rate to flowers during 45-s scans of flowers at 40 equally spaced points along the transect. We counted and then observed visits to as many flowers as we could view simultaneously within an approximately 1 × 1-m area. Visitation rate data are therefore in units of bee visits per flower per time. We censused each transect at standard times of day, beginning at 8 : 30 and 10 : 30 h for tomato and 8 : 00, 9 : 30 and 11 : 00 h for watermelon. After collecting the visitation rate data, we netted bees from crop flowers for 30 min.

We measured two covariates related to floral resource availability: the row length of flowering, bee-attractive crops in the farm field, and the abundance and species richness of weedy flowers growing between the crop rows and in the fallow field margins. For the latter, we used the line intercept method (Kercher, Frieswyk & Zedler 2003).

Data were collected only on days that were sunny, partly cloudy or bright overcast, with wind speeds of <2·5 m s^{-1}. We collected data at each farm when the target crop was at or near its peak period of bloom, as determined by repeated site visits prior to data collection. Cherry tomato data were collected between 30 June and 14 July, and watermelon data between 5 July and 10 August. We surveyed cherry tomato once and watermelon twice at each farm.

In 2004 each crop at each farm was visited only once, and flower visitation rate data were collected once between 8 : 30 and 12 : 00 h. Weedy flower abundance was assessed visually on a scale of 1–5. All data were collected in July 2004.

We compiled information on nesting specialization and sociality of bees from the published literature (Hurd 1979; Michener 2000)

and used this for analyses of trait-specific responses of crop pollinators. We defined wood-nesting bees as those species obligatorily nesting in rotting wood, or using cavities in wood or twigs, but not those nesting in soft-pithed stems. We considered both primitively eusocial and advanced eusocial species to be 'eusocial', and solitary and communal species to be 'solitary'.

GIS ANALYSES

We mapped the centre of each data collection transect, and the perimeter of each farm field, with a Trimble GeoExplorer Global Positioning System (GPS; Trimble Navigation, Sunnyvale, CA, USA) corrected to ±10 m accuracy with GPS PATHFINDER OFFICE (ver. 2·9, Touch Vision, Cypress, CA, USA). We measured crop field size as the boundary of the continuous tilled area. (Geographical Information System) GIS land-cover data for New Jersey were provided by the New Jersey State Department of Environmental Protection, and were based on 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 based on aerial photographs taken in 2000 and subsequently classified to 27 land-cover types. We used the dominant native habitat type, woodland, as the focus of our analyses.

We analysed landscape cover as the proportion of woodland at various radii surrounding each site (see 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 species richness (Winfree *et al.* 2005). We used ARCGIS ver. 9·0 (Environmental Systems Research Institute, Redlands, CA, USA) to determine the proportion of the area surrounding each farm that consisted of woodland, and to measure the linear distance from the centre of our data collection transect to the nearest patch of woodland.

PRELIMINARY ANALYSES

We tested for, and found, no spatial autocorrelation among sites at any scale in terms of either wild bee visitation rate or bee species richness (Moran's *I*, all *P* = 0·07, R PACKAGE; http://www.bio.umontreal.ca/Casgrain/en/labo/R/v4/index.html; we used our larger 2005 data

sets for this analysis). To identify the scale at which surrounding land cover had the most explanatory power, we regressed bee visitation rate against the proportion of woodland surrounding study sites at radii of 500, 1000, 1500, 2000, 2500 and 3000 m. We then compared the resulting r^2 values, and used the scale with the highest r^2 value in all subsequent analyses (Holland, Bert & Fahrig 2004). We did this separately for each crop, because the crops can have distinct pollinator communities (see Results) that may respond to the surrounding landscape at different scales (Steffan-Dewenter *et al.* 2002), and because different sites were used for different crops and years. For watermelon and tomato in 2004, we used the scale of analysis determined for the larger and more detailed 2005 data sets (Table 1). We repeated this analysis using the 2005 watermelon data set of collected specimens to determine the scale of analysis for the wood-nesting, eusocial and solitary bee species (Table 1).

