Journal of Applied Ecology
British Ecological Society

Journal of Applied Ecology 2010, **47**, 841–849 doi: 10.1111/j.1365-2664.2010.01823.x

Pollination services provided to small and large highbush blueberry fields by wild and managed bees

Rufus Isaacs* **and Anna K. Kirk**

Department of Entomology, Michigan State University, East Lansing, MI 48824, USA

Summary

1. Plantings of pollinator-dependent crops vary from large, intensively managed fields to small fields that are managed less intensively, yet there is relatively little information on how pollinator populations and their contribution to crop productivity vary across this gradient.

2. We determined the relative importance of wild bees and managed honey bees *Apis mellifera* L. for crop pollination in the blueberry *Vaccinium corymbosum* L. system of Michigan, USA, by comparing bee communities in small, isolated blueberry fields with those in large blueberry fields (stocked with managed honey bee hives) and measuring the difference in yields of open-pollinated and pollinator-excluded clusters of flowers. We combined these assessments to calculate the contribution of bees to crop production in this system.

3. Wild bees were the dominant pollinators in small fields, comprising 58% of flower-visiting bees, whereas 97% of bees in large fields were honey bees. Large fields had four times as many bees visiting flowers than small fields, but only one-tenth as many bumble bees as small fields.

4. Levels of fruit set exceeded 85% in all fields and were similar between field sizes. Berry weight increased with flower exposure to pollinators and was positively correlated with bee abundance. Berry weights from open-pollinated flowers were twice as high in large fields compared with small fields.

5. By combining berry weight increases attributable to honey bees and wild bees in blueberry fields with measurements of the bee community adjusted for pollinator efficiency, we calculated the relative contributions of honey bees and wild bees to pollination of Michigan blueberries. We estimate that wild bees provide 82% of the pollination in small fields but only 12% of the total pollination services across this system, mostly through their secondary role in large fields.

6. *Synthesis and applications*. Wild bees are the primary pollinators of small blueberry fields, but these insects are at low abundance in large fields, perhaps due to a lack of nesting resources or competition for resources with honey bees. Our findings highlight the dependence of commercial fruit producers on honey bees and suggest that increasing the pollination contribution of other bees, particularly bumble bees, in large fields will require that growers adopt wild bee conservation strategies or stock their fields with managed colonies. Quantifying the contributions of managed and wild pollinating bees across the range of crop production scenarios will help to direct development of integrated crop pollination strategies to minimize the risk of pollination deficits affecting food production.

Key-words: ecosystem service, honey bee, integrated crop pollination, native bee, pollinator

Introduction

Intensive production of pollinator-dependent crops has caused a shift from reliance on wild bees to dependence on managed honey bees to achieve the high rates of pollen transfer required in commercial agricultural systems (DeGrandi-Hoffman 1987). The ease of use and reliability of honey bees for crop pollination has led to beekeepers renting their hives to supply pollination services to farmers. Colonies of honey bees can be moved to fields in large numbers during bloom and removed to safety before pest management activities resume, making them highly suitable for intensive fruit and vegetable production that require pollination and pest control for maximum

*Correspondence author. E-mail: isaacsr@msu.edu

yields. Such pollinator-dependent crops comprise an increasing proportion of global food production (Aizen *et al*. 2008), emphasizing the need to maintain the long-term health of bees for crop pollination. While most fruit farmers rely on *Apis mellifera* for pollination (Delaplane & Mayer 2000), wild bees are also present in crop fields and provide pollination services of considerable economic value (Losey & Vaughan 2006; Klein *et al*. 2007). Wild bee-mediated crop pollination in the United States is estimated to be worth $3·1 billion annually (Losey & Vaughan 2006), compared with $15 billion for honey bees (Morse & Calderone 2000).

The surrounding landscape can be an important factor affecting the pollination of crop fields (e.g. Kremen, Williams & Thorp 2002; Ricketts 2004; Kim, Williams & Kremen 2006; Williams & Kremen 2007), but there are also reports from vegetable farms in the diverse landscapes of the eastern US in which wild bee abundance did not vary significantly with landscape parameters (Winfree *et al*. 2007b). This may reflect the importance of in-field characteristics for bee abundance in farms set in diverse landscapes (e.g. Shuler, Roulston & Farris 2005) with high proportions of wooded land. Recent valuations of pollination services (e.g. Morse & Calderone 2000; Losey & Vaughan 2006; Klein *et al*. 2007) assume consistent contributions of bees to pollination independent of field size because there is relatively little information on the response of bee communities to this scaling factor in agriculture (Ricketts *et al*. 2008). Understanding how wild bees respond to the agricultural intensification reflected in larger field sizes is therefore an important component of accurate valuation of their contribution to crop production. Field size is a useful parameter to represent the degree to which crop production has been intensified (Roschewitz, Thies & Tscharntke 2005; Herzog *et al*. 2006), as farms with small fields are more likely to have other flowering plants as alternative bee forage and lower pesticide inputs. The wild bee community at these farms may be sufficiently large and diverse to provide consistently high levels of pollination (Kim, Williams and Kremen 2006; Holzschuh *et al*. 2007; Winfree *et al*. 2007b). At the opposite end of this spectrum are commercial farms with large fields characterized by a low ratio of natural- to crop-land, use of herbicides to control weeds and use of broad-spectrum insecticides before and after bloom. The combined effect of these practices is expected to reduce the suitability of such fields for wild bees, thereby limiting the services they can provide to nearby crop fields (Corbet, Saville & Osborne 1994; Steffan-Dewenter & Tscharntke 1999; Carvell *et al*. 2006; Kleijn & van Langevelde 2006; Fitzpatrick *et al*. 2007). One consequence of such intensive crop production is that fields become dependent on managed pollinators for productivity, thus increasing the risk that unfavourable weather conditions or pollinator shortages will cause a deficit of pollen deposition and will limit yield (Kevan 1990; Torchio 1990; Allen-Wardell *et al*. 1998). Given current concerns about the long-term health of honey bees from pests and diseases (Watanabe 1994; Berenbaum 2007), it is important to quantify the value of wild bees and honey bees to agricultural crops that depend on pollination and to do this across the range of contexts in which crops are produced.

