

REPORT

The area requirements of an ecosystem service: crop pollination by native bee communities in California

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Abstract

Managing ecosystem services is critical to human survival, yet we do not know how large natural areas must be to support these services. We investigated how crop pollination services provided by native, unmanaged, bee communities varied on organic and conventional farms situated along a gradient of isolation from natural habitat. Pollination services from native bees were significantly, positively related to the proportion of upland natural habitat in the vicinity of farm sites, but not to any other factor studied, including farm type, insecticide usage, field size and honeybee abundance. The scale of this relationship matched bee foraging ranges. Stability and predictability of pollination services also increased with increasing natural habitat area. This strong relationship between natural habitat area and pollination services was robust over space and time, allowing prediction of the area needed to produce a given level of pollination services by wild bees within this landscape.

Keywords

Agriculture, *Apis mellifera*, Apoidea, bee community, bee foraging distance, conservation planning, landscape ecology, pollination service, scale effects.

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INTRODUCTION

Ecosystem services, including climate regulation, soil production, water purification, pest control and crop pollination are critical to human survival (Daily 1997). Management of services could also provide incentives for biodiversity conservation (Daily & Ellison 2002), particularly in human-dominated landscapes where such services are most needed (Scheer & NeNeely 2002). Nonetheless, few natural areas are managed or valued for the services they provide, although many are managed to produce ecosystem goods (e.g. wood, wildlife, fish). In large measure, this is because the ecology of ecosystem services is poorly known, limiting our ability to understand their value and to plan their conservation and management (Palmer *et al.* 2004). Developing such plans

require knowledge of the relationship between the services provided and the area of habitat conserved. This relationship has been estimated for services from plant communities like carbon sequestration and storage (Niles *et al.* 2002) and water flow regulation provided by different vegetation types (Guo *et al.* 2000), but not for any animal-based ecosystem service.

One such service is crop pollination. Thirty per cent of the US food supply by volume depends on animal pollinators (McGregor 1976), of which bee species (Apoidea) are the most important (Roubik 1995; Nabhan & Buchmann 1997). Many farmers rely on colonies of the European honeybee (*Apis mellifera*) that they import temporarily to crop fields to provide pollination during bloom (Free 1993; Delaplane & Mayer 2000). Honeybees are not always the most effective pollinators of a given crop (Parker *et al.* 1987; Kevan *et al.*

1990), and the number of honeybee colonies, both domesticated and feral, have declined by 50–70%, respectively, since 1946 (USDA 1980; data from 1980–2001, E. Mussen, personal communication). Native, unmanaged bee populations also provide important pollination services to various crops, and are generally more diverse and abundant near to natural habitat (Kremen *et al.* 2002b; Klein *et al.* 2003; Ricketts 2004). In this study of native bee pollination of watermelon in northern California, three questions are put forth: (i) what is the appropriate spatial scale for the landscape analysis of pollination services? (ii) Which of several local and landscape environmental factors influence pollination services? (iii) What are the area requirements of pollination services?

METHODS

Farm sites

We studied 22 watermelon (*Citrullus lanatus*) fields located in Yolo, Solano and Sacramento counties of California (Fig. 1) from June to August 2000. Farms varied in the proportion

of natural habitat (riparian forest, chaparral and oak woodland) found nearby. The minimum intersite distance between study fields was 1.9 km; most sites (98.8% of 232 pairwise comparison) were separated by more than 3.2 km (median = 23.4 km; mean = 24.9 km). We classified farms as ‘organic’ ($n = 9$) if they met standards for pesticide and fertilizer use established by the California Organic Foods Act (1990). All other farms ($n = 13$) were classified as ‘conventional’. Most organic farms grew multiple crops in the field alongside watermelon, allowed weeds to grow in or around the crop, and used drip or spray irrigation; in contrast, conventional farms grew only watermelon or watermelon plus muskmelon (*Cucumis melo*) and practiced bare-ground tillage and flood irrigation. Conventional farms varied in the types and amounts of pesticides used. All conventional farms imported honeybee colonies, while only two organic farms did. We mapped the borders of farm fields using a Trimble ProXR Global Positioning System (GPS) (Trimble Navigation, Sunnyvale, CA, USA) corrected to ± 1 m accuracy with Pathfinder v 2.0 (Touch Vision, Cypress, CA, USA). In 2001, we studied 14 watermelon