STATISTICAL ANALYSES

To compare flower visitation rates (bee visits per flower per time) on a given crop between wild bees and honeybees, we used paired *t*-tests, or when normality assumptions were not met, Wilcoxon sign-rank tests.

We compared differences in species composition of the wild bee communities visiting watermelon and tomato using non-metric multidimensional scaling (NMS; PC-ORD ver. 4, MjM Software, Glendeden Beach, OR, USA). Sampling sites were ordinated using the relative Sørensen index, which is based on the proportional rather than the absolute abundance of each species. We used this metric to avoid separating the two crops on the basis of absolute bee abundance, because watermelon is known to be more attractive than tomato to bees. For NMS analysis we used only the 14 farms for which we had data from both watermelon and tomato (2005 data set), so as to control for differences among farms and isolate the effect of crop type. We used only the watermelon data from the first day we visited each farm in order to equalize sampling effort on the two crops. To assess the significance of the difference between the two crops, we used multiresponse permutation procedures (MRPP) for blocked (paired) data in PC-ORD.

To assess the strength of local- vs. landscape-scale environmental variables in predicting bee visitation rate and species richness at crops, we defined six *a priori* general linear statistical models, based on local- and landscape-scale factors that might influence wild bee

Table 2. Statistical models compared to determine the relative importance of local- and landscape-scale variables in predicting wild bee visitation rate and species richness at crop flowers

Models for 2005 data sets	Included variables
Local floral resources	Weedy flower density (cm per 300 m); weedy flower species (number of species per 300 m); flowering crop density (m per 1000 m^2); flowering crop 'species' (number of species per 1000 m^2)
Local farm management	Organic/conventional
Local isolation from natural habitat	Distance from transect centre to nearest woodland (m)
Local, all variables	Weedy flower density, weedy flower species, flowering crop density, flowering crop 'species'; organic/conventional; distance from transect centre to nearest woodland
Landscape cover by natural habitat	Proportion of woodland at most explanatory radius (Table 1)
All local and landscape variables	Weedy flower density, weedy flower species, flowering crop density; flowering crop 'species'; organic/conventional; distance from transect centre to nearest woodland; proportion of woodland

Models for 2004 data sets	Included variables
Local	Weedy flower abundance (ranked 1–5), organic/conventional*
Landscape	Proportion of woodland at most explanatory radius (Table 1)
Local and landscape	Weedy flower abundance, organic/conventional*, proportion of woodland

*This variable was not used for the muskmelon or watermelon data sets, which included only one and two organic farms, respectively.

communities (Table 2). For the 2004 data sets, we used a reduced set of models (Table 2). We compared among these models using the adjusted r^2 values from regression, ANOVA and ANCOVA (JMP ver. 5.1, SAS Institute, Cary, NC, USA). This least-squares method of model selection will produce the same results as Akaike's information criterion model selection, provided model errors are normally distributed (Hilborn & Mangel 1997), which was the case for our data. To improve normality and homoscedasticity, we used the following transformations of the outcome variables: for all data sets except watermelon (2004 and 2005), flower visitation rate was arcsin square-root transformed; counts of wood-nesting bees were transformed as $\ln(x + 1)$; and counts of solitary bees were transformed as square root $(x + 0.5)$ (Sokal & Rohlf 1995).

To analyse the 2005 watermelon data set, for which we made repeat visits to each farm, we used 'robust cluster' regression (STATA ver. 7.0, Stata Corp., College Station, TX, USA). Robust clustering is a bootstrap procedure for sampling from data that are not independent within a cluster (in our case, sample dates within a farm), but that are independent across clusters (in our case, across farms).