Plants dependent on bees for pollen transfer include many perennial fruiting crops, such as the various commercially produced species of blueberry (Delaplane & Mayer 2000). To produce large berries, highbush blueberry requires deposition on the stigma of sufficient pollen tetrads from a compatible cultivar (Marucci & Moulter 1977; MacKenzie 1997; Dogterom 1999; Dogterom, Winston & Mukai 2000). This pollination service is provided by the combined activities of managed *A. mellifera* and wild bees, and many types of wild bees have higher relative pollination efficiencies on blueberry flowers than honey bees (Javorek, MacKenzie & Vander Kloet 2002). Availability of the relative pollination efficiencies of different bee species or groups visiting blueberry flowers from Javorek, MacKenzie & Vander Kloet (2002) provides adjustment factors for calculating adjusted pollination potential from bee abundance data. Highbush blueberry flowers grown in the eastern regions of the United States are visited by a community of wild bees including *Bombus* spp. and numerous species of andrenid and halictid bees (MacKenzie & Winston 1984; Cane & Payne 1993; MacKenzie & Eickwort 1996; Drummond & Stubbs 1997; Sampson & Cane 2000; Tuell, Ascher & Isaacs 2009). Many of these wild bees exhibit the appropriate behaviours to release pollen from the poricidal anthers of blueberry (Buchmann 1983), and they have high fidelity to blueberry flowers during bloom (Cane & Payne 1988; Javorek, MacKenzie & Vander Kloet 2002; Tuell, Ascher & Isaacs 2009). As commercial blueberry production has become more intensive over the past 50 years, field sizes and flower densities during bloom have increased such that in regions of intensive production such as southwest Michigan, USA, well-managed fields produce as many as 30 million flowers per hectare (A.K. Kirk, unpublished data) and large farms may have 50–100 ha of contiguous crop fields. To achieve pollination of this very high density of flowers during a few weeks in the spring, most blueberry producers augment the wild bee population by renting 2–12 colonies of honey bees per hectare (R. Isaacs, unpublished data). Understanding the agricultural settings under which wild bees and honey bees provide crop pollination can help to refine estimates of their value to agriculture and will help focus efforts to maintain the essential services from these insects that help ensure production of fruit and vegetable crops (Klein *et al*. 2007; Kremen *et al*. 2007; Allsopp, De Lange & Veldtman 2008).

Our goal in this study was to determine whether the abundance of wild and managed bees varies with the size of blueberry fields, and to determine whether pollination varies between these different field sizes selected to represent the extreme situations of reliance on wild bees or honey bees. We tested the following hypotheses: (i) bee abundance, species composition and adjusted pollination potential vary between field sizes and positions; (ii) open-pollinated clusters have greater fruit set, berry size and seed number in large fields than in small fields and (iii) the difference in fruit between pollinator-excluded and open-pollinated flowers is greater in large fields than small fields. Finally, the parameter estimates from our measurements under field conditions were used to estimate the relative contributions of wild bees and honey bees to blueberry producers in this region.

Materials and methods

FIELD SITES

All sites for this study were in the primary region of highbush blueberry production across southwest Michigan (Fig. 1) and were of the 'Jersey' cultivar of *Vaccinium corymbosum*. We selected six small non-commercial fields of 0·05–0·40 ha size and six large commercial blueberry fields of 0·6–6·79 ha size, and sampled at the edges and interiors of these fields. Small fields were isolated from other blueberry fields by at least 3 km and were nested within diverse landscapes dominated by woodland, other blueberry fields or other agriculture. Large fields were all part of commercial blueberry farms, with total areas of production exceeding 5 ha. Honey bee stocking density was determined from observations at the fields; large fields were stocked with recommended rates of honey bees (average ± SE of 7·2 ± 1·2 colonies ha^{-1}), whereas only one small field was stocked with colonies (0·4 ± 0·4 colonies ha^{-1}) (U = 2·88, P = 0·004). Large fields also received weed, disease and insect control inputs, fertilizer, tillage of row middles and overhead irrigation, whereas small fields received lower levels of maintenance. Field area and linear distance from the perimeter sampling site (see below) to the nearest woods (the dominant other landscape type) were determined at each sampled field using aerial imagery from the Geospatial Data Gateway (version 3.0 at http://datagateway.nrcs.usda.gov) within a GIS (ArcGIS 9, ESRI, Redlands, CA, USA). Large fields (2·3 ± 0·94 ha) were significantly bigger than the small fields (0·02 ± 0·07 ha) (U = 2·88, P = 0·004). Fields were located in landscapes with varying distance to woodland, but there was no significant difference in distance to woods between large fields (median: 5·3 m) and small fields (7·7 m) (U = 0·80, P = 0·43).

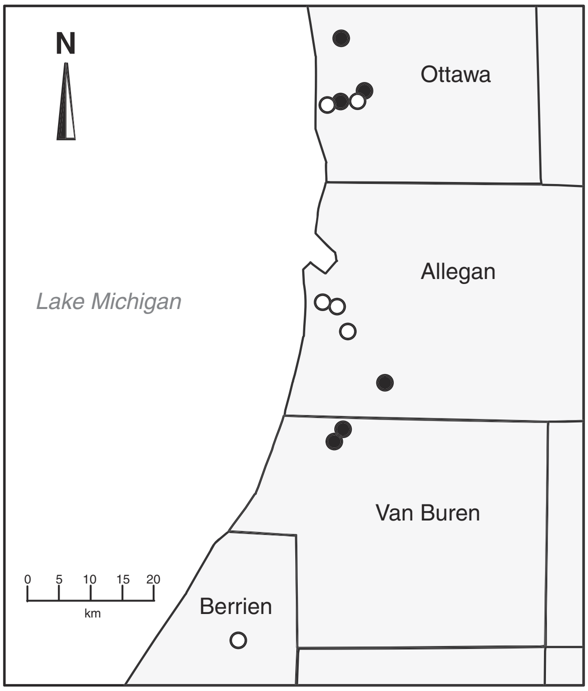

Fig. 1. Location of blueberry fields sampled for the composition of flower-visiting bees and for fruit productivity parameters in southwest Michigan, 2008. The county names are provided, and black stars denote the location of large fields (n = 6), while white stars show the location of small fields (n = 6).

BEE ABUNDANCE DURING BLOOM

The number of pollinating insects visiting blueberry flowers was recorded at each site on two separate days during bloom in May and June 2008. During each sample, the number and identities of bees making legitimate visits to flowers (contacting the stigma end of the flower) were recorded for 5 min in each of 10 sections of the field. During each sample, observers counted bees while walking along the rows and observing one side of *c.* 10 bushes. The 10 samples were distributed across five rows at the field margin and at the interior of each field on the same five rows, for a total sample of 50 bushes per location. Counts of pollinators were performed between 9:30 AM and 6:00 PM (with the majority sampled between 10:00 AM and 4:00 PM) when temperature and wind speed conditions were appropriate for pollinator activity. Insects making legitimate visits to blueberry flowers were recorded as either *A. mellifera* honey bees, andrenid bees, halictid bees, *Bombus* spp. bumble bees (almost all queens) or Eastern carpenter bees *Xylocopa virginica* L. These insects performed more than 99% of the legitimate flower visits to blueberry flowers observed in this study.