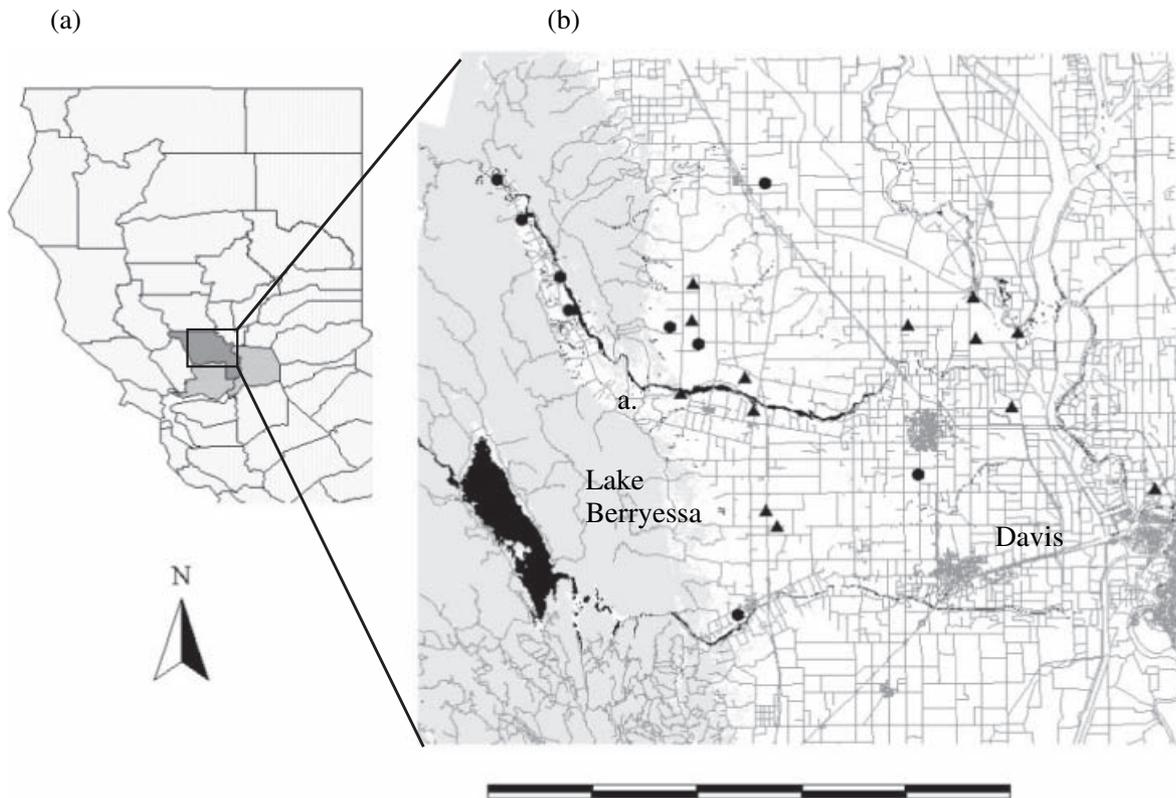


Figure 1 (a) Map of northern California showing the study area in Yolo (dark grey, majority of farm sites), Solano and Sacramento Counties (light grey). (b) Location of farms and surrounding habitat cover. ‘Circles’ denote organic and ‘triangles’ conventional watermelon farms. Grey, upland (oak woodland plus chaparral habitat); black, riparian habitat; white, agricultural or other human-dominated land type. The road network delineates small towns (e.g. Davis). Lake Berryessa is also indicated.

fields in the same landscape (Kremen *et al.* 2002b); of these, we selected the seven organic and five conventional fields that differed in location from the previous year to test model predictions from farms studied in 2000. Farm sites nearest to natural habitat also varied in other environmental characteristics such as elevation (± 100 m); the bee species that we observed in watermelon, however, historically occurred across the gradient (Kremen *et al.* 2002b).

Landsat classification

We conducted a maximum likelihood supervised classification of a Landsat 7 Thematic Mapper image (Raytheon Remote Sensing, Santa Barbara, CA, USA) (July 1999) using the reflective bands (1–5, 7) in ENVI v 3.2 (Research System Inc., Boulder, CO, USA). To improve the classification among vegetation categories, we first separated areas based on the USGS 1 : 24 000 DEM and a slope cut-off of 2% into flat regions dominated by row-crop agriculture from undulating regions that were predominantly rangeland or natural (cf. Guisan *et al.* 1999). Training sets for land cover classes were selected using a 1997 georectified aerial photography layer of the area (provided by Department of Water Resources, Yolo County), the satellite image, and field knowledge. We then classified each region separately and merged the two results. We corrected misclassified pixels in the land cover classification within 5 km of farm sites, by two rounds of ground-truthing combined with detailed examination of the aerial photography layer. The final classified image is *c.* 96% accurate in distinguishing between upland (oak woodland and chaparral), riparian and highly modified land classes (agriculture, urban and grasslands that are dominated by non-native grasses and forbs; Huenneke *et al.* 1990) in the 5 km areas around farm sites.

Bee visitation surveys

At each of the 22 fields, we assessed bee visitation to watermelon flowers by walking 50 m of row in 10 min. In each period, we observed visits to flowers in a 1 m² 'virtual plot' that we moved continuously along the row; to obtain visit rate, we therefore divided the total number of visits/10 min by flower density m⁻², measured in five 1 m² quadrats placed every 10 m along the transect. We walked all transects once between 9:00 AM and 12:30 PM, recording all native and honeybee visits to watermelon flowers of more than 1-s duration, and identifying individuals to the lowest taxonomic level (usually genus or species) and sex (when possible). Taxonomic groupings are described in Kremen *et al.* (2002b) except that in this study, *Halictus tripartitus*, *H. ligatus*, *Lasioglossum (Lasioglossum) titusi* and *L. (Lasioglossum) mellipes* were pooled as 'small striped', as were *L. (Dialictus) spp.*, *Ceratina nanula* and *Hylaenus spp.* (tiny

bee). As honeybee abundances are influenced by the presence of imported colonies, and the purpose of this study was to assess environmental influences on native bee populations and the services they provide, we conducted separate analyses of honeybees and native bees.

We visited each field on three separate dates (except for one conventional field visited only once) in good weather (temperature between 21 and 38 °C, sunny or scattered clouds, wind speed < 4 m s⁻¹). We found no relationship between either of two community metrics for native bees (aggregate abundance and Shannon's diversity index) and independent variables that varied within sites by date (temperature, wind speed, light level, melon flower density, honeybee density) in either single or multiple least squares regression ($P > 0.12$); we therefore subsequently averaged the bee visitation data (three dates and four 10-min samples per date). We minimized field size effects (differential edge effects) by starting all transects about 5 m in from the field edge. To assess edge effects explicitly, on each field in which the length and width of the field were >110 m ($n = 17$), we also conducted 5-min stationary surveys of bees visiting a known number of watermelon flowers (mean = 10) within 1 m² plots located at the beginning (5 m from the nearest edge) and end (55 m from the nearest edge) of our transects.

In 2001, we studied 12 watermelon fields between May and August in identical manner, except that all 12, 10-min samples were taken on a single date per site (Kremen *et al.* 2002b).

Pollination system

Watermelon has separate male and female flowers, large sticky pollen, and requires transfer of 500–1000 pollen grains by an insect vector to set a marketable fruit (Adlerz 1966; Stanghellini *et al.* 1997). In northern California, 28 native solitary and two native social bee species pollinate watermelon (Kremen *et al.* 2002a,b), depositing four to 197 grains per visit (median values per species; Kremen *et al.* 2002b). The honeybee, *A. mellifera*, deposits 21 grains per visit (median value; Kremen *et al.* 2002b). We used estimates of total pollen deposition per flower as a proxy for pollination services. While pollen deposition is strongly related to fruit production, it is not a linear relationship. Pollen could be deposited unevenly across flowers, leaving some flowers over-pollinated and some under-pollinated. Alternatively, resource limitation at the level of the individual plant may cause fully pollinated flowers not to produce fruit. Despite these caveats, estimation of pollen grain deposition is an accepted measure of pollination service (Kearns & Inouye 1993), and is the most direct measure for landscape-level studies in which other factors influencing fruit production (e.g. soil type, cultivation practices) cannot be standardized.