For the analyses of how particular species groups that share a life-history trait respond to land use, our measure of bee abundance was the number of bee specimens collected rather than visitation rate, because these analyses require data resolved to the species level. We limited analysis to the 2005 watermelon data set, which contained 70% of the specimens collected. For eusocial and solitary bee species, we used the six models in Table 2. For wood-nesting bee species, we investigated only associations with the two predictor variables related to woodland (distance to nearest woodland patch; proportion of woodland in the surrounding landscape), which are the main variables of interest for this group. We were unable to investigate the full set of models with this data set that had many zero values and did not meet the models' statistical assumptions.

Results

Over the 2 years of the study, we observed 7434 bee visits (4592 by wild bees and 2842 by honeybees) to 32 171 crop flowers, and collected 1738 wild bee specimens, which were identified to 54 species (see Appendix S1 in Supplementary Material).

In 2004 we found that tomato and pepper were visited significantly more frequently by wild bees than by honeybees (tomato, Wilcoxon sign-rank test with $n = 17$, $W = 0$, $P < 0.001$; pepper, paired t-test with df $= 21$, $t = -4.22$, $P < 0.001$), whereas for watermelon and muskmelon, wild bee and honeybee visitation rates did not differ significantly (watermelon, paired t-test with df $= 11$, $t = -0.02$, $P = 0.98$; muskmelon, Wilcoxon sign-rank test with $n = 14$, $W = 28$, $P > 0.10$). In our more extensive data sets from 2005, tomato and watermelon were both visited significantly more often by wild bees (tomato, Wilcoxon sign-rank test with $n = 13$, $W = 0$, $P < 0.001$; watermelon, paired t-test with df $= 22$, $t = -2.45$, $P = 0.02$; Fig. 2; Winfree *et al*. 2007b). Crop flower visitation rates by honeybees and wild bees were not negatively correlated, suggesting that competitive exclusion did not occur.

The wild bee communities visiting watermelon and tomato were significantly different (Fig. 3; MRPP test, $A = 0.09$, $P = 0.004$). The r^2 value for the NMS ordination, which measures the proportion of variance explained by the rank correlation between the true pairwise similarity values (in our case, the relative Sørensen index) and the physical distances between sites on the ordination plot, was 0.76.

Neither local- nor landscape-scale land-use variables strongly predicted wild bee visitation rate or species richness at crops (Table 3). Even after selecting the best model for each data set, only two of the eight models were statistically significant at the $P = 0.05$ level, and none of the models was significant after adjusting the critical P value for multiple comparisons (adjusted $P = 0.006$, Dunn-Šidák correction). Similarly, no individual variables were strongly or consistently predictive (Table 3).

Table 3. The most explanatory model for each data set, and the slope coefficient B (or t for categorical variables), and SE (or P value for categorical variables) of each included variable

Data set	Most explanatory model†	Whole model r^2	Whole model P	Model variables	B**	SE***
Watermelon 2005	Visitation: local model 1	0.19	0.02	Weedy flower density	0.0018	0.0009
				Weedy flower species	0.0106	0.0122
				Flowering crop density	0.0000	0.0002
				Flowering crop species	0.0147	0.0139
	Species richness: landscape model 5	0.05	0.12	Percentage of woodland 2000 m	−0.0600	0.0371
Tomato 2005	Visitation: local model 2	0.06	0.42	Organic	0.84‡	0.42§
	Species richness: local model 3	0.16	0.18	Distance to woodland	0.0060	0.0041
Watermelon 2004	Visitation: landscape model 1	0.04	0.51	Percentage of woodland 2000 m	0.0015	0.0022
Tomato 2004	Visitation: local model 1	0.12	0.42	Weedy flower abundance	−0.3281	1.2122
				Organic	1.34‡	0.20§
Muskmelon 2004	Visitation: local and landscape model 3	0.49	0.03	Weedy flower abundance	2.2794	1.6295
				Percentage of woodland 1000 m	0.2802	0.1214
Pepper 2004	Visitation: local and landscape model 3	0.32	0.07	Weedy flower abundance	−0.2458	1.8087
				Percentage of woodland 500 m	0.2056	0.1536
				Organic	1.73‡	0.10§

