Agriculture, Ecosystems and Environment 264 (2018) 34–43

Contents lists available at ScienceDirect

Agriculture, Ecosystems and Environment

journal homepage: www.elsevier.com/locate/agee

The intertwined effects of natural vegetation, local flower community, and pollinator diversity on the production of almond trees

David Alomar, Miguel A. González-Estévez, Anna Traveset, Amparo Lázaro*

Mediterranean Institute for Advanced Studies, Global Change Research Group, C/Miquel Marquès 21, 07190, Esporles, Balearic Islands, Spain

ARTICLE INFO

Keywords:
Agro-systems
Crop pollination
Ecosystem service
Fruit set
Honeybees
Landscape characteristics
Local flower community
Pollinator-species richness
Percentage of natural habitat
Prunus dulcis

ABSTRACT

Wild pollinators are a valuable natural resource for crops, as they often increase their production and quality. For this reason, there is currently a great interest in the development of management and conservation tools that help to maintain a wide variety of wild pollinators in agro-systems. To achieve this, it becomes a priority to study the diversity of wild pollinators in relevant crops as well as the local and landscape characteristics that benefit them. The almond tree (*Prunus dulcis*) is a crop of high economic interest, with a large dependence on pollinators due to the self-incompatibility of most of its varieties and, thus, it is very vulnerable to pollinator losses. By using field data and habitat characterization of 18 almond fields in Mallorca Island (Spain), we assessed how the abundance and diversity of pollinators varied with local and landscape characteristics (at 1 and 2 km buffer zones) of the fields, and how those affected almond production (fruit set). Almond trees were mostly pollinated by honeybees, but they were also visited by a large number of wild pollinators. The percentage of natural area in the 2 km buffer zones increased both pollinator-species richness and honeybee visits. At the field level, the flower community in the ground positively influenced almond production, both directly and indirectly by increasing the diversity of wild pollinators. Pollinator-species diversity directly increased fruit production but was negatively affected by honeybee abundance, which suggests that a high density of honeybees might result in negative effects on almond production through competition with wild pollinators. Management strategies to improve almond production might include favoring wild pollinators through the maintenance of natural habitats surrounding crop fields, and preserving the flowering herb community that occurs spontaneously in the groundcover of almond fields in Mediterranean areas.

1. Introduction

Pollination is an essential ecosystem service (Klein et al., 2007) currently threatened by the increasing disappearance of both wild pollinators and honeybees (Biesmeijer et al., 2006, Winfree et al., 2007; Burkle et al., 2013). This pollinator loss is causing great concerns in agriculture production, mainly because two-thirds of the plant species cultivated by humans are pollinated by insects, and 35% of world food production depends on animal pollination (Gallai et al., 2009). Although the use of honeybee hives for crop pollination is common practice (Winfree et al., 2007), it is known that wild pollinators are an important and valuable natural resource for crops, as they usually increase their production (Klein et al., 2007; Garibaldi et al., 2013) and quality (Brittain et al., 2014); and therefore also the net profits earned by farmers (Morandin and Winston, 2005). In addition, wild bees are often more effective crop pollinators than honeybees (Sadeh et al., 2007; Garibaldi et al., 2013; Zhang et al., 2015). For this reason, there is currently a great interest in the development of management and conservation tools that help to maintain a wide variety of wild pollinators in agro-systems (Aizen and Harder, 2009; Potts et al., 2010; Garibaldi et al., 2013). However, the actual role that wild pollinators play in crops of some important productive areas of the world is still unknown. Further research is also needed on the relationship between managed honeybees and wild pollinators. While high local densities of managed honeybees could lead to competition between them and wild pollinators (Goulson, 2003, 2004), a more balanced relationship between wild and managed bees might be beneficial, given that an increase in wild pollinators might enhance honeybee movement (Carvalheiro et al., 2011) and positively influence honeybee effectiveness per visit (Brittain et al., 2013a).