Estimation of pollen deposition

We estimated the mean total number of pollen grains deposited by bees per flower in 10 min at each field, using the following equation:

$$\sum v_{is}e_{is} \quad (1)$$

where v_{is} is the number of visits per 10 min per flower for species group i and sex s , and e_{is} is the pollination efficiency in pollen grains/visit (from Kremen *et al.* 2002b). Estimates of pollen deposition for these 10-min samples strongly predicted estimates of pollen deposition from visitation studies conducted across the entire flowering day (7:00 AM–14:00 PM; four full day samples from four farms in 2000, and 19 samples from 14 farms in 2001; $r^2 = 0.93$, $F_{[1,22]} = 282.86$, $P = 0.0001$). We used this relationship (full-day pollen = $-20.2 + 32.92$ pollen deposition/10 min) to estimate the total amount of pollen deposited per flower per day at each field site. To assess the stability of pollination services across time, we also estimated the pollen deposition at each farm separately for each of the three sample dates in 2000, and used these estimates to calculate the coefficient of variation in pollen deposition at a site (Tilman & Lehman 2001).

Site and landscape variables

To characterize the environment surrounding sites, we measured the proportional area of wild habitats and the insecticide use within specified radii of the watermelon transects, and plant species richness on and around the farm field. Proportional areas of upland (oak, mixed-oak and chaparral classifications), riparian, and wild (upland + riparian) were calculated from the Landsat image at five scales (600, 1200, 1800, 2400 and 4800 m radii originating at the centroid of the watermelon transects) using an Avenue script in Arcview 3.2. We used proportional area rather than an index that incorporates both patch areas and the distances to patches for two reasons. First, our study landscape has few separate patches because most of the natural habitat is concentrated in several large blocks (Fig. 1); thus there will be little difference between proportional area and more complex indices. Second, we are interested in the community of pollinating species, which includes species varying in dispersal and foraging ranges. The accuracy of the dispersal parameter greatly influences the calculation of distance-weighted indices (Moilanen & Nieminen 2002) and therefore is not appropriate for community level studies. Our approach assumes that the presence of wild habitat patches anywhere within a given radius of the sample point affects the community of bees dwelling there, but that habitat beyond

this radius does not. We use the analysis of scale effects (see below) to observe the scale at which this community-level effect might occur.

To develop a spatial index of insecticide use, we obtained a spatially explicit data set of pesticide usage on all fields for 2000 (Department of Agriculture, Yolo County). We then classified all insecticides ($n = 79$ products) used within 4800 m of our watermelon transects using a four-point scale based on LD50 for honeybees and on residual toxicity (Johansen & Mayer 1990). For six insecticides not listed in Johansen & Mayer (1990), we used data from Metcalf & Luckmann (1994) and matched the most toxic level in each study. For each of the five spatial scales (radii), we then calculated a toxicity index for the entire area as the sum of the area of each field times the toxicity class of each chemical applied on that field, over all fields within that radius and all chemicals applied from the beginning of the year up until the last bee survey date at that watermelon field (including multiple applications of the same product on the same field). While it is a relatively coarse metric (for example, it treats all insecticides as equally important regulators of bee populations no matter when the applications occurred), it nevertheless provides a mechanism for differentiating similarly managed sites that occur within differing pesticide landscapes: for example, organic farms surrounded largely by conventional rather than by other organic farms. As a sensitivity analysis, we also calculated the index in the same manner, but only for chemicals applied during the 2 weeks prior to the first bee survey date on a given farm. We did not attempt to discount the influence of an insecticide by distance from the sample point. Instead, we assumed that the application of an insecticide anywhere within a given radius would affect the populations of bees dwelling there, and therefore the abundances of bees that could be present at the watermelon field. We then used the analysis of scale effects (see below) to determine the appropriate scale for the analysis.

To assess local plant species richness on farm sites, we identified all species found in 24 circular plots of 5-m radius, placed every 25 m along eight 50-m transects. Each of the first set of four transects was placed along one of the four sides of the watermelon field such that half of the plot fell in the field and half outside, capturing weeds growing on the border and in the field. Each of the second set of four transects was placed along the border of the adjacent fields to the N, S, E and W of the watermelon field. We studied plant diversity on these adjacent fields, generally located within 30 m of the studied field, because the weedy composition of farm fields tends to be influenced by field preparation and crop type (Leeson *et al.* 2000; Bellinder *et al.* 2004), and thus is likely to differ widely over the short distance from the sampled field border to that of adjacent fields.

Analytical methods

Two of the environmental variables of interest, proportion of wild habitat and toxicity index, occurred along a west to east spatial gradient, with sites in the western portion of the study region being both closer to wild habitat and having lower insecticide levels. As random assignment of sites to environmental conditions was not possible (a common situation in real-world studies), we first assessed the degree of spatial auto-correlation in the data (Legendre 1993) before proceeding to other analyses. We regressed the aggregate native or honeybee abundance at each site against the proportion of wild habitat and the toxicity index, repeating this analysis at each of the five scales, and then examined each of the five sets of residuals for spatial autocorrelation using Moran's index (Lichstein *et al.* 2002) with eight distance classes based on Yule's Rule (Legendre & Legendre 1983). This analysis of spatial autocorrelation, like the better-known partial Mantel test, separates the variation explained by space alone from the variation explained by the environmental variables (Legendre 1993). The advantage of this method over a partial Mantel test is that it retains the original environmental variables, rather than arbitrarily pooling them (Lichstein *et al.* 2002). Calculations of Moran's index were performed in the R-Package (P. Casgrain, <http://www.fas.umontreal.ca/biol/casgrain/en/labo/R/v4/index.html>). We used mean aggregate native or honeybee abundance (eqn 1, $\sum v_{is}$) for the spatial autocorrelation analyses rather than pollen deposition, the ultimate variable of interest in this study, because this was the variable measured across space, whereas pollen deposition was derived from it.

To determine the best scale for conducting subsequent analyses on the variable of interest, pollen deposition, we compared the coefficients of determination from significant regressions at the five different spatial scales (Ricketts 2001; Tilman & Lehman 2001; Pearman 2002; Steffan-Dewenter *et al.* 2002).

To analyse the importance of different environmental variables in determining the level of pollen deposition at each farm, we first performed least squares regressions of pollen deposition against each variable (proportional area of upland habitat, proportional area of riparian habitat, toxicity level, plant species richness, farm management type, field size and honeybee abundance). Next we included all seven variables in the global model (multiple least squares regression). We then selected only variables whose parameter estimates were significant at $P < 0.1$ for inclusion in the final model. We validated the final model by using it to predict pollen deposition values for different farm fields studied in the same landscape in 2001, and then compared the observed with expected values using Spearman's rank correlation. Finally, we analysed how variability in pollen deposition over

the three sample dates per farm was related to the variables identified in the final model, using the coefficient of variation as the dependent variable (Tilman & Lehman 2001).