The abundance of all bees and of each separate group of bees observed visiting blueberry flowers was compared using a two way analysis of variance (ANOVA) using field size (large vs. small) and sample position (edge vs. interior) as the main factors (PROC MIXED, SAS 9.2, Cary, NC, USA). Preliminary analysis keeping the two sample dates separate did not reveal any significant between-date variation so the two samples were averaged for each site. To determine the efficiency-adjusted pollination potential at each site, the abundance of the different pollinators was multiplied by the appropriate efficiency factor to account for variation in pollen deposition rate and tempo among the different bee groups. Efficiency values were based on Javorek, MacKenzie & Vander Kloet (2002), in which bumblebees are 6·5 times and *Andrena* spp. are 3·5 times more efficient than *A. mellifera* at blueberry pollination. We also applied a 3·5 efficiency factor to halictid bees because of their similar size and behaviour on blueberry flowers (R. Isaacs, pers. obs.). *Xylocopa* are considered nectar robbers but have also been shown to provide pollination of rabbiteye blueberry *V. ashei* (Sampson, Danka & Stringer 2004). Consequently, their abundance was not adjusted for relative efficiency and they were assumed to be as efficient as honey bees.

BLUEBERRY FRUIT SET AND QUALITY

At each sampled field, five bushes at the perimeter and five bushes at the interior were selected, spread across five adjacent rows in each location. Interior samples were at the field center, or up to 60 m into the fields. On each selected bush, a group of three similar-aged flower clusters with flowers close to opening (hereafter, clusters) were marked with flagging tape on each of two shoots. One shoot was randomly designated to be open pollinated while the other had pollinators excluded by surrounding the group of clusters with a loose mesh bag attached to the stem with a wire twist-tie. Comparison between open-pollinated and pollinator-excluded flower clusters allowed for estimation of the amount of fruit set and yield attributable to insect visitation to flowers, and helped to account for between-field variation in field health. The number of unopened flowers on clusters was counted on each shoot between 15 May and 10 June 2008 when the number of flowers was easily observed. Approximately, 1 month later, the number of fruit on clusters was counted, and the proportion of fruit set was determined. When *c.* 50% of the berries were ripe, berries from clusters were collected and brought to the laboratory. This provides berries in which seeds are set, it avoids loss of overripe berries to predation or disease, and provides similar fruit weight data compared with harvesting each berry as it ripens (J.K. Tuell, unpublished data). The total weight of berries and number of berries per cluster was recorded, and these berries were also squashed inside a plastic bag and the numbers of mature seeds recorded.

Flower and fruit data were analysed using the same ANOVA method described above. Before analysing the fruit data, the number of flowers in each cluster was compared between management intensity and position to first determine whether there was any bias in the sample size. The same analysis was performed on fruit parameters of open clusters and on the difference in fruit parameters between bagged and open clusters. All proportion fruit set data were arcsine transformed prior to analysis. To determine the relationship between bee abundance and the increase in blueberry fruit set or berry weight, regression analysis was performed using PROC REG (SAS 9.2) for both field sizes separately and all fields together.

VALUE OF POLLINATION

To estimate the economic value of pollination in small and large blueberry fields, data from a survey of Michigan blueberry farms (USDA-NASS, 2008) were used to calculate the proportion of fields that were ≤0·4 ha (1 acre) and larger than this area, i.e. in the two classes of fields sampled in this study. These values were then combined with our measured values of flower density, fruit set and change in berry weight to estimate the total yield from pollination in small and large fields. Using the relative proportion of adjusted pollination potential provided by honey bees and wild bees, the proportion of the yield supported by these two groups of bees was determined for both large and small fields.

Results

POLLINATOR COMMUNITY

Blueberry flowers were visited by a community of bee species including *A. mellifera*, *Bombus impatiens*, andrenid bees (dominated by *Andrena carlini* and *A. carolina*), halictid bees and *Xylocopa virginica* (Table 1). Overall, significantly more bees were observed during bloom in large fields than in small fields ($F_{1,20}$ = 25·5, P < 0·0001) with no significant variation based on position of the samples ($F_{1,20}$ = 0·16, P = 0·69). This pattern of bee abundance was dominated by *Apis mellifera* which was by far the most abundant flower-visiting bee at large farms (96·8% of the 2202 bees observed). In contrast, *A. mellifera* was less common than wild bees at small farms (42·3% of the 442 bees observed) (Fig. 1). More than 10 times as many *A. mellifera* were observed at large farms than at small farms ($F_{1,20}$ = 30·7, P < 0·0001), reflecting the varying stocking strategies. This pollinator was distributed evenly across the fields in both field types, with no significant variation between the sampling positions ($F_{1,20}$ = 0·14, P = 0·72) and no significant interaction between field size and position ($F_{1,20}$ = 0·01, P = 0·97).

The abundance of other pollinators varied according to the type of wild bee, with some varying according to the field size and others not affected by this factor. Bumble bees comprised 32·4% of the bees observed visiting flowers in small fields and 0·4% in large fields, and their abundance in fields of different sizes was opposite to that of honey bees: small fields had over 10 times more bumble bees than the large fields ($F_{1,20}$ = 10·3, P = 0·004) (Table 1). Bumble bees were also distributed evenly across fields, with no significant variation between the two sampled positions ($F_{1,20}$ = 0·002, P = 0·99). Andrenid bees comprised 12·2% of the bees observed in small fields and 1·3% in large fields, while *X. virginica* comprised 10% in small fields and 0·9% in large fields. Halictid bees were the least abundant native bees, comprising 3·2% of the bees in small fields and 0·5% in large fields (Fig. 1). For each of these bee types, due to inter-farm variability there was no significant variation in their abundance between field sizes or positions ($F_{1,20}$ < 1·4, P > 0·25) (Table 1).

Calculation of the adjusted pollination potential from bee abundance data and efficiency values resulted in a smaller discrepancy between field sizes than was seen for abundance data (Fig. 2), although honey bees remained the dominant pollinator in large fields. The adjustment for pollinator efficiency revealed that small fields receive an estimated 82% of their pollination from wild bees while large fields receive only *c.* 11% from wild bees, the remainder from honey bees. The overall adjusted pollination potential was *c.* 70% higher in large than in small fields (194·5 ± 26·5 vs. 113·7 ± 26·5 estimated honey bee equivalents) ($F_{1,20}$ = 4·63, P = 0·044) (Fig. 2).