†The 2004 and 2005 data sets use different models (see Table 2).
‡t is reported for categorical variables.
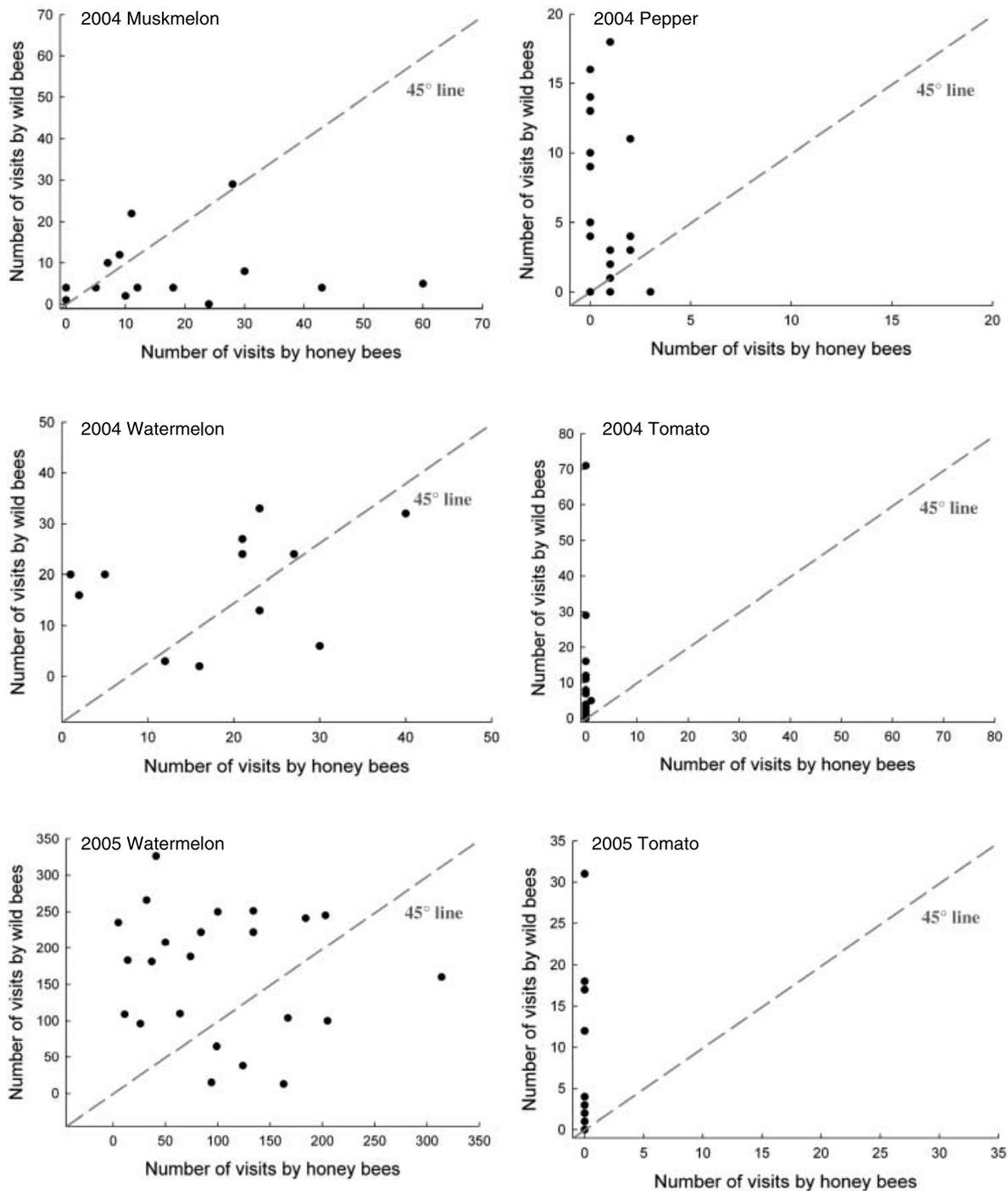§P is reported for categorical variables.