Statistical analyses were carried out in STATA (Intercooled v. 7.0; StataCorp LP, College Station, TX, USA) and JMP 3.2.5 (SAS Institute, Cary, NC, USA). Power analysis was conducted using G*Power (Buchner *et al.* 1997). Dependent variables were log-transformed when necessary to meet assumptions of normality (Chatterjee & Price 1991).

RESULTS

We observed 2046 visits to watermelon flowers by native bees (12 species groups) and 5316 by honeybees during 42.7 h of sample time in 2000, and 1303 visits by native bees and 1707 by honeybees in 28 h of sample time in 2001. Native bee species are as listed in Kremen *et al.* (2002b).

Spatial effects

We found no significant spatial autocorrelation in the data at any lag distance or scale for native bee abundance (Bonferonni-adjusted $\alpha' = 0.006$, $P > 0.029$ for all lags; Legendre & Legendre 1983). Regressions of native bee abundance against the two spatial variables, proportional area of wild habitat and the toxicity index, were non-significant at 600 m (Bonferonni-adjusted $\alpha' = 0.01$, $P = 0.06$), but were consistently significant ($P < 0.001$) and explained a similar level of variation ($0.3 < r_{adj}^2 < 0.34$) at radii from 1200 to 4800 m (Fig. 2). The scale of 2400 m was

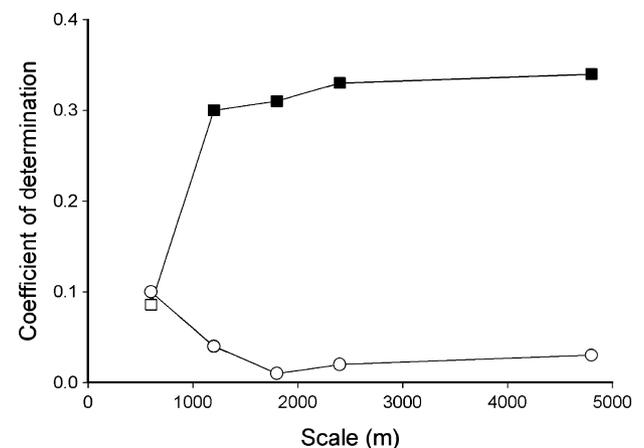


Figure 2 Analysis of scale effects. Total native bee or honeybee abundances were regressed against two scale-dependent variables, the proportional area of wild habitat (riparian + upland) and the toxicity level in the surrounding landscape. The coefficients of determination (r_{adj}^2) of the native bee (squares joined by lines) and honeybee (circles joined by lines) regressions are plotted against scale. Significant regressions are indicated by filled symbols.

selected for the remaining analyses because it had the largest coefficient of determination; however the scale of 1200 m, where the effect began to plateau, may be equally biologically relevant, and was also analysed. There was no significant effect of either spatial variable on honeybee abundance at any spatial scale ($P > 0.37$; Fig. 2).

Across our fields, visits per flower did not differ between edge and interior plots for native bees ($P = 0.31$), although honeybees, in contrast, were significantly more abundant in edge than interior plots (nonparametric paired t -test, mean difference = 0.07 visits/flower/min, Wilcoxon signed ranks = 48.5, $P = 0.01$, one-tailed).

Environmental factors influencing pollen deposition by native bees

For native bees, mean pollen deposition per flower was significantly related to proportion of riparian or upland habitat and farm type in single regressions (Table 1). In a multiple regression including all the variables, the overall model was significant ($F_{7,13} = 2.98$, $r^2_{adj} = 0.41$, $P = 0.04$) but only upland had $P < 0.1$. The best-supported model is therefore the single regression with upland only (Table 1; Fig. 3a); this result was confirmed by also testing the reduced models of upland + riparian, and upland + farm type; in

Table 1 Least squares single and multiple regressions of native bee pollen deposition (natural log-transformed). Honeybee pollen deposition displayed no significant relationships to any of these environmental variables in single or multiple regressions

Variable	Parameter estimate	r^2_{adj}	$T_{1,20}$	P -value
(a) Single regressions				
Upland	3.54	0.42	4.01	0.0007
Farm type	1.34	0.30	3.19	0.005
Riparian	12.5	0.20	2.5	0.02
Field area	-0.000002	0.05	-1.45	0.16
Plant richness	0.03	0.03	0.85	0.41
Insecticide ¹	-0.005	0.02	-0.65	0.52
Honeybee abundance	-0.02	0.02	-0.64	0.53
T				
(b) Multiple regression				
Upland	2.95		2.04	0.06
Farm type	0.79		1.30	0.22
Riparian	5.33		0.87	0.40
Field area	0.00000006		0.04	0.97
Plant richness	-0.04		-1.03	0.32
Insecticide ¹	0.008		0.88	0.40
Honeybee	-0.02		-0.70	0.5

¹Values reported for the insecticide index refer to insecticides applied during the entire year up until the sample date; results were similar when using the index based only on insecticides applied in the 2 weeks prior to the first bee survey date.