Table 1. Average number of bees per 50 bush sample observed making legitimate visits to blueberry flowers during sampling at the edge and interior of small and large blueberry fields in southwest Michigan, 2008

	Small fields (n = 6)		Large fields (n = 6)		P value	
Pollinator	Edge	Interior	Edge	Interior	Field size	Sample position
Apis mellifera	21·3 ± 10·4	9·8 ± 3·8	182·7 ± 37·9	172·7 ± 43·1	0·0001	0·72
Bombus spp.	11·3 ± 4·8	12·0 ± 5·0	1·0 ± 0·5	0·5 ± 0·2	0·005	0·96
Halictids	1·5 ± 0·4	0·8 ± 0·5	1·5 ± 1·3	0·5 ± 0·2	0·83	0·28
Andrenids	3·7 ± 1·4	5·3 ± 3·2	1·2 ± 0·7	3·7 ± 1·5	0·28	0·29
Xylocopa virginica	4·8 ± 2·5	2·5 ± 1·2	2·3 ± 1·8	1·0 ± 0·8	0·25	0·29

Each location was sampled for a total of 50 min.

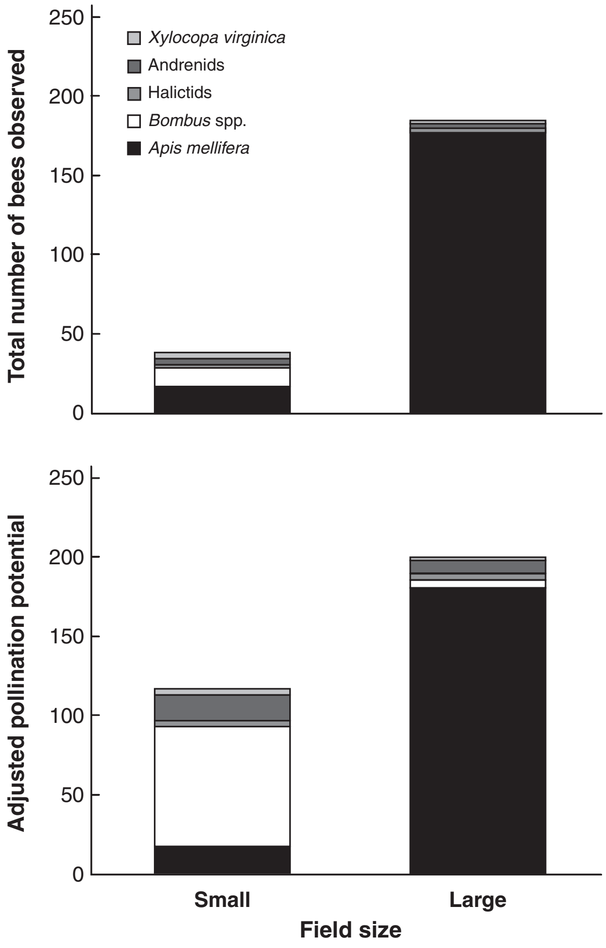

Fig. 2. Pollinator community composition in small and large highbush blueberry fields, presented as the average number of bees observed in 50-min sampling (top) and the adjusted pollination potential, i.e. adjusted for relative pollinator efficiency after Javorek, MacKenzie & Vander Kloet (2002) (bottom).

BLUEBERRY FRUIT SET AND QUALITY

The number of flowers on the three clusters measured for fruit productivity assessments was similar in small (27·2 ± 0·9 flowers per sample) and large (28·5 ± 0·9 flowers per sample) blueberry fields, and was similar across sampling locations, indicating no bias in the size of clusters measured. In addition, the fruit set, berry weight and seed counts of clusters that were bagged to exclude pollinators (and thereby measure parthenocarpic set fruit) were not statistically different between field sizes or positions, indicating little variation in the underlying ability of flowers to set fruit. The proportion of open-pollinated flowers that were set to become berries was slightly higher in large fields (0·92 ± 0·02%) than in small fields (0·89 ± 0·02%), but this difference was not statistically significant ($F_{1,20}$ = 1·14, P = 0·29), and there was no significant variation in fruit set between sampling positions (Table 2). Fruit on open-pollinated clusters weighed 50% more in large fields compared with small fields ($F_{1,20}$ = 18·27, P = 0·0004) (Table 2) and there was no difference between sampling positions ($F_{1,20}$ = 0·3, P = 0·87). This increase in fruit size was associated with an increase in the number of seeds per berry, with higher seed counts in berries from large fields compared with those from small fields, but no variation between the field positions (field size $F_{1,20}$ = 14·6, P = 0·0011; field position $F_{1,20}$ = 0·31, P = 0·58) (Table 2).

Calculation of the difference in fruit parameters between the bagged and open clusters on each bush provides a measure of the benefit provided by pollination, taking into account the underlying parthenocarpic productivity potential of each blueberry bush (Eck 1988). There was little change in fruit set between pollinator-excluded and open-pollinated clusters (3·24% increase in large fields and 5·2% increase in small fields), with no difference in fruit set between field sizes ($F_{1,20}$ = 0·14, P = 0·72) or field position ($F_{1,20}$ = 0·00, P = 0·98). Exposure to pollinators had a much larger effect on berry weight: berries in large fields were 0·38 g heavier on average in large fields when exposed to pollinators, but only 0·14 g heavier in small fields when exposed ($F_{1,20}$ = 12·28, P = 0·002), and with no difference between field positions ($F_{1,20}$ = 0·13, P = 0·72). There was also a much higher number of mature seeds per berry in open-pollinated fruit from large fields (22·6 ± 2·7) than from small fields (13·5 ± 3·1) ($F_{1,20}$ = 14·47, P = 0·0011), with no significant variation between the sampling positions ($F_{1,20}$ = 0·39, P = 0·54) (Table 2). Pollinator-excluded clusters contained berries with < 25% of the seeds found in open-pollinated berries, and with no significant difference in seed counts between field sizes. There were 2·5 ± 0·7 mature seeds per berry in fruit from large fields compared with 3·2 ± 0·8 in the small fields ($F_{1,20}$ = 0·56, P = 0·47).

Across all 24 sampling locations, bee abundance adjusted for pollination efficiency was positively correlated with the change in berry weight (r^2 = 0·36, $F_{1,22}$ = 25·5, P < 0·001). The response to pollination was different between the field sizes; berry weight change between bagged and open clusters ranged from −0·08 to 0·32 g in small fields where bee abundance was lower, whereas it ranged from 0·08 to 0·82 g in large fields that had the highest level of bee abundance (Fig. 3). Regression analysis of bee abundance and change in berry weight conducted separately for small or large fields revealed a positive correlation in small fields (r^2 = 0·38, $F_{1,10}$ = 6·22, P = 0·03), and in large fields there was a similar trend, although no significant correlation (r^2 = 0·29, $F_{1,10}$ = 4·05, P = 0·07) (Fig. 3).