Fig. 2. Total number of visits to crop flowers by honeybees vs. wild bees. Each point is a study farm. Points above the 45° line indicate that wild bee visitation exceeded honeybee visitation.

The abundance of eusocial bees showed little association with land-use variables. The best model was number six (Table 2; whole model $r^2 = 0.06$, $P = 0.13$), which included only the proportion of woodland cover in the surrounding landscape. The abundance of solitary bees showed little association with land-use variables, but was positively associated with the abundance of weedy flowers in the farm field. The best model was number 1 (Table 2; whole model $r^2 = 0.20$,

$P = 0.01$), and the model's overall significance was driven by the variable weedy flower abundance ($t = 3.11$, $P = 0.005$). For wood-nesting bees, we examined only the two variables related to woodland cover. The abundance of wood-nesting bees was associated with neither the distance to the nearest woodland patch ($t = -1.39$, $P = 0.18$) nor the proportion of woodland in the surrounding landscape at a 1000 m radius ($t = 0.42$, $P = 0.68$).
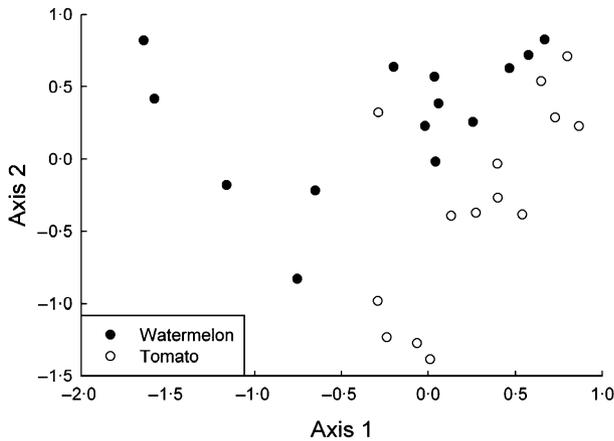
Fig. 3. Non-metric multidimensional scaling ordination of study farms and crops according to bee species composition. The ordination is based on the relative Sørensen index, which separates sites according to proportional rather than absolute species composition. Cumulative $r^2 = 0.76$, stress = 21.8, instability = 0.005.

Discussion

HUMAN LAND USE AND WILD BEE VISITATION TO CROPS

Contrary to our expectations, we found no strong associations between land-use intensity (at either local or landscape scale) and wild bee visitation to crops (Table 3). The best models were statistically significant for only two of our eight data sets, and none was significant after correcting for multiple comparisons.

Natural history traits such as sociality and nesting requirements can determine how bees respond to land use (Klein, Steffan-Dewenter & Tscharntke 2003a; Steffan-Dewenter *et al.* 2006), and variation in traits among species could lead to findings of no significant effect for the bee community as a whole. However, our analyses by natural history trait revealed only one pattern not found at the community scale: solitary species were positively associated with the abundance of weedy flowers in the farm field. Even obligatorily wood-nesting bees did not have strong associations with woodland cover at either the local or the landscape scales.

Previous studies of crop visitation by wild pollinators have found negative effects of human land use at the local and/or landscape scale (Klein *et al.* 2007; Kremen & Chaplin-Kramer 2007). Why then did land-use intensity have such weak effects in our study? We suggest four possible reasons, which are not mutually exclusive. First, we considered the possibility that we were unable to detect the true effects of human disturbance because our data sets were too small and/or variable, especially given the known variability of wild bee populations (Williams, Minckley & Silveira 2001). This may have been the case for our smaller data sets from 2004. However, the statistical models for the more extensive 2005 data sets showed even less association between wild bees and land use than those from 2004. In particular, our 2005

