# Wild pollination services to California almond rely on semi-natural habitat

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## Summary

**1.** Global declines in honeybees have led to concerns about negative impacts on food production because of low levels of pollination. This is exemplified in California where the demand for honeybees *Apis mellifera* to pollinate almond *Prunus dulcis* is increasing, but problems with honeybee health suggest it may not be sustainable to rely solely on the pollination service of a single species.

**2.** We investigated the effect of the quantity of surrounding natural habitat, organic management and strips of semi-natural vegetation on flower visitation frequency of wild and managed pollinators and fruit set in 23 California almond orchards (15 conventional, 8 organic). Five conventional and four organic orchards were surrounded by a low percentage ($< 5\%$) of natural or semi-natural habitat in a 1-km radius and another five conventional and four organic orchards were surrounded by a high percentage of these habitats ($> 30\%$). A further five conventional orchards with a low percentage of surrounding natural habitat had an adjacent strip of semi-natural vegetation and were included in the study to represent a realistic option for orchard management in intensive agricultural landscapes.

**3.** Wild bee species visited almond flowers but only in orchards with adjacent semi-natural habitat or vegetation strips. Organic management increased the flower visitation frequencies of hover flies and wild bees. The presence of a strip of semi-natural vegetation in orchards with a low percentage of surrounding natural habitat increased the number of species and the flower visitation frequency by wild pollinators but only at orchard edges and not to the degree seen when natural habitat was abundant.

**4**. Wild bee species richness and flower visitation frequency, but not honeybee frequency, were related to fruit set. Fruit set increased with increasing percentage of natural habitat surrounding the orchards. Organic farming or the presence of a vegetation strip did not increase fruit set.

**5.** *Synthesis and applications.* The restoration of high quality habitat strips along the edges of crop fields in highly intensified agricultural landscapes should be encouraged and monitored to conserve pollinators and to determine whether benefits for agriculture can be realized. Although honeybees are the main and most important pollinating insects for many plants, wild pollinators may be necessary to ensure high fruit set. Organic farming alone will not sustain wild pollination services for almond in California.

**Key-words:** agricultural landscapes, biodiversity, ecosystem service, habitat quality, honeybees, landscape restoration, *Prunus dulcis*, sustainable agriculture, Syrphidae, wild bees

## Introduction

High levels of over-wintering colony losses in the managed honeybee *Apis mellifera* L. in the USA and globally over the past 4–6 years (Johnson *et al.* 2009; Neumann & Carreck 2010) have heightened concerns that a scarcity of honeybees will negatively affect food production (Aizen & Harder 2009). Wild insects contribute to the pollination of many crops (Klein *et al.* 2007; Garibaldi *et al.* 2011) and may provide insurance in times when honeybee colonies are weak or weather conditions are unfavourable for honeybee flight (Corbet *et al.* 1993; Winfree *et al.* 2007). The flower visitation frequency and

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diversity of wild pollinators in crop fields can be negatively affected by the isolation of the crop field from natural habitat (Ricketts *et al.* 2008; Garibaldi *et al.* 2011) but can benefit from the amount of surrounding natural or semi-natural habitat (Kremen, Williams & Thorp 2002; Steffan-Dewenter 2002) or by organic management (Morandin & Winston 2005; Gabriel *et al.* 2010) and by the potential interaction between landscape and crop management variables (Holzschuh *et al.* 2007; Rundlof, Nilsson & Smith 2008; Batáry *et al.* 2011). Crops may also benefit from planted hedgerow strips of native vegetation that are otherwise isolated from natural areas because they have positive effects on the abundance of beneficial insects (Pollard & Holland 2006; Morandin *et al.* 2011). Whether the positive effect on the abundance of beneficial insects associated with vegetation strips translates into increased crop production in highly intensified landscapes is unknown.

Almond *Prunus dulcis* (Mill.) D.A. Webb production in California is an important test case of the usefulness of vegetation strips and natural areas for crop production. California produces over 80% of the world's almonds (United States Department of Agriculture 2009, http://www.fas.usda.gov), and growers rely almost exclusively on managed honeybees for pollination. Almond flowers in February in California, when wild bee populations are just starting to emerge from diapause and thus honeybees have been considered to be the only management option. Each year, almond production in California requires the import of approximately one-half of the hives in the USA (Sumner & Boriss 2006). The demand for honeybee colonies for almond pollination in California is likely to increase as the area of land devoted to almond, now at over 300 000 ha, continues to grow (http://www.almond-board.com). Shortages of honeybee colonies have already increased the cost of renting hives threefold between 2003 and 2009 (United States Department of Agriculture, http://www.ars.usda.gov). This has stimulated interest among growers in the potential contribution of wild bees to almond pollination services.