VALUE OF WILD AND HONEY BEES IN SMALL AND LARGE FIELDS

To estimate yield in large and small blueberry fields, we assumed two constant values: a standard bush spacing of 4 × 9 ft, equivalent to 2691 bushes per hectare (b), and 11 016 flowers per mature *V. corymbosum*, cv. Jersey bush (f) (A.K. Kirk, unpublished data) (Table 3). Using our average values of proportion fruit set (fs) in open-pollinated clusters, and the change in berry weight between bagged and open clusters (Δbw) averaged across field positions for each separate replicate field in each size category, we predicted average ± SE

Table 2. Average (±SE) values of fruit productivity for blueberry clusters exposed to the pollinator community present at farms of different sizes, and the significance of field size and the position of the sampling (edge vs. interior)

	Small fields (n = 6)		Large fields (n = 6)		P value	
Yield component	Edge	Interior	Edge	Interior	Field size	Sample position
Fruit set (%)	87·9 ± 3·7	91·2 ± 2·4	91·8 ± 2·7	91·0 ± 2·4	0·29	0·65
Weight per berry (g)	0·40 ± 0·05	0·41 ± 0·04	0·59 ± 0·04	0·63 ± 0·11	0·0004	0·87
Mature seeds per berry	14·9 ± 5·1	12·0 ± 3·9	23·2 ± 2·9	22·0 ± 5·0	0·0011	0·59

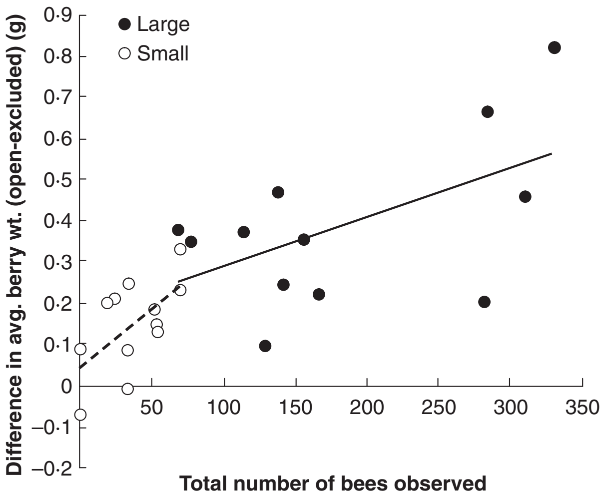

Fig. 3. Change in average berry weight from flower exposure to bees, as a function of bee abundance in small and large blueberry fields. Pollinator-excluded berries had similar weight in small and large fields. The best fit lines for small fields (dashed line) and large fields (solid line) are shown, with the best fit regression line for all data points being change in berry weight (g) = 0·0013 Total bees + 0·069, r^2 = 0·36. n = 5 bushes for each data point.

yield supported by pollination of 3753 ± 854 kg ha^{-1} in small fields and 10 267 ± 1683 kg ha^{-1} in large fields (Table 3). The areas of small and large fields across the Michigan blueberry industry determined from the USDA-NASS survey (a_S and a_L respectively) were used to estimate the total yield (in tonnes) from each size category. The yield in each field size was then partitioned into being derived by the pollinating action of honey bees (Y_{hb}) or wild bees (Y_{wb}) using values of the proportion of yield from honey bees and wild bees, P_{hb} and P_{wb}, calculated for each field from the adjusted pollination potential values. These yield contributions for honey bees and wild bees were calculated using eqns 1 and 2 respectively. In these equations, subscripts $_S$ and $_L$ refer to values from small and large fields respectively.

$$Y_{hb} = (b \cdot f \cdot fs_S \cdot \Delta bw_S \cdot a_S \cdot P_{hbS}) + (b \cdot f \cdot fs_L \cdot \Delta bw_L \cdot a_L \cdot P_{hbL}) \quad \text{eqn1}$$

$$Y_{wb} = (b \cdot f \cdot fs_S \cdot \Delta bw_S \cdot a_S \cdot P_{wbS}) + (b \cdot f \cdot fs_L \cdot \Delta bw_L \cdot a_L \cdot P_{wbL}) \quad \text{eqn 2}$$

From these calculations, we estimate that over 99% of the blueberries produced in Michigan are from large fields. As a result of their dominance in large fields, honey bees support 88·2% of the total yield increase from pollination in this blueberry industry (Table 3). The remaining 11·8% is from wild bees that support the vast majority of yield increase in small fields, but which have the greatest contribution to this whole system through their secondary role in the more dominant large field scale of blueberry production.

Discussion

Our results show that agricultural intensification strongly affects the abundance of wild bees and their contribution to crop pollination in blueberry fields, both at individual field and state-wide scales. The lower contribution of wild bees in large compared with small fields was seen in absolute and relative terms: fewer bumble bees were observed in large fields and these fields also had high abundance of honey bees from managed colonies that provided the majority of pollination services. Wild bees are the primary pollinators in small fields, but because this size of field constitutes a small fraction of Michigan blueberry fields, and because honey bees are the most common in large fields, we estimate that wild bees provide just over 10% of the pollination services to the Michigan blueberry industry. Our findings emphasize the need to consider the degree of agricultural intensification when valuing the pollination services provided by wild and managed bees.

Intensive crop production is expected to negatively impact wild bee populations through the combined effects of reduced habitat, lower diversity and abundance of flowering plants through the season or increased pesticide use (Kevan 1990; Banaszak 1992; Corbet, Saville & Osborne 1994; Winfree *et al.* 2009). The lower counts of bumble bees in large fields in this study are likely to be due to a combination of such factors, as modern blueberry production methods include these land use changes and management inputs (Pritts & Hancock 1992; Mallampalli & Isaacs 2002). We did not detect a response to field size/management intensity in two other abundant groups of blueberry pollinators, andrenid and halictid bees, which are the primary non-*Apis* bees present in blueberry fields during bloom (Tuell, Ascher & Isaacs 2009). The variable sensitivity to field size may reflect the varying life histories, in which bumble bees require access to toxin-free habitat and flowers through the season, whereas solitary bees that specialize on *Vaccinium*, such as *Andrena carolina* and *A. carlini*, are active primarily during the period of blueberry bloom (Tuell, Ascher & Isaacs 2009) when only bee-safe insecticides are applied. Such phenology might buffer more specialized crop-pollinating