Almond trees (*Prunus dulcis* Mill., F. Rosaceae) are very appreciated world-wide for their nuts and flowers. Currently, Spain has become the second largest almond producer of the world after United States of America, producing the 11.9% (2.31 millions of tons) of world production (FAO, 2010), and the Balearic Islands is one of the main regions of almond production in this country (FAO, 2010). Despite this, there is

* Corresponding author.
E-mail address: amparo.lazaro@imedea.uib-csic.es (A. Lázaro).

https://doi.org/10.1016/j.agee.2018.05.004
Received 27 September 2017; Received in revised form 4 May 2018; Accepted 8 May 2018
0167-8809/ © 2018 Elsevier B.V. All rights reserved.

scarce information either on their pollinator assemblage or the impact that wild pollinators have on almond production in these islands. This crop is very vulnerable to eventual pollinator losses (Garibaldi et al., 2013), as most varieties are self-incompatible (Certal et al., 2002), and it flowers early in the season, when wild bee populations are just starting to emerge from diapause. For this reason, many almond fields depend on rented honeybee hives for their pollination (Vargas and Romero, 1987; Delaplane and Mayer, 2000), but fruit production in commercial almond fields is still usually limited, with fruit sets of ca. 30% (Gary et al., 1976; Tombesi et al., 2016). To solve this problem, several studies have focused on testing the efficiency of other managed bees, such as *Osmia cornuta* (Bosch and Blas, 1994; Márquez et al., 1994), *Osmia lignaria* (Artz et al., 2013), and *Bombus terrestris* (Dag et al., 2006) on the pollination of almond flowers. Some works have also described the diversity of almond trees' wild pollinators (Ortiz-Sánchez and Tianut, 1993; Mandelik and Roll, 2009; Klein et al., 2012; Brittain et al., 2013b), and the local or/and landscape characteristics that benefit them in some areas where it is cultivated, such as Israel (Mandelik and Roll, 2009), California (Klein et al., 2012), Australia (Saunders et al., 2013), and Egypt (Norfolk et al., 2016). These studies show that the increase in local flowering resources and/or the percentage of surrounding natural habitat favor both wild pollinators (Mandelik and Roll, 2009; Klein et al., 2012; Saunders et al., 2013; Norfolk et al., 2016) and fruit production (Klein et al., 2012; Norfolk et al., 2016). However, the relative importance of local versus landscape context on almond production is still little explored, and nothing is known about almond production in productive insular habitats that are characterized by depauperated pollinator communities (e.g. Barrett, 1996; Anderson et al., 2001).

In this paper, we study the role of wild pollinators on almond tree pollination in Mallorca (Balearic Islands, Spain), by analyzing flower visitation frequencies (as a proxy for pollination) and fruit production. Specifically, we determined the abundance and identity of flower visitors and assessed their effect on fruit set in 18 crop fields across Mallorca Island during two years. Furthermore, we evaluated the effect of local (flower abundance and diversity in the groundcover of almond fields) and landscape (percentage of natural habitat surrounding the fields, and field size) characteristics on pollinator visits and fruit production on this crop. Particularly, we asked: (1) Does the frequency of wild pollinator visits to almond trees increase with natural resources for pollinators (natural habitat, floral resources) at the local and landscape levels?; (2) Does the diversity (richness and Simpson's diversity index) of pollinators increase with the availability of natural resources at the local and landscape levels?; (3) Does the presence of managed honeybees affect the abundance and diversity of wild pollinators visiting almond trees? (4) Does almond production increase with the visits of wild pollinators?; and, (5) Does almond production increase with the natural resources for them at the local and landscape levels? We expected almond pollination and fruit production to be positively related to the amount of natural habitat for pollinators both at the local and landscape level. Moreover, we predicted that a large abundance of honeybees might have a negative influence on wild-pollinator visitation.

2. Material and methods

2.1. Study species and sites

The deciduous tree *Prunus dulcis* (Mill.) belongs to the Rosaceae family and is one of the main fruit crops that requires pollination by insects (Garibaldi et al., 2013). Its flowers are open, whitish, and 3 to 5 cm in diameter; they normally appear solitary or in groups of 2 or 4. The fruits, almonds, take 5 to 6 months to mature and are used as food for their nutritional properties (fatty acids, vitamin E, fiber, riboflavin and minerals) and also to make oil and emollients.