watermelon data set included 23 sites, 3828 wild bee visits to 15 888 watermelon flowers, and 1221 collected specimens, yet all variables relating to land-use intensity were highly non-significant. In contrast, many studies finding significant effects of land use on wild bees in other systems had smaller or similar sample sizes, e.g. 104 wild bee visits to grapefruit in Argentina (Chacoff & Aizen 2006); 615 wild bee visits to coffee in Costa Rica (Ricketts 2004); and 3349 wild bee visits to watermelon in California (Kremen, Williams & Thorp 2002; Kremen *et al.* 2004). Furthermore, for our 2005 watermelon data set we considered the range of values for the number of wild bee visits per flower per day that were included within the 95% confidence intervals for the slope in single regressions against each of our metrics of woodland cover (this approach is preferable to power analysis; Colegrave & Ruxton 2005). Across the gradient, the lower 95% CI prediction was 38–108 visits per flower per day (for proportion woodland) or 65–109 (for distance to woodland), both of which are more than the number of visits required for full fruit set (10–40 visits; R.W., unpublished data). This means that, even when we consider the range of possible slopes that might be consistent with our data, wild bees provide sufficient visitation to supply plants with crop pollination services across the entire land-use gradient.

Second, we may have found few differences between organic and conventional farm management because, in our system, many of the features often associated with organic farming (Hole *et al.* 2005) are common to both management categories. Organic and conventional farms did not differ significantly in farm field size (mean ± SD for organic 4789 ± 4475 m^2, conventional 6525 ± 4048 m^2; *t*-test, $t = 0.92$, $P = 0.37$), number of crops grown (organic 2.0 ± 2.4 different crops per 1000 m^2, conventional 0.7 ± 0.4 per 1000 m^2; Wilcoxon test, $\chi^2 = 1.0$, $P = 0.32$), weedy flower density (organic 68 ± 80 cm flowers per 600 cm, conventional 41 ± 35 cm flowers per 600 cm; Wilcoxon test, $\chi^2 = 0.45$, $P = 0.50$), or the density of weedy flower species (organic 6.0 ± 2.6 species per 600 cm, conventional 6.6 ± 2.4 species per 600 cm; *t*-test, $t = 0.50$, $P = 0.62$). Synthetic pesticide, herbicide and fertilizers are used only on the conventional farms, and some of the synthetic pesticides used in our area are known to be highly toxic to bees (e.g. malathion and permethrin). However, organic farms are also permitted to use certain non-synthetic pesticides. Overall, our findings are consistent with the suggestion of Benton, Vickery & Wilson (2003) that the local habitat heterogeneity resulting from factors such as weediness and field size may be more important than organic farming *per se* in supporting biodiversity. Our results are also consistent with previous findings that farm management exerts a stronger effect on insect diversity in homogeneous landscapes (Tscharntke *et al.* 2005; Rundlöf & Smith 2006), whereas our landscapes were heterogeneous.

Third, the phenology of floral resources in our study system may be complementary between woodlands and human-disturbed habitats (Heinrich 1976). In our study system, flowers and pollinators are abundant in spring woodlands, but by the time the forest canopy closes in June,

there is little bloom and few pollinators (R.W., unpublished data). In contrast, by June many species are flowering in agricultural areas, old fields, and gardens, and such habitats can continue to provide floral resources through the autumn. Our data set was dominated by bee species with long flight seasons [e.g. *Bombus*, *Lasioglossum* (*Dialictus*), *Halictus*, *Ceratina*], which could take advantage of this complementarity over time. Several other studies in temperate forest ecosystems have also found that although forests support certain bee species, they support lower bee densities than human-disturbed habitats (Banaszak 1992, 1996; Klemm 1996; Steffan-Dewenter *et al*. 2002; Winfree *et al.* 2007a).