Table 3. Estimated contribution of honey bees and wild bees to yield of highbush blueberry in Michigan

Parameter	Symbol	Small	Large	Total
Bushes per hectare[e]	b	2691	2691	
Flowers per bush[a]	f	11 016	11 016	
Proportion of fruit set	fs	0·89	0·91	
ch. wt per berry (g)	Δbw	0·14	0·38	
Yield from pollination (kg ha^{-1})	$b.f.fs.$Δbw	3753 ± 854	10 267 ± 1683	
Area in production (ha)	A	38·3	7193·4	
Total yield from pollination (T)	$b.f.fs$ Δbw.A	152 ± 33	73 854 ± 12 105	74 006
Proportion of pollination[b]				
From honey bees	P_{hb}	0·18 ± 0·21	0·89 ± 0·12	
From wild bees	P_{wb}	0·82 ± 0·21	0·11 ± 0·12	
Yield contribution (T)				
From honey bees	Y_{hb}	43 ± 17	65 252 ± 10 918	65 209
From wild bees	Y_{wb}	150 ± 21	8601 ± 2969	8752

Yield contributions were calculated by partitioning the yield increase from pollinator visitation into honey bee and wild bee contributions based on their abundance and efficiency, for both small and large fields. Average ± SE values were calculated from the replicate fields in which measurements were taken Yield contributions were calculated by partitioning the yield increase from pollinator visitation into honey bee and wild bee contributions based on their abundance and efficiency, for both small and large fields. Average ± SE values were calculated from the replicate fields in which measurements were taken.
[a]Values of b and f were assumed to be constant across field sizes.
[b]Proportion expressed after adjustment for pollination efficiency, after Javorek, MacKenzie & Vander Kloet (2002).

bees from the stresses associated with agricultural intensity (Cane 1997), suggesting that wild bee conservation programmes should focus on pollinators with life histories that put them at risk from poor habitat quality in large crop fields.

Our findings of smaller increases in the number of mature seeds and berry weight between bagged and open-pollinated clusters in small fields compared with large fields suggest that the small blueberry fields have greater pollination limitation than large fields. If so, fruit size may be increased through greater pollinator abundance, whether by implementing conservation strategies for wild bees or by greater investment in managed bees. Although fruit size is probably sensitive to other management practices that co-vary with field size such as fertilization, irrigation, etc., a detailed study to determine the relative contribution of other crop inputs was outside the scope of this study. However, our findings of similar fruit set, numbers of mature seeds and berry weight in pollinator-excluded clusters sampled in large or small fields indicates that the underlying horticultural conditions were similar across this study.

Many common cultivars of highbush blueberry have a degree of parthenocarpy that results in high fruit set, even though there is limited berry weight, in non-fertilized fruit (Eck 1988). Fruit set was not responsive to pollination in the 'Jersey' cultivar used for this study, whereas we found that the primary response to bee-mediated pollination was higher fruit weight, stimulated by improved seed set in well-pollinated fruit. The benefits of pollination to crops are often seen in higher per-fruit weight and quality rather than in fruit set levels, and the importance of this response varies widely across different blueberry species and cultivars (MacKenzie 1997, 2009; Delaplane & Mayer 2000). Even though highbush blueberry cultivars vary in their levels of parthenocarpy, their yields are often improved by pollination through improved fruit quality and larger berries (MacKenzie 1997). Similar findings for other crops including grapefruit *Citrus paradisi* Macf. (Chacoff & Aizen 2007) emphasize that pollination benefits need to be calculated in terms of the quantity, quality and price of fruit produced through the action of bees.

This study highlights the context-dependent nature of pollination services from different types of bees. The greater efficiency of wild bees as blueberry pollinators (e.g. Cane & Payne 1988; Javorek, MacKenzie & Vander Kloet 2002) combined with being more abundant than honey bees in small fields, results in wild bees being the dominant contributor to blueberry yield in small blueberry fields. This suggests that a loss of honey bees is unlikely to have a significant impact on the yields currently provided from small blueberry fields, supporting the findings of Winfree *et al.* (2007a) from long-blooming summer vegetable crops in small diverse crop systems. In contrast, honey bees from managed colonies dominate the bee community in large blueberry fields. Despite their relatively low efficiency, honey bees still provide 89% of the pollination to large blueberry fields, and because large fields constitute the vast majority of the area of Michigan's blueberry production we conclude that honey bees are responsible for pollinating over 88% of the yield increase from pollination in this industry. We caution that by using a standard value for flowers per bush (f, derived from measurements in highly productive mature fields) for our yield estimates, we have overestimated the absolute magnitude of pollination contribution from bees across the study system. The relative contributions of honey bees and wild bees are expected to be the same, but the absolute values would be expected to be smaller due to a high proportion of fields with lower f values.

Our findings demonstrate the high dependence of blueberries on honey bees, and suggest a similar situation for other intensively managed, pollinator-dependent fruit and nut crops that bloom early in the spring. During bloom of these crops, wild bee populations are generally low in abundance and social species have yet to build the size of their colonies, forcing growers with intensive production methods to rely on honey bees or other managed bees (DeGrandi-Hoffman 1987; James & Pitts-Singer 2008). We do not discount the role of wild bees for providing insurance against further losses of honey bees from diseases and mites (e.g. Winfree *et al.* 2007a), but our results indicate that the amount of this insurance from wild bees is currently insufficient to provide full seed set and berry size in large fields. Field size is likely to be a parameter encompassing various factors that reduce field suitability for bee habitat and may interact with the background template of landscape structure that affects the size of wild bee populations at larger spatial scales. The concentrated bloom period with high flower densities found in spring flowering crops such as blueberry, apple, cherry and almonds during times when native bee populations are relatively small and weather conditions are variable support the expectation that it will be challenging to provide full pollination with wild bees in these crops (Kremen *et al.* 2008). Increasing the pollination contribution from wild bees will require further research into strategies for their conservation in farmland and how to optimally combine honey bees and wild bees to ensure full crop pollination. Such integrated crop pollination (ICP) approaches should be developed to serve the pollination needs of agriculture across the spectrum of production scenarios. In the same way that integrated pest management provides a structure for crop managers to choose a combination of appropriate responses to prevent economic losses to pests (Pedigo & Buntin 1994; Radcliffe, Hutchison & Cancelado 2009), ICP can help to formalize how pollination tactics can best be combined for the specific agricultural setting, crops, and local population of wild bees capable of pollination. This should then guide farmers towards sustainable strategies for maintaining pollination services across the range of situations in which pollinator-dependent crops are grown.