We selected 18 almond fields across Mallorca Island, Balearic Islands, Spain (Fig. 1). Sites were distributed across all the area where almond trees are cultivated in Mallorca, with a minimum distance of 850 m between sites. Sites were chosen to differ in size, visual differences in surrounding landscape, and presence of managed honeybee hives (Table A1, Appendix). Almond trees within the fields were of similar size and were planted in rows with each tree being separated by its closer neighbor by 5–10 m. Each study field included several varieties of almond trees, sometimes unknown by the farmers. The mix of varieties also differs among fields, with those flowering earlier having traditional Mallorcan varieties whereas those flowering later having foreign varieties (see Table A1 for varieties in each study site; all the varieties included in this study were auto-incompatible).

2.2. Landscape and local characteristics

To determine landscape characteristics, we calculated the size of each study almond field by means of orto-photos (year 2006). In addition, we estimated the percentages of both natural area (different types of forest and shrublands) and cultivated (mainly trees with dry fruit – such as almond and carob trees –, but also some olive groves and citrics) area in the 1 km- and 2 km- radius buffer zone surrounding the sampling area in each field, as different pollinators may respond to the landscape at different scales (e.g., Steffan-Dewenter et al., 2002; Kennedy et al., 2013). For this, we used ArcMap 10.3 (Environmental Systems Research Institute, Redlands, CA) and maps of land use coverage (Instituto Geográfico Nacional, 2010).

To estimate floral abundance and diversity in the groundcover of almond fields, we used 20 sampling squares (50 × 50 cm), randomly placed across the field each day the pollinator censuses were conducted (see below). Within each square we recorded the abundance and identity of the different plant species with open flowers. With these data we calculated: 1) flower abundance, as the total number of open flowers found in the sampled area; 2) flower richness, as the total number of flowering species found in the sampled area; and 3) flower diversity, as the inverse Simpson (1949) calculated as: $1/\Sigma_i^S p_i^2$, and where p_i was the proportional number of flowers of the species i, and S was the flowering species richness. This index varies from 0 (lowest diversity) to a maximum of [1 − 1/S].

2.3. Pollinator visitation

We observed flower visits to almond tree flowers during two flowering seasons (2015 and 2016), from late January to late March, covering the whole flowering period of this species in Mallorca. To observe flower visitors, we haphazardly selected and marked 20 individual trees located approximately in the middle of each of the 18 orchards. Each sampling day, we performed focal observations of flower-visitors to each of the marked individual trees, using 5 min observation periods (5 min x 20 trees = 100 min observation per site and sampling day each year). Censuses were conducted always between 09:30 and 18.00 h, on days with weather conditions that allowed pollinator activity. The observation protocol was optimized during preliminary observations. Each study year, every site was visited between 3 and 5 days during its flowering peak (always including morning, midday and afternoon), except for 'Sa Marineta' which was observed only one day the first year, and 'Son Blai' which could only be studied the first year (4 sampling days) because almond trees were cut the second sampling year. Excluding from the analyses 'Sa Marineta' the first year, did not change the results (results not shown) and, therefore, we kept this sampling day in the analyses. Table A1 (Appendix) shows the number of sampling days in each site each year.

Observations of flower visitors were conducted on selected branches or areas of the canopy, where we counted the number of flowers (those branches contained a mean of 414 ± 12.76 flowers). During each census period, we recorded the number and identity of flower visitors and the number of flowers contacted by them. A pollinator visit was considered only when the visitor's body contacted the flower