Fourth, high dispersion of natural habitat fragments and high habitat heterogeneity throughout our study system may make it better for many bee species. Habitat heterogeneity is a key factor promoting biodiversity in agricultural landscapes (Tscharntke *et al*. 2005; Rundlöf & Smith 2006). Bees may benefit from habitat heterogeneity because their foraging, nesting and overwintering resources are often located in different habitat types (Westrich 1996). One indication of high heterogeneity in our study system is the large range of variation in terms of the proportion of woodland cover in the landscape surrounding each farm at a 2 km radius (8–60%; all metrics were calculated for our 2005 watermelon data set), compared with the small range of variation in distance to the nearest patch of woodland (18–343 m). Furthermore, these two measures are uncorrelated (Pearson's $r = -0.28$, $P = 0.19$). Thus a farm site could have very low proportional woodland in the surrounding landscape, but still have a patch of woodland within tens of metres of the farm site. Our system contrasts with California's Central Valley, where several studies finding a negative effect of habitat loss on bees have been carried out (Kremen, Williams & Thorp 2002; Kremen *et al*. 2004; Greenleaf & Kremen 2006a, 2006b). In California, the range of variation in the proportion of natural habitat in the surrounding landscape is similar to ours (0–62%), but the distance to the nearest natural habitat patch also varies greatly (35–5980 m; C.K., unpublished data), and is highly negatively correlated with landscape cover (Spearman's $\rho = -0.93$, $P < 0.0001$). This comparison suggests that there is local-scale heterogeneity in the New Jersey/Pennsylvania system across the entire landscape gradient, whereas in the California system local-scale heterogeneity is found only in the landscapes with most natural habitat.

Two other measures related to heterogeneity can be contrasted between our system and other studies that found negative effects of human land use on bees. In the work of Morandin & Winston (2005), crop field sizes were at least two orders of magnitude larger than those in our study; in studies that reported the maximum distance to the nearest patch of natural habitat, these distances ranged from 900 to 1600 m (Klein, Steffan-Dewenter & Tscharntke 2003a, 2003b; Ricketts 2004; Chacoff & Aizen 2006), compared with 318 m in our study.

Habitat heterogeneity in our system can also be compared with studies relating landscape-scale heterogeneity to biodiversity of other taxa in agricultural systems. In a study of butterflies, 'heterogeneous' agricultural landscapes were defined as those for which pasture constitutes a large proportion (on average 19%) of all agricultural lands (Rundlöf & Smith 2006). In our system, pasture constitutes 22% of all agricultural lands (USDA-NASS 2004). Furthermore, in our system hay fields constitute 44% of all non-pasture croplands (USDA-NASS 2004). Heterogeneity is further added to our system by suburban/urban development, which ranged from 11 to 73% at a 2-km radius. Other studies have found suburban/urban areas to support diverse bee faunas (Cane *et al*. 2006; Winfree *et al*. 2007a). Another definition that has been used in the published literature is that complex or heterogeneous agricultural landscapes are those containing ≥20% non-crop habitat (Tscharntke *et al*. 2005). Our entire study system meets this criterion, because the maximum proportion of agriculture was 66%.

CROP VISITATION BY MANAGED VS. UNMANAGED BEES

Most of the pollinator visitation to summer vegetable crops in our study region is by wild bee species. This is a striking finding from a farm management perspective, because most of the farmers in our region rent honeybees to pollinate their crops, and few are aware of the pollination provided by wild species.