In this study, we quantified flower visitation frequency to almond in 23 orchards surrounded by either a low (<5%) or a high (>30%) percentage of natural or semi-natural habitat (hereafter referred to as natural habitat) in a 1-km radius. Five of the conventional orchards with a low percentage of surrounding natural habitat had an adjacent strip of semi-natural vegetation and were included to represent a realistic option for orchard management in intensive agricultural landscapes, where restoring extensive patches of natural habitat would generally not be feasible. In this study, we specifically ask the following questions: (i) Are wild insects available to pollinate early-blooming almond flowers in California? If wild insects are available then, (ii) Are the flower visitation frequency and richness of wild insects related to the percentage of surrounding natural habitat? (iii) Does organic management increase the flower visitation frequency and richness of wild insects? (iv) Does the presence of a nearby strip of semi-natural vegetation in an otherwise isolated orchard increase the flower visitation frequency and richness of wild insects? (v) Is fruit set altered by the management options and the flower visitation frequency and richness of wild insects?

## Materials and methods

### STUDY AREA AND SITE SELECTION

The study was conducted in 23 almond orchards located in Colusa and Yolo Counties in the Sacramento Valley, Northern California (38°42′ to 38°57′ N and 121°57′ to 122°14′ W, Fig. 1), part of California's agriculturally intensive Central Valley. To explore the effects of organic management, natural habitat in the landscape and their interaction, we selected eight organic and 10 conventional orchards; in each case, half were surrounded by <5% and half by more than 30% natural habitat (1 km radius). Less than 5% natural habitat in a 1-km radius is considered as a cleared agricultural landscape (Tscharntke *et al.* 2005, 2012). We selected an additional set of five conventional orchards in areas with a low percentage of surrounding natural habitat (<5%) that had an adjacent strip of semi-natural vegetation. The strips were generally 10–25 m wide, along one side of the orchard and consisted of vegetation common to scrubby riparian habitats. We were not able to locate comparable organically managed orchards. The minimum distance between orchards was 1 km with a mean inter-site distance of 3 km.



**Fig. 1.** Study area and locations of study orchards in Yolo and Colusa County in northern California. The black circles indicate organically and the white circles conventionally managed orchards.

The organic orchards were certified according to the California Organic Foods Act (1990) and did not use any insecticide or herbicide. Between-row vegetation was controlled in organic orchards by mowing or burning, but by herbicide application in conventional orchards. In conventional orchards, insecticides were applied only after the almond bloom finished and if pest levels were high. All orchards, except for one conventional and two organic, were sprayed with fungicides during the almond bloom.

### LANDSCAPE CHARACTERIZATION

Natural habitat near orchards consisted primarily of valley and foothill riparian woodland, oak *Quercus* ssp. woodland or chaparral with a flora comprised largely of native species (Ward 1987). To determine the area of surrounding natural habitat within a 1-km radius of each orchard edge, we classified 2009 aerial imagery data from the National Agricultural Imagery Program (NAIP, 1 $m^2$ resolution) for Yolo and Colusa Counties (available at MapMart, http://www.mapmart.com) using heads-up digitizing in ArcGIS 9.3.1 (Environmental Systems Research Institute, Redlands, CA, USA). The 2009 data were the closest available to our sample dates; little change in land use occurred in and around our sample sites during the 1-year interval. We mapped the edge of each orchard closest to natural habitat with a Trimble GeoExplorer Global Positioning System (GPS; Trimble Navigation, Sunnyvale, CA, USA) corrected to $\pm 10$ m accuracy with GPS Pathfinder Office (version 2.9; Touch Vision, Cypress, CA, USA) and then calculated the percentage of natural habitat area using ArcGIS. We also measured the size of orchards from the aerial images (using heads-up digitizing) with ArcGIS.