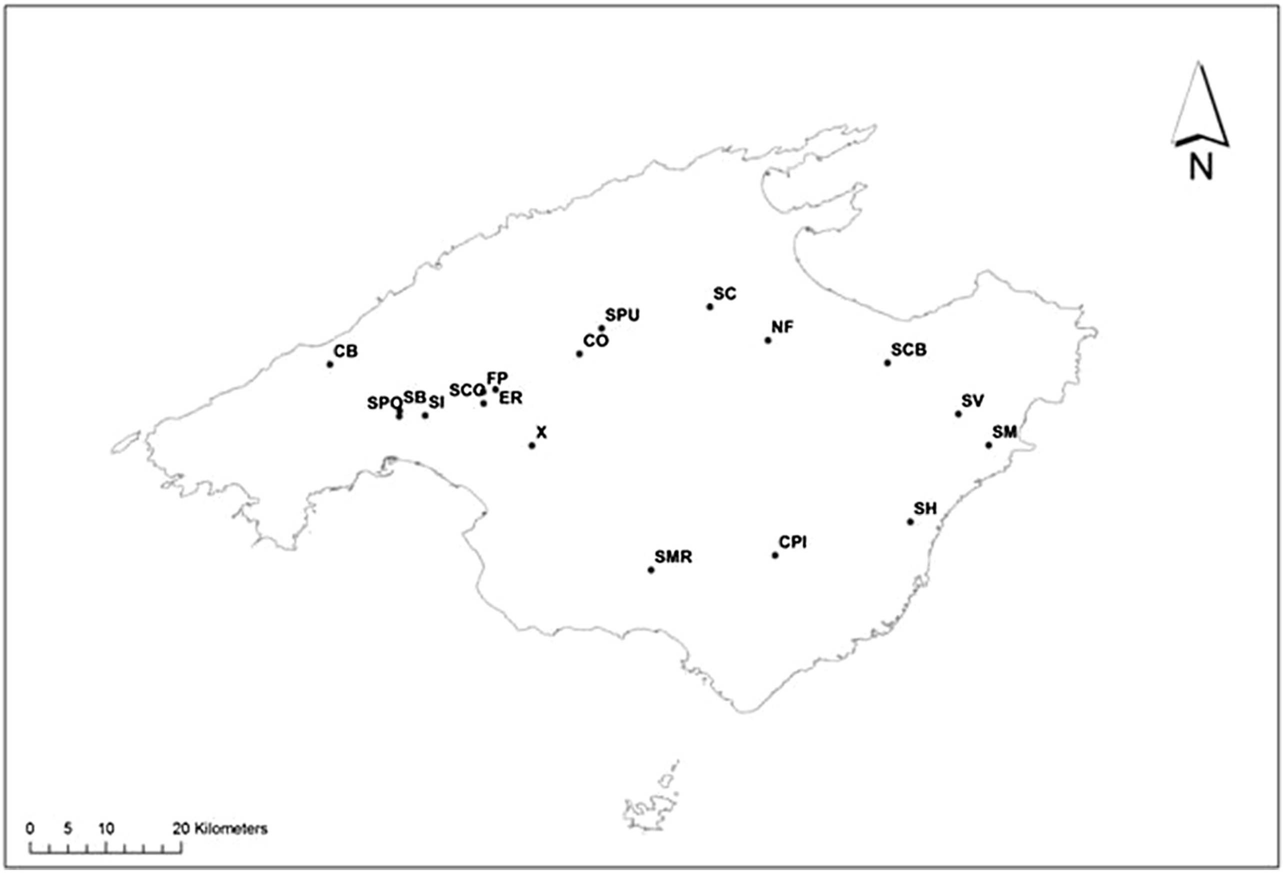

Fig. 1. Map of the 18 almond study fields across Mallorca Island, Balearic Islands, Western Mediterranean. CB: Can Beia; CO: Cooperativa; ER: Es Rafal; FP: Festival Park; SC: Sa Canova; NF: Na Fillola; SM: Sa Marineta; SCB: Ses Cabanasses; SH: S'Hospitalet; SI: S'Indioteria; SB: Son Blai; SCO: Son Cos; SMR: Son Marrano; CPI: Can Pinya; SPO: Son Pou; SPU: Son Pujol; SV: Son Vives; X: Xorrigo.

reproductive organs. We categorized pollinators into the following functional groups (Fenster et al., 2004): honeybees (*Apis melifera*), wild bees, hoverflies (Syrphidae), flies (other Diptera), wasps (Braconidae and Vespidae), butterflies (Lepidoptera) or beetles (Coleoptera). Whenever flower visitors could not be identified to species level in the field, we collected them for subsequent identification by specialized taxonomists. Collected specimens were deposited at the Laboratory of Terrestrial Ecology of the Mediterranean Institute for Advanced Studies (IMEDEA; UIB-CSIC, Spain). After each insect census, we estimated the total number of flowers in each almond tree (almond floral display, hereafter).