Acknowledgements

We thank Scott Prajzner for assistance with GIS analysis and preparation of fig. 1 and Julianna Tuell for technical advice and assistance. This manuscript was greatly improved by feedback from Scott Swinton, Luis Teixeria, Nate Walton, Anna Fiedler and three anonymous reviewers. Our thanks to Dave Kleweno and Marty Saffell at The Michigan field office of USDA-NASS for access to the field size dataset. This study was funded by a College of Agriculture Pre-Doctoral Recruitment Fellowship and a MSU Plant Science Program Fellowship to AKK, and by the Michigan Agricultural Experiment Station.

References

Aizen, M.A., Garibaldi, L.A., Cunningham, S.A. & Klein, A.M. (2008) Long-term global trends in crop yield and production reveal no current pollination shortage but increasing pollinator dependency. *Current Biology*, **18**, 1572–1575.

Allen-Wardell, G., Bernhardt, P., Bitner, R., Burquez, A., Buchmann, S., Cane, J., Cox, P.A., Dalton, V., Feinsinger, P., Ingram, M., Inouye, D., Jones, C.E., Kennedy, K., Kevan, P., Koopowitz, H., Medelllin, R., Medellin-Morales, S., Nabhan, G.P., Pavlik, B., Tepedino, V., Torchio, P. & Walker, S. (1998) The potential consequences of pollinator declines on the conservation of biodiversity and stability of food crop yields. *Conservation Biology*, **12**, 8–17.

Allsopp, M.H., De Lange, W.J. & Veldtman, R. (2008) Valuing insect pollination services with cost of replacement. *PLos Biology*, **3**, 1–8.

Banaszak, J. (1992) Strategy for conservation of wild bees in an agricultural landscape. *Agriculture, Ecosystems & Environment*, **40**, 179–192.

Berenbaum, M.R. (2007) Colony collapse disorder and pollinator decline. Statement to Congress of U.S.A. 29 March 2007.

Buchmann, S.L. (1983) Buzz pollination in angiosperms. *Handbook of Experimental Pollination Biology* (eds C.E. Jones & R.J. Little), pp. 73–113. Van Nostrand Reinhold, New York, NY.

Cane, J.H. (1997) Ground-nesting bees: the neglected pollinator resource for agriculture. *Acta Horticulturae*, **437**, 309–324.

Cane, J.H. & Payne, J.A. (1988) Foraging ecology of the bee *Habropoda laboriosa* (Hymenoptera: Anthophoridae), an oligolege of blueberries (Ericaceae: *Vaccinium*) in the southeastern USA. *Annals of the Entomological Society of America*, **81**, 419–427.

Cane, J.H. & Payne, J.A. (1993) Regional, annual, and seasonal variation in pollinator guilds: intrinsic traits of bees (Hymenoptera: Apoidea) underlie their patterns of abundance at *Vaccinium ashei* (Ericaceae). *Annals of the Entomological Society of America*, **86**, 577–588.

Carvell, C., Roy, D.B., Smart, S.M., Pywell, R.F., Preston, C.D. & Goulson, D. (2006) Declines in forage availability for bumblebees at a national scale. *Biological Conservation*, **132**, 481–489.

Chacoff, N.P. & Aizen, M.A. (2007) Pollination requirements of pigmented grapefruit (*Citrus paradisi* Macf.) from Northwestern Argentina. *Crop Science*, **47**, 1143–1150.

Corbet, S.A., Saville, N.M. & Osborne, J.L. (1994) Farmland as a habitat for bumble bees. *Forage for Bees in an Agricultural Landscape* (ed. A. Matheson), pp. 35–46. International Bee Research Association, Cardiff, UK.

DeGrandi-Hoffman, G. (1987) The honeybee component of horticultural crop production systems. *Horticultural Review*, **9**, 237–272.

Delaplane, K.S. & Mayer, D.F. (2000) *Crop Pollination by Bees*. CAB Publishing, Wallingford.

Dogterom, M.H. (1999) *Pollination by Four Species of Bees on Highbush Blueberry*. PhD thesis, Simon Frazer University, Vancouver, BC.

Dogterom, M.H., Winston, M.I. & Mukai, A. (2000) Effect of pollen load size and source (self, outcross) on seed and fruit production in highbush blueberry cv. 'Bluecrop' (Vaccinium corymbosum; Ericaceae). *American Journal of Botany*, **87**, 1584–1591.

Drummond, F.A. & Stubbs, C.S. (1997) Sampling bee populations in lowbush blueberry in Maine. *Acta Horticulturae*, **446**, 101–108. In: *Proceedings of the sixth international symposium on Vaccinium culture*, Orono, Maine.

Eck, P. (1988) *Blueberry Science*. Rutgers University Press, New Brunswick.

Fitzpatrick, U., Murray, T.E., Paxton, R.J., Breen, J., Cotton, D., Santorum, V. & Brown, M.J.F. (2007) Rarity and decline in bumblebees – a test of causes and correlates in the Irish fauna. *Biological Conservation*, **136**, 185–194.

Herzog, F., Steiner, B., Bailey, D., Baudry, J., Billeter, R., Bukácek, R., De Blust, G., De Cocke, R., Dirksen, J., Dormann, C.F., De Filippi, R., Frossard, E., Liira, J., Schmidt, T., Stöckli, R., Thenail, C., van Wingerden, W. & Bugter, R. (2006) Assessing the intensity of temperate European agriculture at the landscape scale. *European Journal of Agronomy*, **24**, 165–181.

Holzschuh, A., Steffan-Dewenter, I., Kleijn, D. & Tscharntke, T. (2007) Diversity of flower-visiting bees in cereal fields: effects of farming system, landscape composition and regional context. *Journal of Applied Ecology*, **44**, 41–49.

James, R. & Pitts-Singer, T.L. (2008) *Bee Pollination in Agricultural Ecosystems*. Oxford University Press, Oxford.

Javorek, S.K., MacKenzie, K.E. & Vander Kloet, S.P. (2002) Comparative pollination effectiveness among bees (Hymenoptera: Apoidea) on lowbush blueberry (Ericaceae: *Vaccinium angustifolium*). *Annals of the Entomological Society of America*, **95**, 345–351.

Kevan, P.G. (1990) Pollination: keystone process in sustainable global productivity. *Acta Horticulturae*, **288**, 103–110.

Kim, J., Williams, N. & Kremen, C. (2006) Effects of cultivation and proximity to natural habitat on ground-nesting native bees in California sunflower fields. *Journal of the Kansas Entomological Society*, **79**, 309–320.

Kleijn, D. & van Langevelde, F. (2006) Interacting effects of landscape context and habitat quality on flower visiting insects in agricultural landscapes. *Basic and Applied Ecology*, **7**, 201–214.