### OBSERVATIONS OF FLOWER-VISITING INSECTS

Observations of visitors to almond flowers in the 23 orchards were made from 25 February to 18 March in 2008 under sunny to lightly overcast skies, when temperatures were above 13 °C (Delaplane & Mayer 2000) and the wind speed was $< 2.5$ m $s^{-1}$. In each of the 23 orchards, we observed flower visitors on three separate days. Prior to the observations, the level of orchard bloom was measured as the percentage of partially or fully open flowers based on counts from 100 flowers from one or more branches on 10 trees per orchard and the temperature and wind speed were measured. For each orchard and observation day, we selected five trees at the orchard edge nearest to the natural habitat or strip, if present, and five trees in the orchard interior at 50–60 m (five small orchards) or 100–110 m from the edge (18 large orchards) which were in full bloom (pollen was not completely dehisced). At each tree, we observed eight groups of flowers ($17.5 \pm 0.1$, mean $\pm$ SE min 2, max 55) for 20 s each, two each in the inner top, inner bottom, outer top and outer bottom quadrants of the tree. Flowers for observation were selected such that the observer could see the interior of each flower; a step ladder was utilized as needed. The number of flowers observed per time period was therefore a result of feasibility. Observation time was 26.7 min per orchard on a given day and 80 min per orchard in total over 3 days. For each 20-s observation period, we recorded the number of flowers observed, the number of flower visits (frequency) by *Apis mellifera*, non-*Apis* wild bees assigned either to species or to morphospecies, hover flies (family Syrphidae) and other visitors (mainly Diptera) (vouchered specimens deposited at the RM Bohart Museum of Entomology, University of California, Davis; Table S1, Supporting Information). Owners of the orchards provided data on the number of honeybee hives per ha placed in orchards used in our study.

### FRUIT SET

In late March 2008, we counted the number of post-anthesis flowers along a 1-m length of a tagged branch on five trees at each orchard edge closest to the natural habitat if available. In July, before birds and small mammals started feeding on the developed fruits, the number of developed fruits was counted on the same branches used to calculate fruit set. Extremely small and deformed fruits were noted and excluded from analysis as they do not contain edible or marketable nuts.

### STATISTICAL ANALYSES

Prior to statistical analysis, the flower visitation frequency by honeybees was pooled over the eight observations per tree per day, yielding 15 frequency measures (5 trees × 3 days) at the orchard edge and 15 in the interior. As there were more zeros in the data for wild bees, hover flies and all-other visitors, (a catch-all category of remaining taxa, mostly Diptera) than for honeybees, the data were first pooled per tree as above and then over all five trees at the same distance from the edge, yielding three frequency measures at the orchard edge and three in the interior. The richness data were pooled in the same way as for the visitation frequency of wild bees. The richness of wild bees was based on the species or morphospecies identified during the study. The richness of all visitors was calculated using species or morphospecies identifications for bees and 10 additional broader taxonomic groups (e.g. Bombyliidae, Coleoptera; Table S1, Supporting Information).

Using separate generalized linear mixed models (GLMM), we tested the effects of the surrounding landscape (percentage natural area in surrounding 1 km) and orchard management (conventional or organic) on the flower visitation frequency by the four different visitor groups (honeybees, wild bees, hover flies and all-others), on the richness of visitors (all visitors and wild bees only) and on fruit set (proportion of flowers setting fruit on a 1-m branch). We also ran all models with visitation frequencies by using the proportion of flowers visited (visitation rate). Model results were the same, and we present frequency only. Fruit set was measured at the orchard edge. Thus, all models testing for effects on fruit set included data of the orchard edge only.

Explanatory variables included distance from the edge, orchard management, percentage of surrounding natural habitat (log transformed) and paired interactions between those variables. The other potential explanatory variables were the percentage of open almond flowers in the orchard, the number of honeybee hives per ha, orchard size (ha), temperature ( °C) and wind speed (m $s^{-1}$). Some of the potential explanatory variables for inclusion in the models were correlated (Table S2, Supporting Information). When two of these variables were correlated, the variable which had the most explanatory power in the model (lowest AIC value, maximum likelihood comparison) was included. Daily variables such as wind speed, temperature and the number of flowers observed were not included in the model for fruit set, because fruit set integrated across multiple days in which these variables were not measured.

The models for flower visitation frequency and visitor richness had a log-normal Poisson error distribution. For honeybees, the random variables were observation day nested within distance from the edge, nested within the orchard. For the wild bees, hover flies, all-other visitors and visitor richness, the random variables were the distance from the edge nested within the orchard. The model for fruit set had a binomial error distribution,

and orchard was used as a random factor. An observation level random variable (unique for each frequency measure) was included to account for overdispersion where necessary (Maindonald & Braun 2010). Model simplification was performed by stepwise deletion (where $P > 0.05$). After the removal of an explanatory variable, the models with and without the variable were compared by analysis of variance (maximum likelihood fitting) to test the loss of explanatory power from the removal of the variable. When there was no significant difference ($P > 0.05$) between the models, the explanatory variable was removed. All analyses were carried out in R 2.13.1 (R Development Core Team 2011).

The effect of the vegetation strip could not be incorporated in the above analysis framework, as there were no organic orchards with a strip. Therefore, separate analyses of conventionally managed orchards only (5 with and 10 without strips) were performed to test for the effect of the adjacent vegetation strip. The same analyses were carried out as detailed above but without the orchard management variable and with the explanatory variable percentage surrounding natural habitat replaced by a three level categorical variable: (i) high percentage surrounding natural habitat, (ii) low percentage natural habitat (as defined above) and (iii) low percentage natural habitat but with a vegetation strip bordering the orchard. Model simplification was carried out in the same way as detailed above.