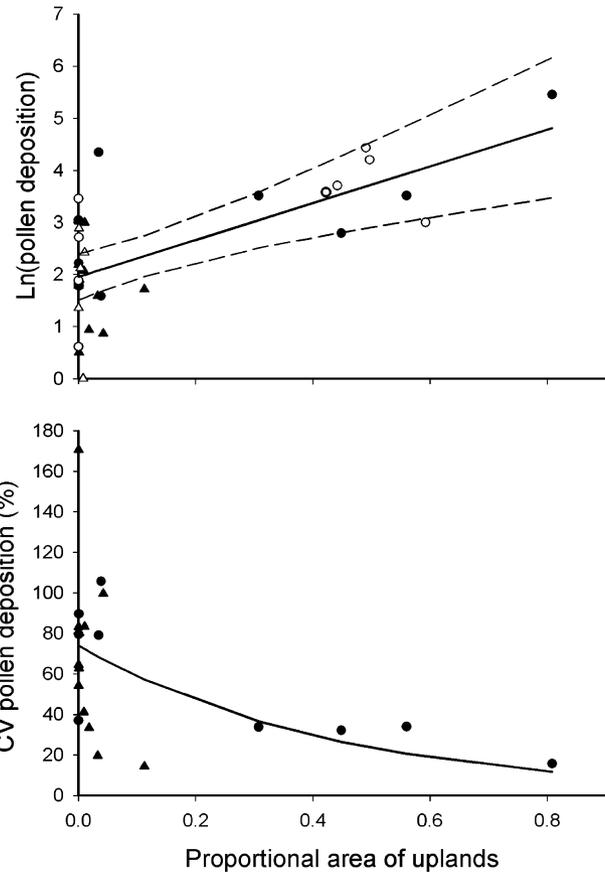


Figure 3 The relationship between the amount and variability of pollen deposition provided by native bees and the proportion of upland habitat within 2.4 km of the farm site. (a) Mean estimated pollen deposition/10 min (natural log-transformed) against the proportion of upland habitat. ‘Circle’ denotes organic farms and ‘triangle’, conventional farms; ‘filled’, data from 2000. The model (solid line), based on data from 2000, is $\ln(\text{pollen deposition}) = 1.95 + 3.54 * \text{upland}$; the dashed lines are 95% confidence intervals. Open symbols represent observations from 2001, used to test the model. (b) Coefficient of variation in pollen deposition (natural-log transformed) between three sampling dates against the proportion of upland habitat. The line indicates a fitted exponential decay curve (see Results).

both cases, only upland was significant ($P < 0.01$). However, as we have no conventional watermelon farms at the high end of the upland gradient (Fig. 1), it is possible that we could not detect the effect of farm type because the farm type and landscape variables are confounded. We therefore also tested the effect of farm type on the subset of farms at the low end of the upland gradient ($n = 17$, proportional area of uplands < 0.04) but still found no significant effect of farm-type ($P = 0.11$), although the power to reject the null hypothesis was low ($1 - \beta = 0.43$, *post hoc* test for unequal sample sizes, effect size = 0.82). Results for the 1200-m scale of analysis were similar for both single and multiple regressions. None of the

variables showed a significant effect on pollen deposition by honeybees ($P > 0.14$).

Comparison of observed data from 2001 with values predicted from the 2000 model validated the predictive power of the model based on proportional area of upland habitat. The observed data were significantly correlated with the predicted values (Spearman's $\rho = 0.77$, $P = 0.003$), and an analysis of covariance for the data from both years, with 'year' as the classifying variable, showed that there was no difference in the effect of upland habitat in each year (year \times habitat interaction, $F = 0.001$, $P = 0.97$), or between-years (Table 2). The model explains the data better at the high than the low end of proportional area of upland habitat (Fig. 3a).

Variability of pollination services

Pollination services from the native bee community were less variable among sample dates on farm sites with higher proportional areas of upland habitat. An exponential decay model fit the data better than a linear model (Fig. 3b; nonlinear: $CV = 74.06 \cdot (0.101)^{\text{proportional area}}$, $F = 39.66$, $P = 0.0000$, $r^2_{\text{adj}} = 0.79$; linear: $CV = 71.77 - 79.77 \cdot \text{proportional area}$, $F = 5.50$, $P = 0.03$, $r^2_{\text{adj}} = 0.18$), suggesting that stability of pollination services provided by the native bee community increases as proportional area of upland habitat increases around a farm. In contrast, there was no change in coefficient of variation for pollination services from honeybees across the upland gradient ($P = 0.53$).

Area requirements of pollination services

To determine the area requirements for providing a given level of pollination services by native bees, we generated a model based on the data from both years against upland habitat (Fig. 4), and converted the y-axis to units of pollen deposited during the entire lifetime of a female flower (see *Methods*). Female watermelon flowers require between 500 and 1000 grains to set a marketable fruit (Adlerz 1966; Free 1993); therefore if farmers were to rely entirely on native bee

Table 2 ANCOVA table for the effects of year and proportion of upland habitat on pollen deposition (natural log-transformed). Both the interaction term (removed here, see text) and year terms were non-significant; thus, the relationship between pollen deposition and upland habitat was virtually unchanged from year to year

Source of variation	Est.	d.f.	F	P-value
Upland habitat	3.65	1	28.61	< 0.0001
Year	0.066	1	0.044	0.83
Overall model ($r^2 = 0.45$)		2, 32	14.72	< 0.0001

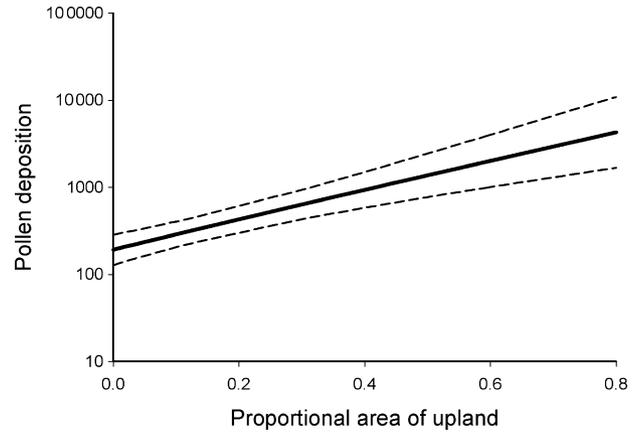


Figure 4. The estimated total pollen deposition per day from native bees (solid line) with 95% confidence intervals (dashed lines). The model based on data from both years [$\ln(\text{pollen deposition}/10 \text{ min}) = 1.864 + 3.76 \cdot \text{upland habitat}$, $F = 32.83$, $P < 0.0001$, $r^2_{\text{adj}} = 0.49$] was converted to full-day pollen (see *Methods*). A target of 10% upland habitat could provide 20–40% of pollination needs for watermelon, and potentially greater benefits for many other fruits and vegetables with lower pollination requirements (Delaplane & Mayer 2000; Kremen *et al.* 2002a).

communities for pollination, their farms would need to be situated in areas containing $\geq 40\%$ of natural habitat within a 2.4 km radius as natural habitat (Fig. 4), or $\geq 30\%$ within 1.2 km (data not shown). The largest bee species visiting watermelon in this system have estimated maximum foraging distances of 2.2 km (S. Greenleaf, N. Williams, R. Winfree and C. Kremen, unpublished data). Much smaller proportions of natural habitat are sufficient to ensure a substantial, partial contribution to watermelon pollination, and even farms with no natural habitat obtain services from native bees (Fig. 4).