Klein, A.-M., Vassière, B.E., Cane, J., Steffan-Dewenter, I., Cunningham, S., Kremen, C. & Tscharntke, T. (2007) Importance of pollinators in changing landscapes for world crops. *Proceedings of the Royal Society B: Biological Sciences*, **274**, 303–313.

Kremen, C., Williams, N.M. & Thorp, R.W. (2002) Crop pollination from native bees at risk from agricultural intensification. *Proceedings of the National Academy of Sciences*, **99**, 16812–16816.

Kremen, C., Williams, N., Aizen, M.A., Gemmill-Herren, B., LeBuhn, G., Minckley, R., Packer, L., Potts, S., Roulston, T., Steffan-Dewenter, I., Vazquez, D., Winfree, R., Adams, L., Crone, E., Greenleaf, S., Keitt, T.H., Klein, A.-.M., Regetz, J. & Ricketts, T.H. (2007) Pollination and other ecosystem services produced by mobile organisms: a conceptual framework for the effects of land-use change. *Ecology Letters*, **10**, 299–314.

Kremen, C., Daily, G.C., Klein, A.-M. & Schofield, D. (2008) Inadequate assessment of the ecosystem service rationale for conservation: reply to Ghazoul. *Conservation Biology*, **22**, 795–798.

Losey, J.E. & Vaughan, M. (2006) The economic value of ecological services provided by insects. *BioScience*, **56**, 311–323.

MacKenzie, K.E. (1997) Pollination requirements of three highbush blueberry (*Vaccinium corymbosum* L.) cultivars. *Journal of the American Society of Horticultural Science*, **122**, 891–896.

MacKenzie, K. (2009) Pollination practices and the use of bees in *Vaccinium* crops. *Acta Horticulturae*, **810**, 527–538.

MacKenzie, K.E. & Eickwort, G.C. (1996) Diversity and abundance of bees (Hymenoptera: Apoidea) foraging on highbush blueberry (*Vaccinium corymbosum* L.) in central New York. *Journal of the Kansas Entomological Society*, **69**, 185–194.

MacKenzie, K.E. & Winston, M.L. (1984) Diversity and abundance of native bee pollinators on berry crops and natural vegetation in the lower Fraser Valley, BC. *Canadian Entomologist*, **116**, 965–974.

Mallampalli, N. & Isaacs, R. (2002) Distribution of egg and larval populations of cranberry fruitworm (Lepidoptera: Pyralidae) and cherry fruitworm (Lepidoptera: Tortricidae) in highbush blueberries. *Environmental Entomology*, **31**, 852–858.

Marucci, P.E. & Moulter, H.J. (1977) Blueberry pollination in New Jersey. *Acta Horticulturae*, **95**, 345–351.

Morse, R.A. & Calderone, N.W. (2000) The value of honey bees as pollinators of U.S. crops in 2000. *Bee Culture*, **128**, 1–15.

Pedigo, L.P. & Buntin, G.D. (1994) *Handbook of Sampling Methods for Arthropods in Agriculture*. CRC Press, Boca Raton, FL.

Pritts, M.P. & Hancock, J.F. (1992) *Blueberry Production Guide*. N.E. Regional Agricultural Engineering Service, Ithaca, NY.

Radcliffe, E.B., Hutchison, W.D. & Cancelado, R.E. (2009) *Integrated Pest Management: Concepts, Tactics, Strategies and Case Studies*. Cambridge University Press, Cambridge.

Ricketts, T.H. (2004) Tropical forest fragments enhance pollinator activity in nearby coffee crops. *Conservation Biology*, **18**, 1262–1271.

Ricketts, T.H., Regetz, J., Steffan-Dewenter, I., Cunningham, S.A., Kremen, C., Bogdanski, A., Gemmill-Herren, B., Greenleaf, S.S., Klein, A.-M., Mayfield, M.M., Morandin, L.A., Ochieng, A. & Viana, B.F. (2008) Landscape effects on crop pollination services: are there general patterns? *Conservation Biology*, **22**, 799–801.

Roschewitz, I., Thies, C. & Tscharntke, T. (2005) Are landscape complexity and farm specialisation related to land-use intensity of annual crop fields? *Agriculture, Ecosystems & Environment*, **105**, 87–99.

Sampson, B.J. & Cane, J.H. (2000) Pollination efficiencies of three bee (Hymenoptera: Apoidea) species visiting rabbiteye blueberry. *Journal of Economic Entomology*, **93**, 1726–1731.

Sampson, B.J., Danka, R.G. & Stringer, S.J. (2004) Nectar robbery by bees (*Xylocopa virginica* (L.) and *Apis mellifera* L.) contributes to the pollination of rabbiteye blueberry. *Journal of Economic Entomology*, **97**, 735–740.

Shuler, R.E., Roulston, T.H. & Farris, G.E. (2005) Farming practices influence wild pollinator populations on squash and pumpkin. *Journal of Economic Entomology*, **98**, 790–795.

Steffan-Dewenter, I. & Tscharntke, T. (1999) Effects of habitat isolation on pollinator communities and seed set. *Oecologia*, **121**, 432–440.

Torchio, P.F. (1990) Diversification of pollination strategies for U.S. crops. *Environmental Entomology*, **19**, 1649–1656.

Tuell, J.K., Ascher, J.S. & Isaacs, R. (2009) Wild bees (Hymenoptera: Apoidea: Anthophila) of the Michigan highbush blueberry agroecosystem. *Annals of the Entomological Society of America*, **102**, 275–287.

Watanabe, M.E. (1994) Pollination worries rise as honey bees decline. *Science*, **265**, 1170.

Williams, N.M. & Kremen, C. (2007) Resource distributions among habitats determine solitary bee offspring production in a mosaic landscape. *Ecological Applications*, **17**, 910–921.

Winfree, R., Williams, N.M., Dushoff, J. & Kremen, C. (2007a) Native bees provide insurance against ongoing honey bee losses. *Ecology Letters*, **10**, 1105–1113.

Winfree, R., Williams, N.M., Gaines, H., Ascher, J.S. & Kremen, C. (2007b) Wild bee pollinators provide the majority of crop visitation across land-use gradients in New Jersey and Pennsylvania, USA. *Journal of Applied Ecology*, **45**, 793–802.

Winfree, R., Aguilar, R., Vázquez, D.P., LeBuhn, G. & Aizen, M.A. (2009) A meta-analysis of bees' responses to anthropogenic disturbance. *Ecology*, **90**, 2068–2076.

Received 2 November 2009; accepted 30 April 2010
Handling Editor: Michael Pocock