Our study contributes to the growing literature demonstrating the importance of crop pollination by wild bees (Kremen & Chaplin-Kramer 2007), and is notable for finding that wild, native bees provide more visitation than managed or feral *Apis mellifera*, being responsible for 62% of the flower visits over the entire study system. Previous studies of canola (Morandin & Winston 2005) and coffee in Indonesia (Klein, Steffan-Dewenter & Tscharntke 2003b, 2003a) found that wild bees (which include wild, native *Apis* species for coffee) contributed >98% of the flower visits. All other studies have found that wild bees contribute a smaller proportion of visits than we found, when summed over all sites in the system (although particular sites can have higher visitation than the means presented here). Wild bees accounted for 59% of visits to coffee in Costa Rica (Ricketts 2004); 51% of visits to longan in Australia (Blanche, Ludwig & Cunningham 2006); about 37% (Heard & Exley 1994) or 0% (Blanche, Ludwig & Cunningham 2006) of visits to macadamia in Australia; 34% of visits to watermelon in California (Kremen, Williams & Thorp 2002; Kremen *et al*. 2004); 28% of visits to sunflower (Greenleaf & Kremen 2006b) in California; 2–30% of visits to a variety of crops in Poland (Banaszak 1996); and 3% of visits to grapefruit in Argentina (Chacoff & Aizen 2006). Although flower visitation rate is not equivalent to pollination, which also depends on per-visit pollen deposition, visitation is the most important predictor of actual pollination (Vázquez, Morris & Jordano 2005).

Lastly, the wild bee communities visiting watermelon and tomato crops were distinct (Fig. 3), even when we controlled for farm and for the differential attractiveness of the two crops. This result lends credence to the argument that conservation of diverse communities is necessary in order to retain the full range of ecosystem services (Tilman 1999).

CONCLUSIONS AND MANAGEMENT RECOMMENDATIONS

In contrast to previous studies of crop pollination by wild bees, in our system neither local- nor landscape-scale land use affected wild bee visit frequency to crop flowers. Organic farming was not associated with wild bee diversity or abundance, but in our system organic and conventional farming are not distinct in terms of field size, crop diversity or the abundance of flowering weeds. Our study therefore supports the hypothesis that these farm-site characteristics are more important than organic farming *per se* (Benton, Vickery & Wilson 2003). Our entire study system has high habitat heterogeneity compared with some other study systems, where negative effects of human land use on crop visitation by wild bees have been found. This might explain why wild bees are abundant and diverse, even in areas with a low proportion of natural habitat. It may also explain the weak effect of organic farm management (Tscharntke *et al*. 2005; Rundlöf & Smith 2006).

Currently, there is debate over the most effective way to restore biodiversity in agricultural landscapes (Kleijn *et al*. 2006). Agri-environment schemes and similar programmes, such as those administered by the US Department of Agriculture, cost nearly 4 billion annually in Europe and North America (Donald & Evans 2006). Our findings suggest that restoration of habitat heterogeneity is important and should remain a goal of such programmes. Our findings also suggest that such programmes should target intensively used, homogeneous landscapes for restoration, given that heterogeneous landscapes already appear to support diverse pollinators. Maintaining such landscape heterogeneity is also important to prevent them from crossing thresholds past which they no longer support this critical ecosystem service.

The bee communities we found visiting crops were dominated by species with long flight seasons, which need floral resources spanning the entire growing season. Such resources may be provided by the habitat heterogeneity in our system. In other, more homogeneous agricultural landscapes, growers may want to actively manage for hedgerows and buffer plantings that flower at times of year, when crops are not in bloom, a practice that is widely believed to increase pollinator populations (Vaughan *et al*. 2004). This recommendation is supported by our finding that even weeds co-flowering with crops did not appear to draw pollinators away from crops; indeed, for solitary bees we found a significant positive effect of co-flowering weeds on crop visitation.

Lastly, wild bees were responsible for the majority of crop flower visitation to three of the four summer vegetable crops we studied, even though most farmers in our system own or rent domesticated honeybees for pollination purposes. Furthermore, different bee communities were found on different crops, suggesting that maintaining diverse bee communities leads to more complete pollination services. These are striking findings with regard to the ecosystem services delivered by wild species.

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Supplementary material

The following supplementary material is available for this article.

Appendix S1. List of bee species collected on watermelon (*Citrullus lanatus* (Thunb.) Matsum. & Nakai), tomato (*Solanum lycopersicum* L.), muskmelon (*Cucumis melo* L.) and bell pepper (*Capsicum annuum* L.) crops

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