DISCUSSION

In order to manage the ecosystem services provided by natural or semi-natural habitats, it is essential to know the area of natural habitat required. Water purification and carbon sequestration are the best-known ecosystem services (Palmer *et al.* 2004); but even here we lack full understanding of their area requirements. Various metropolitan areas, including New York, the world's largest city, rely solely on protected watersheds to purify water (Heal 2000). Nonetheless, the areas designated for this important function have not been determined from ecological knowledge but *ad hoc* (P. Jaffe, Princeton University, personal communication); the per capita watershed areas protected for this function vary over three orders of magnitude for different cities (Reid 2001). Similarly, carbon storage and sequestration services provided by forests are often estimated by

calculating the areas of different forest types and assigning a carbon stock value to each (Mathews *et al.* 2000; Niles *et al.* 2002). Amounts of carbon for a given forest type will vary greatly, however, depending on plant community composition, age structure, soil fertility and other local environmental conditions (Caspersen *et al.* 2000; Oren *et al.* 2001; Balvanera *et al.* 2005); as actual rates of carbon storage and sequestration have been measured in only a few forests (Watson *et al.* 2000), these area-based estimates will have large errors. For animal-based ecosystem services such as crop pollination or pest regulation, we know of no prior studies determining area requirements.

We found that crop pollination services provided by native bee communities in California strongly depended on the proportion of natural upland habitat within 1–2.5 km of the farm site (Fig. 2), a spatial scale that accords well with maximal foraging distances for similar bee species (Walther-Hellwig & Frankl 2000; Steffan-Dewenter *et al.* 2002). This relationship can permit farmers in this region to predict the amount of pollination that they are likely to receive from native pollinators based on the surrounding landscape. The model based on upland habitat was robust and predictive across years and sites, despite significant changes in the abundances of some species among years that altered the rank importance of these different pollinator species (Kremen *et al.* 2002b). This consistency suggests that in the aggregate, pollination function is more stable than the populations of individual bee species, as predicted by theory (Tilman *et al.* 1998).

While the relationship between pollen deposition and upland habitat was robust, the final model explained only 49% of the variation in the data. This may be the result of both limitations in the variables we were able to measure and omission of important variables. For example, other field studies have shown negative effects of insecticide use on honey and native American bee species (Johansen & Mayer 1990; Metcalf & Luckmann 1994); thus the lack of significance of our toxicity index may reflect its incomplete ability to capture effects of insecticides on bee communities at the landscape scale. Similarly, the detection of a farm-type effect may have been hampered by low power in comparing conventional with organic farms at the low end of the upland habitat gradient, and the lack of conventional farms at its high end. In a separate study on sunflower pollination in organic and conventional fields spanning the natural habitat gradient, however, we again only found a significant effect of natural habitat while farm type was a trend (S. Greenleaf and C. Kremen, unpublished data), suggesting that natural habitat is truly a much more important predictor of variation in pollination services in this landscape than farm management type. Finally, potentially important variables that we were not able to measure include landscape variables that measure nest site and floral availability,

including the area of crops providing floral resources (e.g. Westphal *et al.* 2003).

The relationship between upland habitat and pollen deposition was tighter at high than at low levels of upland habitat (Fig. 3a). There are two likely explanations for the larger residuals found at low levels of upland habitat. First, some of the organic isolated farms with large positive residuals also grew squash on their farms and therefore attracted *Peponapis pruinosa*, a bee species that obligately forages on squash for pollen (Hurd *et al.* 1974) and nectars on watermelon, contributing to its pollination (Kremen *et al.* 2002b). Second, farms with strong positive residuals tended to have ground-nesting bees not often found in isolated sites, possibly because of the availability of appropriate nesting substrates (e.g. undisturbed bare ground) on or near the farm. For example, the isolated site with the largest positive residual occurred near both a small, undisturbed dry canyon and a town, both of which could provide nesting resources (Frankie *et al.* 2002) for the ground-nesting bees found on this but not other isolated farms (e.g. *Melissodes* sp., *Bombus* sp.). In the same landscape, the number of ground-nesting bees found nesting on sunflower farms not only decreased with distance from natural habitat, but also became more variable by an order of magnitude (Kim 2004), supporting the hypothesis that increasing patchiness of nesting resources at isolated sites contributes to increasing variability in bee abundances and pollination services.

Our data indicate that honeybees are the dominant pollinator of watermelon in this landscape. While honeybees can influence native bee abundances at flowers by depleting floral resources (Goulson 2003), honeybee abundances did not vary across the gradients of interest in this study; thus, any competitive effects that occurred at watermelon flowers would represent a constant, background condition across farms. If honeybees continue to become less abundant as current trends in the number of managed colonies suggest (USDA 1980, E. Mussen, personal communication), the relative importance of native bees as pollinators of this and other crops will increase. While honeybee abundances in this landscape were not related to upland habitat, honeybees also obtain floral resources from many native plant species found in upland habitat in this area (Kremen *et al.* 2002a) and feral honeybees may nest there. Regional beekeepers use upland areas to provide sources of forage for honeybees when hives are not placed at blooming crops (observations). Upland habitat thus also contributes to the support of domesticated and feral honeybee colonies ensuring a phenological continuity of forage. Our assessment of the importance of natural habitat based on native bee communities (Fig. 4) therefore underestimates the utility of upland habitat for providing pollination services.

Despite this caveat, the predictive relationship between natural habitat area and crop pollination services from

native bee populations is useful in two ways. First, it provides some of the critical information needed to determine the marginal benefits of reserving an additional unit of land for services (Armsworth & Roughgarden 2003). There will be an economic optimum at which maximum gains in crop productivity are realized; this will necessarily be at some intermediate level of natural habitat, because each unit of land reserved, although it contributes to crop pollination, is then no longer available for crop production. The stability of the service also has a value that may depend on natural habitat (Armsworth & Roughgarden 2003, equation 3). Our data show that both the amount and the stability of pollination services from native bees increased with increased proportional area of upland habitat (Fig. 3a,b). Conservation of upland habitat could allow farmers to reduce their reliance on managed honeybees, thereby reducing both production costs and risk to farmers, while increasing food security for society. To be clear, this is a recommendation for farmers to diversify their sources of pollination services, but not to abandon the use of domesticated honeybees.