We explored the relationship between flower visitation frequency and fruit set, or richness and fruit set of all 23 orchards using binomial GLMMs. The orchard and an observation level variable were included as random variables. Flower visitation frequencies by all visitors, honeybees, wild bees, hover flies and all-others were each run in separate GLMMs because of colinearity. The same was performed for the richness of all visitors and of wild bees.

## Results

### ALMOND FLOWER-VISITOR COMMUNITY

In total, we observed 2416 flower visits by honeybees *Apis mellifera* (70% of all visits), 378 by wild bees of at least 19 species (11% of all visits), 327 by hover flies (10% of all visits) and 314 by other insects of various taxa (9% of all visits). Other insects included flies (primarily Bombyliidae and Muscidae), ants (Formicidae) and other infrequent visitors (Table S1, Supporting Information). The most flower visits by wild bees were provided by the ground-nesting sand bee *Andrena cerasifolii* (Cockerell) accounting for more than 2% of all flower visits. Sweat bees also frequently visited flowers, especially an undescribed *Lasioglossum* (*Evylaeus*) species and *Lasioglossum incompletum* (Crawford). These wild bees were present only in orchards with nearby natural habitat. The blue orchard bee *Osmia lignaria propinqua* Cresson, a species that could be managed for almond production in California (Bosch & Kemp 2002), was only observed once.

### EFFECT OF SURROUNDING NATURAL HABITAT AND ORGANIC MANAGEMENT

The flower visitation frequency by honeybees was consistently greater than the visitation frequencies of the other pollinator taxa and was positively related to the stocking density of hives in the orchard (Table 1), but was not related to the surrounding natural habitat (Fig. 2a). In contrast, the visitation frequency by wild bees, hover flies and all-other visitors was positively related to the percentage of surrounding natural

**Table 1.** Results from (GLMM) analyses of the flower visitation frequency, richness of visitors and fruit set in 23 almond orchards. The table shows the $\chi^2$ values (***$P < 0.001$, **$P < 0.01$, *$P < 0.05$; d.f. = 2 for honeybee hives, d.f. = 1 for all other variables) from likelihood ratio tests for variables in the minimum models and the direction of the relationships. Blanks represent variables dropped following stepwise deletion or correlated variables not included in the model (see also Table S2, Supporting Information)

| | Natural habitat (%) | Orchard management† | Distance from edge‡ | Orchard size (ha) | Open flowers (%) | Temperature (°C) | # honeybee hives | Wind (m s⁻¹) |
|---|---|---|---|---|---|---|---|---|
| **Visitation frequency** | | | | | | | | |
| Honeybees | | | | 06·46* + | | 06·07* − | 23·38*** + | |
| Wild bees | 57·62*** + | 05·19* o > c | 11·36*** e > i | | 24·51*** + | | | |
| Hover flies | 25·54*** + | 17·03*** o > c | | | 10·48** + | | | |
| All-others | 31·91*** + | | 10·65*** e > i | 07·09** − | 07·10** + | | | |
| **Richness of visitors** | | | | | | | | |
| All visitors | 40·43*** + | | 21·34*** e > i | | 08·61** + | | | |
| Wild bees | 54·76*** + | | 12·87*** e > i | | 22·22*** + | 04·50* + | | |
| Fruit set | 5·57* + | NA | | | | | | |

†Orchard management was organic (o) or conventional (c).
‡0 m at the edge (e) of the orchard vs. 100 m into the interior (i) of the orchard (50 m for smaller orchards).
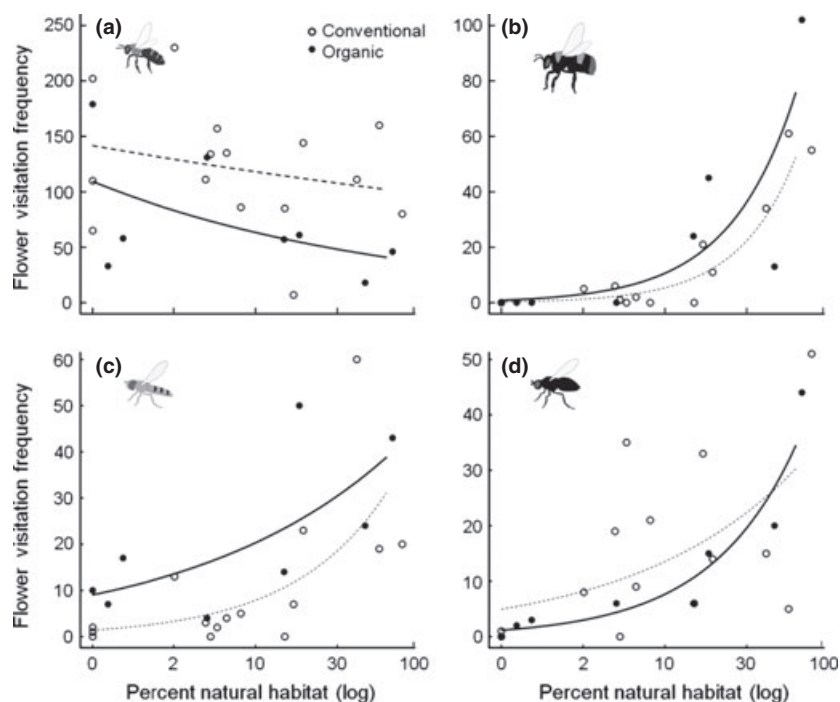
**Fig. 2.** Flower visitation frequency for (a) honeybees, (b) wild bees, (c) hover flies and (d) all-other visitors observed during 80 min in conventional (open, dashed line) and organic (filled, solid line) almond orchards (each point represents one orchard, for statistics see Table 1).

habitat (all $P$ values $< 0.001$, Table 1, Fig. 2b–d, respectively). Furthermore, the richness of visitors (all and wild bee) (estimate $\pm$ SE of the minimum model: $2.5 \pm 0.4$) and almond fruit set ($0.4 \pm 1.2$) were also positively related to the percentage of surrounding natural habitat (Table 1, Figs S1 and S2, Supporting Information).

The flower visitation frequency by wild bees ($P = 0.015$) and hover flies ($P < 0.001$) was greater in organic than conventionally managed orchards (Table 1, Fig. 2). The richness of all visitors did not differ between organic (mean $\pm$ SE: $5.9 \pm 1.5$) and conventional ($5.7 \pm 1.0$) orchards, nor did the species richness of wild bees ($2.9 \pm 0.7$, $3.5 \pm 0.8$, respectively). Flower visitation frequency by wild bees ($P < 0.001$) and all-other visitors ($P = 0.012$) was greater at the orchard edge than the interior. The level of orchard bloom measured as the percentage of flowers open positively influenced the flower visitation frequency by wild bees, hover flies, all-other wild visitors and the species richness of bees and richness of all visitors (all $P$ values $< 0.01$). Other variables including orchard size, temperature and wind had effects on only one or few groups of visitors (Table 1).

### EFFECT OF SEMI-NATURAL VEGETATION STRIPS

In conventional orchards with a low percentage of surrounding natural habitat, the presence of the strip significantly increased the flower visitation frequency by wild bees, hover flies and all-other visitors ($P < 0.01$, Fig. 3), but not by honeybees. The presence of strips also increased

the species richness of wild bees (mean $\pm$ SE: $1.0 \pm 0.0$ low, $2.2 \pm 0.5$ strip, $7.4 \pm 0.9$ high) and richness of all visitors ($1.8 \pm 0.4$ low, $4.8 \pm 0.7$ strip, $10.6 \pm 0.9$ high, Table 2, Fig. S1, Supporting Information). Strips did not increase fruit set in orchards with a low percentage of surrounding natural habitat ($\chi^2 = 1.44$, $P = 0.236$) and for honeybees, the stocking level of hives was a more powerful explanatory variable than the category of surrounding natural habitat ($P < 0.001$, Table 2).

For wild bees, there was a greater flower visitation frequency at the orchard edge than in the interior, both with a strip and when the orchard was surrounded by a high percentage of natural habitat (Table 2, Fig. 3b). For the all-others group of visitors, there was a significant interaction between the distance from the edge and the orchard's surrounding natural habitat ($P = 0.026$, Table 2, Fig. 3d). In orchards with a strip, the visitation frequency at the orchard edge was comparable to levels in orchards with a high percentage of surrounding natural habitat, but in the orchard interior visitation frequency remained low (Table 2, Fig. 3d).