Second, this predictive relationship between habitat area and pollination services could allow land-use planners to establish conservation targets in this landscape. Targets are commonly applied in planning networks of protected areas to conserve biodiversity (Margules & Pressey 2000; Cowling *et al.* 2003), but their use would be novel in planning the sustainable production of ecosystem goods and services (Balvanera *et al.* 2001; Heal *et al.* 2001). Once established, targets could be reached through conservation and restoration on private and public lands. In northern California, much of the existing upland natural habitat is either managed by the Bureau of Land Management for primitive recreation and wildlife habitat (<http://www.ca.blm.gov/ukiah/cachecreek.html>), or is held by private ranchers. Farms in the valleys near these existing upland areas (Fig. 1) currently enjoy the benefits of the pollination services upland habitats provide, although these benefits may be reduced in the future by growing urbanization and vineyard expansion (Stephen 1995; Merenlender *et al.* 1998; Merenlender 2000; Kremen *et al.* 2002b). Farms in the Central Valley, in contrast, are almost universally far from natural habitat. Here active restoration with native plants on and off farms, such as hedgerow plantings (Bugg *et al.* 1998), or larger-scale restoration, would be required to enhance the level and stability of services provided by native bee populations. Reaching a target of 10% might be feasible through combined public/private action, if farmers were willing to convert much of the non-farmed portions of their properties (field and roadside borders, irrigation ditches, levees, borders around barns and equipment yards) into habitat for native bees and other beneficial insects. On-farm restoration would also provide other ecosystem services of

value to farmers as well as potential eligibility for compensation under the Farm Bill (http://www.usda.gov/farmland/bill/conservation_fb.html). The agri-environment programme of the European Union (Commission of the European Communities 2000; Kleijn *et al.* 2004) provides a hopeful example of what can be accomplished when farmers are given incentives for stewardship of ecosystem services.

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REFERENCES

- Adlerz, W.C. (1966). Honey bee visit numbers and watermelon pollination. *J. Econ. Entomol.*, 59, 28–30.
- Armsworth, P.R. & Roughgarden, J.E. (2003). The economic value of ecological stability. *Proc. Natl Acad. Sci. USA*, 100, 7147–7151.
- Balvanera, P., Daily, G.C., Ehrlich, P.R., Ricketts, T.H., Bailey, S.A., Kark, S. *et al.* (2001). Conserving biodiversity and ecosystem services: conflict or reinforcement? *Science*, 291, 2047.
- Balvanera, P., Kremen, C. & Martinez, M. (2005). Applying community structure analysis to ecosystem function: examples from pollination and carbon storage. *Ecol. Appl.* in press.
- Bellinder, R.R., Dillard, H.R. & Shah, D.A. (2004). Weed seedbank community responses to crop rotation schemes. *Crop Protect.*, 23, 95–101.
- Buchner, A., Erdfelder, E. & Faul, F. (1997). How to use G*Power. Available at: http://www.psych.uni-duesseldorf.de/aap/projects/gpower/how_to_use_gpower.html.
- Bugg, R.L., Anderson, J.H., Thomsen, C.D. & Chandler, J. (1998). Farmscaping in California: hedgerows, roadside plantings and wild plants for bio-intensive pest management. In: *Enhancing Biological Control: Habitat Management to Promote Natural Enemies of Agricultural Pests* (eds Pickett, C.H. & Bugg, R.L.). University of California Press, Berkeley, 339–374.
- Caspersen, J.P., Pacala, S.W., Jenkins, J.C., Hurtt, G.C., Moorcroft, P.R. & Birdsey, R.A. (2000). Contributions of land-use history to carbon accumulation in US forests. *Science*, 290, 1148–1151.