### EFFECT OF FLOWER VISITATION FREQUENCY AND RICHNESS ON FRUIT SET

Fruit set was positively related to the flower visitation frequency by hover flies and wild bees but not by honeybees (Table 3, Fig. 4a). Fruit set was also positively related to the richness of flower visitors and the species richness of wild bees (Table 3, Fig. 4b).
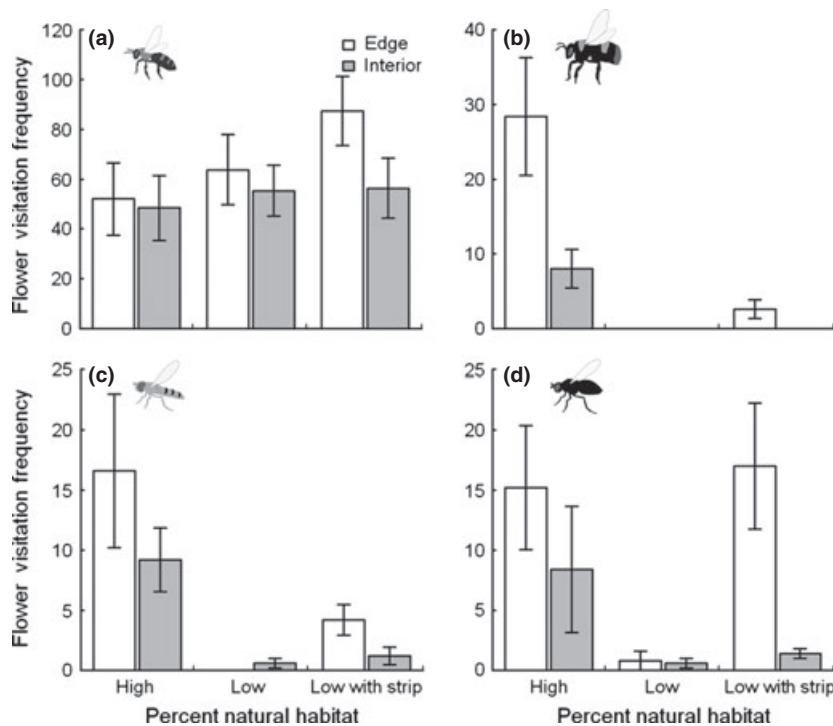
**Fig. 3.** Flower visitation frequency for (a) honeybees, (b) wild bees, (c) hover flies and (d) all-other visitors observed during 40 min at the orchard edge and 40 min at the interior in conventional almond orchards grouped according to the orchards' surrounding natural habitat (1 km): high (>30%), low (<5%), low with a strip of adjacent semi-natural vegetation. Each of the three categories comprises five orchards and means ± SE are given, see also Table 2.

## Discussion

### NATURAL HABITAT AND ORGANIC FARMING TO INCREASE WILD POLLINATION SERVICES

The natural habitat surrounding some almond orchards in California harbours a wide variety of potential pollinators, particularly wild bees and flies. The flower visitation frequencies by these wild pollinators increased with increasing surrounding natural habitat and this seems to have improved almond fruit set. Other studies in California and elsewhere have shown that the amount of natural habitat or isolation from natural habitat does affect wild pollination services of other crop systems (Ricketts *et al.* 2008; Garibaldi *et al.* 2011 and references therein). These studies argue that the benefits for pollination from natural habitat are in part a result of the nesting and food resources provided by the natural habitat, promoting the build-up and persistence of populations of wild flower-visiting insects (Potts *et al.* 2005).

Previous studies have shown mixed effects of organic management on crop flower visitation frequency or abundance of bees and other pollinators (Kremen, Williams & Thorp 2002; Morandin & Winston 2005; Winfree *et al.* 2008; Brittain *et al.* 2010), and this may have been partly related to the fact that surrounding habitat interacts with organic farming (see also Holzschuh, Steffan-Dewenter & Tscharntke 2008). In our study, organic almond orchards enhanced visitation frequency by both wild bees and hover flies but the benefits for these two pollinator groups were different: while visitation frequency by hover flies was enhanced by organic farming independent of the surrounding natural habitat (Fig. 2c), visitation frequency by wild bees was only enhanced by organic farming when orchards were surrounded by natural habitat of at least 10% (Fig. 2d). Hover flies are previously described as being less sensitive to general land intensification than wild bees (Jauker *et al.* 2009) and therefore depend less on extensive natural habitat than wild bees.

Our results support 'the intermediate landscape complexity hypothesis' (Tscharntke *et al.* 2012) postulating that 'cleared landscapes' (<5% natural habitat) will be unlikely to gain any ecosystem services benefits from organic farming alone. In contrast, in 'simple landscapes' (those with 5–10% of natural habitat), organic farming may promote wild pollinators and their services (Haenke *et al.* 2009; Batáry *et al.* 2011). Finally, in 'complex landscapes' (those with more than 30% of natural habitat), the positive effects of nearby natural habitat may dominate with local management playing a minor role (Tscharntke *et al.* 2005; Williams & Kremen 2007; Tscharntke *et al.* 2012; also visible in Fig. 2d for house flies and other minor flower-visiting taxa).

Although we found a strong relationship between flower visitation frequency of hover flies and of wild bees on fruit set, the direct and indirect contributions of these groups to pollination remain to be tested experimentally. The benefit of natural habitat, but not organic farming, on the overall visitation frequency of wild pollinators was strong enough to significantly enhance

**Table 2.** Results of analyses (GLMM) of the flower visitation frequency, richness of visitors and fruit set for the 15 conventional almond orchards only. The orchards were classified into three categories of surrounding natural habitat (1 km): low, low with an adjacent vegetation strip and high (d.f. = 2, see Materials and methods for detail). The table shows the $\chi^2$ values (***$P$ < 0·001, **$P$ < 0·01, *$P$ < 0·05; d.f. = 2 for natural habitat category and honeybee hives, d.f. = 1 for all other variables) from likelihood ratio tests for variables in the minimum models and the direction of the relationship. Blanks represent variables dropped following stepwise deletion or correlated variables (see also Table S2, Supporting Information) not included in the model reduction process

| | Natural habitat (category) | Low with strip × low | Low with strip × high | Low × high | Distance from edge† | Natural habitat × Distance | Orchard size (ha) | Open flowers (%) | Temperature (°C) | No. of honeybee hives |
|---|---|---|---|---|---|---|---|---|---|---|
| **Visitation frequency** | | | | | | | | | | |
| Honeybees | | | | | | | | | 04·68* − | 26·98*** + |
| Wild bees | 42·57*** d.f. 2 | 09·17** low < str. | 23·84*** str. < high | 39·24*** low < high | 10·44** e > i | | | 07·16** + | | |
| Hover flies | 35·62*** d.f. 2 | 11·58*** low < str. | 13·60*** str. < high | 35·32*** low < high | | | | | | |
| All-others | 28·30*** d.f. 2 | 18·71*** low < str. | 2·76 str. = high | 27·16*** low < high | 11·85*** e > i | 07·39* d.f. 2‡ | 07·33** − | | | |
| **Richness of visitors** | | | | | | | | | | |
| All visitors | 34·80*** d.f. 2 | 06·52* low < str. | 18·03*** str. < high | 33·92*** low < high | 17·84*** e > i | | | | | |
| Wild bees | 42·20*** d.f. 2 | 07·67** low < str. | 23·2*** str. < high | 38·22*** low < high | 11·40*** e > i | | | 06·51* + | | |
| Fruit set | (*)§ | | | (*) | NA | NA | | | | |

†0 m at the edge (e) of the orchard vs. 100 m into the interior (i) of the orchard (or 50 m for smaller orchards)
‡Where there is a significant interaction the individual variables should be interpreted with caution
§the model for fruit set with natural habitat category gives an overall $P$-value of 0·06 with a tendency of having more fruits in orchards with high than with low percentage of natural habitat indicated with (*).

**Table 3.** Results of binomial mixed models for the effect of the flower visitation frequency and richness of visitors on fruit set measured at the edge of 23 almond orchards. Visitation frequency was considered for all visitors summed and for the four main visitor groups (honeybees, wild bees, hover flies and all-others). The table shows the $\chi^2$ values and positive directions are indicated with + (***$P < 0.001$, **$P < 0.01$, *$P < 0.05$; d.f. = 1) from likelihood ratio tests with null models

| Pollinator group variable | Fruit set |
|---|---|
| All visitation frequency | 1·70 |
| Honeybee visitation frequency | 0·66 |
| Wild bee visitation frequency | 4·02* (+) |
| Hover fly visitation frequency | 16·45*** (+) |
| All-other visitation frequency | 2·20 |
| All visitation richness | 6·72** (+) |
| Wild bee visitation richness | 6·24* (+) |

fruit set. Without any natural habitat in agricultural landscapes, no benefits of wild pollination services for almond can be expected from organic farming. The lack of relationship between natural habitat and honeybee visitation frequency and between honeybee visitation and fruit set suggests the exciting potential for highest crop yield through combined management for honeybees and wild bees. The high pollination service quality with wild bee visitations may be a result of species interactions making honeybees more effective pollinators (Greenleaf & Kremen 2006) in addition to the fact that some wild bee species pollinate almond more effectively on a per flower basis (Bosch & Blas 1994). Understanding the effects of species interactions on pollination services is therefore a crucial future research goal.

Although our study is based on data of a single year, data of multiple years will most likely not change the main results. We did collect pan trap data of flying insects in most of the orchards investigated here in 2008, 2009 and 2010 and found high species and individual numbers of wild bees and syrphid flies in orchards with high percentage of natural habitat in each of the 3 years (A-M. Klein, C. Brittain & C. Kremen, unpublished data). We noted climatic conditions of the study area over a period of 5 years (2008–2012) and 2008 (when this study took place) was not exceptional different with respect to climatic conditions from the other years.