- Chatterjee, S. & Price, B. (1991). *Regression Analysis by Example*, 2nd edn. Wiley, New York.
- Commission of the European Communities (2000). Communication from the commission to the council and the European parliament: indicators for the integration of environmental concerns into the common agricultural policy. URL http://europa.eu.int/eur-lex/en/com/cnc/2000/com2000_0020en01.pdf.
- Cowling, R.M., Pressey, R.L., Rouget, M. & Lombard, A.T. (2003). A conservation plan for a global biodiversity hotspot – the Cape Floristic Region, South Africa. *Biol. Cons.*, 112, 191–216.
- Daily, G.C. (1997). *Nature's Services: Societal Dependence on Natural Ecosystems*. Island Press, Washington.
- Daily, G. & Ellison, K. (2002). *The Economy of Nature*. Island Press, Washington.
- Delaplane, K.S. & Mayer, D.F. (2000). *Crop Pollination by Bees*. CABI Publishing, New York.
- Frankie, G.R.T., Schindler, M.H., Ertter, B. & Przybylski, M. (2002). Bees in Berkeley. *Fremontia*, 30, 50–58.
- Free, J.B. (1993). *Insect Pollination of Crops*. Academic Press, San Diego.
- Goulson, D. (2003). Effects of introduced bees on native ecosystems. *Ann. Rev. Ecol. Syst.*, 34, 1–26.
- Guisan, A., Weiss, S.B. & Weiss, A.D. (1999). GLM versus CCA spatial modeling of plant species distribution. *Plant Ecol.*, 143, 107–122.
- Guo, Z.W., Xiao, X.M. & Li, D.M. (2000). An assessment of ecosystem services: water flow regulation and hydroelectric power production. *Ecol. Appl.*, 10, 925–936.
- Heal, G. (2000). *Nature and the Marketplace: Capturing the Value of Ecosystem Services*. Island Press, Covelo.
- Heal, G., Daily, G.C., Ehrlich, P.R., Salzman, J., Boggs, C., Hellmann, J. et al. (2001). Protecting natural capital: ecosystem service districts. *Stanford Environ. Law Q.*, 20, 333–364.
- Hueneke, L.F., Hamburg, S.P., Koide, R., Mooney, H.A. & Vitousek, P.M. (1990). Effects of soil resources on plant invasion and community structure in Californian serpentine grassland. *Ecology*, 71, 478–491.
- Hurd, P.D., Jr, Linsley, E.G. & Michelbacher, A.E. (1974). Ecology of the squash and gourd bee *Peponapis pruinosa* on cultivated cucurbits in California USA, Hymenoptera: Apoidea. *Smithsonian Contrib. Zool.*, 168, 1–17.
- Johansen, C.A. & Mayer, D.F. (1990). *Pollinator Protection: a Bee and Pesticide Handbook*. Wicwas Press, Cheshire.
- Kearns, C.A. & Inouye, D.W. (1993). *Techniques for Pollination Biologists*. University Press of Colorado, Niwot, CO.
- Kevan, P.G., Clark, E.A. & Thomas, V.G. (1990). Insect pollinators and sustainable agriculture. *Am. J. Alternative Agr.*, 5, 12–22.
- Kim, J.H. (2004). *Effects of cultivation and proximity to natural habitat on ground-nesting native bees in California sunflower fields*. Senior thesis, Ecology and Evolutionary Biology Princeton University, Princeton, NJ.
- Kleijn, D., Berendse, F., Smit, R., Gilissen, N., Smit, J., Brak, B. et al. (2004). Ecological effectiveness of agri-environment schemes in different agricultural landscapes in the Netherlands. *Cons. Biol.*, 18, 775–786.
- Klein, A.M., Steffan-Dewenter, I. & Tscharnke, T. (2003). Fruit set of highland coffee increases with the diversity of pollinating bees. *Proc. R. Soc. Lond. Ser. B*, 270, 955–961.
- Kremen, C., Bugg, R.L., Nicola, N., Smith, S.A., Thorp, R.W. & Williams, N.M. (2002a). Native bees, native plants and crop pollination in California. *Fremontia*, 30, 41–49.
- Kremen, C., Williams, N.M. & Thorp, R.W. (2002b). Crop pollination from native bees at risk from agricultural intensification. *Proc. Natl Acad. Sci. USA*, 99, 16812–16816.
- Leeson, J.Y., Sheard, J.W. & Thomas, A.G. (2000). Weed communities associated with arable Saskatchewan farm management systems. *Can. J. Plant Sci.*, 80, 177–185.
- Legendre, P. (1993). Spatial autocorrelation – trouble or new paradigm. *Ecology*, 74, 1659–1673.
- Legendre, L. & Legendre, P. (1983). *Numerical Ecology*. Elsevier, Amsterdam.
- Lichstein, J.W., Simons, T.R., Shriener, S.A. & Franzreb, K.E. (2002). Spatial autocorrelation and autoregressive models in ecology. *Ecol. Mono.*, 72, 445–463.
- Margules, C.R. & Pressey, R.L. (2000). Systematic conservation planning. *Nature*, 405, 243–253.
- Mathews, E., Payne, R. & Murray, S. (2000). *Pilot Analysis of Global Ecosystems: Forest Ecosystems*. World Resource Institute, Washington.
- McGregor, S.E. (1976). *Insect Pollination of Cultivated Crop Plants*. USDA-ARS, Washington.
- Merenlender, A. (2000). Mapping vineyard expansion provides information on agriculture and the environment. *Calif. Agr.*, 53, 7–12.
- Merenlender, A.M., Heise, K.L. & Brooks, C.P. (1998). Effects of subdividing private property on biodiversity in California's north coast oak woodlands. *Transac. West. Sec. Wildl. Soc.*, 34, 9–20.
- Metcalfe, R.L. & Luckmann, W.H. (1994). *Introduction to Insect Pest Management*, 3rd edn. John Wiley and Sons, Inc., New York.
- Moilanen, A. & Nieminen, M. (2002). Simple connectivity measures in spatial ecology. *Ecology*, 83, 1131–1145.
- Nabhan, G.P. & Buchmann, S. (1997). Services provided by pollinators. In: *Nature's Services: Societal Dependence on Natural Ecosystems* (ed. Daily, G.C.). Island Press, Washington, pp. 133–150.
- Niles, J.O., Brown, S., Pretty, J., Ball, A.S. & Fay, J. (2002). Potential carbon mitigation and income in developing countries from changes in use and management of agricultural and forest lands. *Trans. R. Soc. London, Philos. Ser. A*, 360, 1621–1639.
- Oren, R., Ellsworth, D.S., Johnsen, K.H., Phillips, N., Ewers, B.E., Maier, C. et al. (2001). Soil fertility limits carbon sequestration by forest ecosystems in a CO₂-enriched atmosphere. *Nature*, 411, 469–472.
- Palmer, M., Bernhardt, E., Chornesky, E., Collins, S., Dobson, A., Duke, C. et al. (2004). Ecology for a crowded planet. *Science*, 304, 1251–1252.
- Parker, F.D., Batra, S.W.T. & Tepedino, V.J. (1987). New pollinators for our crops. *Agri. Zool. Rev.*, 2, 279–304.
- Pearman, P.B. (2002). The scale of community structure: habitat variation and avian guilds in tropical forest understory. *Ecol. Mono.*, 72, 19–39.
- Reid, W.V. (2001). Capturing the value of ecosystem services to protect biodiversity. In: *Managing Human-Dominated Ecosystems* (ed. Hollowell, V.C.). Missouri Botanical Garden Press, St Louis, MO, pp. 197–225.
- Ricketts, T.H. (2001). The matrix matters: effective isolation in fragmented landscapes. *Am. Nat.*, 158, 87–99.
- Ricketts, T.H. (2004). Do tropical forest fragments enhance pollinator activity in nearby coffee crops. *Conserv. Biol.*, 18, 1–10.

- Roubik, D.W. (1995). *Pollination of Cultivated Plants in the Tropics*. Food and Agriculture Organization, Rome, Italy.
- Scheer, S.J. & McNeely, J.A. (2002). *Ecoagriculture: Strategies to Feed the World and Save Wild Biodiversity*. Island Press, Washington, DC.
- 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. *Am. Bee J.*, 137, 386–391.
- Steffan-Dewenter, I., Munzenberg, U., Burger, C., Thies, C. & Tschardtke, T. (2002). Scale-dependent effects of landscape context on three pollinator guilds. *Ecology*, 83, 1421–1432.
- Stephen, W.P. (1995). Alfalfa pollination in Manitoba. *J. Econ. Entom.*, 48, 543–548.
- Tilman, D. & Lehman, C. (2001). Biodiversity, composition, and ecosystem processes: theory and concepts. In: *The Functional Consequences of Biodiversity: Empirical Progress and Theoretical Extensions* (eds Kinzig, A., Pacala, S.W. & Tilman, D.). Princeton University Press, Princeton, pp. 9–41.
- Tilman, D., Lehman, C. & Bristow, C. (1998). Diversity–stability relationships: statistical inevitability or ecological consequence. *Am. Nat.*, 151, 277–282.
- USDA (1980). *Beekeeping in the United States: Agricultural Handbook Number 335*. Science and Education Administration, Washington.
- Walther-Hellwig, K. & Frankl, R. (2000). Foraging habitats and foraging distances of bumblebees, *Bombus* spp. (Hymenoptera: Apidae), in an agricultural landscape. *J. Appl. Entomol. – Zeitschrift Für Angewandte Entomologie*, 124, 299–306.
- Watson, R., Noble, A., Bolin, B., Ravindranath, N.H. & Verardo, D. (2000). *Intergovernmental Panel on Climate Change Special Report; Land Use, Land-use Change and Forestry*. Cambridge University Press, Cambridge.
- Westphal, C., Steffan-Dewenter, I. & Tschardtke, T. (2003). Mass flowering crops enhance pollinator densities at a landscape scale. *Ecol. Lett.*, 6, 961–965.

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