### HABITAT STRIPS TO INCREASE WILD POLLINATION SERVICES

Strips of semi-natural habitat adjacent to conventional orchards in an otherwise isolated landscape increased the visitation frequency of wild pollinators. However, the increased visitation rate was predominantly confined to the orchard edge, and for wild bees and hover flies, flower visitation remained significantly lower than in orchards surrounded by substantial natural habitat. Habitat strips like hedgerows may support flies (Syrphidae and Tachinidae) (Morandin *et al.* 2011) and wild bees (Hannon & Sisk 2009), because they may provide nesting opportunities and more continuous food resources to support a more abundant and diverse community of flower-visiting insects. Although the habitat strips in this study did not increase fruit set, this may have been because of their relatively poor quality in terms of food resources. Habitat strips may also increase natural pest control in almond orchards (Eilers & Klein 2009; Haenke *et al.* 2009) and if widely implemented provide some connectivity promoting biodiversity within agricultural landscapes (Tscharntke *et al.* 2005; Menz *et al.* 2010). With our study design, we cannot draw conclusions about possible combined effects of organic farming and habitat strips. Future research should study the combined effects of high quality vegetation strips and organic farming for pollination services.

### MANAGEMENT RECOMMENDATION AND APPLICABILITY

Although our results support the conservation of remaining natural habitat because of 'free' pollination services (Chaplin-Kramer, Tuxen-Bettman & Kremen 2011), the great majority of crop growers in our study area and probably elsewhere will not have access to this service. Almond orchards are often isolated from natural habitat, and restoring large amounts of land into semi-natural habitat to increase the accessibility to free pollination services is unlikely to be a financially realistic option. Furthermore, nearby natural habitat does not
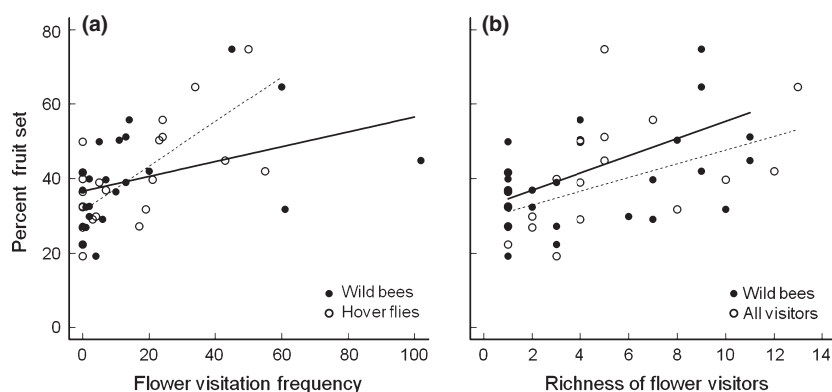


**Fig. 4.** Percentage fruit set in relation to flower visitation frequency by (a) wild bees and hover flies and (b) the richness of flower visitors (wild bees and all visitors) observed during 80 min per orchard in 23 almond orchards. The richness of flower visitors was based on species or morphospecies identifications for bees and 10 additional broader taxonomic groups, see Table 3 for statistics.

guarantee increased yields because multiple interacting processes such as soil fertility, insect pests (Eilers & Klein 2009) and predators (birds, squirrels and rodents) also affect yield (Ghazoul 2007; Klein, Olschewski & Kremen 2008). Organic farming alone will not benefit wild bee pollinators unless orchards are surrounded for at least 10% of natural habitat.

Restoration of flowering hedgerows that support wild pollinators could represent a practical way in which orchard managers can supplement pollination services by honeybees in their orchards with wild pollinators. Active management of such strips may be necessary to improve their nectar, pollen and nesting resources so as to sustain wild bees and increase crop fruit set, but more research needs to identify habitat strip elements essential to increasing their quality. We also found a significant decay of wild pollinators from the orchard edge to the interior, highlighting the need to consider the optimal spatial arrangements of habitat strips.

In conclusion, although we do not suggest that wild insects could replace honeybees for large-scale almond pollination; growers may consider reducing hive stocking rates when orchards are surrounded by natural habitat. Organic growers can consider using slightly lower stocking rates than conventional growers when more than 10% of natural habitat is available. A full economic assessment is needed to determine whether short or long-term monetary benefits can be achieved by investing in restoration of vegetative strips while reducing honeybee hive rentals, under both, organic or conventional management.

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## Supporting Information

Additional Supporting Information may be found in the online version of this article:

**Table S1.** List of flower-visiting taxa and species.

**Table S2.** Correlation matrix of explanatory variables to flower visitation.

**Fig. S1.** Richness of flower visitors in relation to landscape variables.

**Fig. S2.** Fruit set in relation to natural habitat.

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