To use comparable measures of pollinator visitation, we estimated the number of pollinator visits to 500 flowers for each individual almond tree in a 5-min observation period. We separately calculated honeybee visitation and wild-pollinator visitation (all wild pollinator groups were pooled to obtain greater sample sizes for more robust statistical analyses), to study the response of these two groups of pollinators. To evaluate the diversity of pollinator visits in the fields, we used pollinator-species richness as the number of species visiting an almond tree during an observation period, and the inverse Simpson Index (Simpson, 1949) of pollinator visits (pollinator-species diversity, hereafter). Inverse Simpson Index was calculated as explained above, but in this case p_i was the proportional visitation for the pollinator i, and S was the pollinator species richness, i.e. the number of pollinators visiting a plant species. This index includes both richness and evenness and gives higher weight to common taxa (Gurevitch et al., 2006), which prevents us from overemphasizing incidental pollinator visits.

2.4. Fruit set

At the beginning of the flowering period (end of January to mid of March, depending on the field) each study year, we haphazardly marked one branch in each of the 20 individual trees used to observe pollinators. At the end of July, when fruits were ripe and before almond harvest, we counted the number of developed fruits in these marked branches. We estimated fruit set for each individual tree at each site as the number of developed fruits divided by the number of flowers in the marked branch. Aborted fruits were noted and not counted as developed fruits, because they did not contain edible or marketable almonds.

2.5. Data analysis

All the statistical analyses reported here were conducted in R 3.2.4 (R Development Core Team, 2014). To study the effects of local and landscape characteristics on the abundance and diversity of pollinators, and on fruit production, we used generalized linear mixed models (GLMM, libraries lme4 and glmmADMB), including site and individual nested within site as categorical random variables to avoid pseudoreplication. As response variables, we used the total number of honeybee visits (honeybee visitation, hereafter) and wild pollinators (wild-pollinator visitation, hereafter) to plants estimated per 500 flowers, pollinator-species richness, pollinator-species diversity (Simpson, 1949), and fruit set, in separate models. The local field characteristics, included in the models as continuous predictor variables, were: total abundance and diversity (both flowering-species richness and inverse Simpson diversity index) of wildflowers in the groundcover of almond fields, and the number of open flowers in the individual trees (almond floral display). The landscape characteristics included in the models as

Table 1
Results of the best models showing the relationship between local and landscape characteristics and pollinator visitation rates, species richness and diversity, and the fruit set of almond trees. For each variable that appear in the best models, the χ^2, the degrees of freedom (*df*) and the *P*-values are shown, as well as the direction of the effect for significant continuous variables. The variables involved in significant interactions were also included in the full model.

Model	*Variable*	*Effect direction*	χ^2	*df*	*P*
A) Wild–pollinator visitation	Year		8.64	1	**0.003**
	Flower richness	+	6.72	1	**0.010**
	Honeybee visitation	+	25.02	1	**< 0.0001**
	Almond floral display	–	64.50	1	**< 0.0001**
	Date		2.42	1	0.119
B) Honeybee visitation	Year		10.32	1	**0.001**
	% Natural area 2 km buffer zone	+	3.78	1	0.052
C) Pollinator-species richness	% Natural area 2 km buffer zone	+	9.50	1	**0.002**
	Honeybee visitation	+	4.54	1	**0.033**
	Number of flowers observed	+	5.05	1	**0.025**
D) Pollinator-species diversity	Flower abundance	+	6.70	1	**0.010**
	Honeybee visitation	–	23.81	1	**< 0.0001**
	Almond floral display	–	9.59	1	**0.002**
	% Natural area 2 km buffer zone		2.03	1	0.154
	Date		2.27	1	0.132
E) Fruit set	Year		3.74	1	**0.053**
	Flower abundance	+	75.58	1	**< 0.0001**
	Pollinator-species diversity	+	4.30	1	**0.038**
	Almond floral display	–	141.20	1	**< 0.0001**
	% Natural area 1 km buffer zone		2.49	1	0.114

continuous predictor variables were: the size of almond fields, the percentage of natural area and the percentage of cultivated area in the 1 km- and 2 km-radius buffer zones surrounding the fields. In all models, year was included as a categorical fixed predictor variable, and date (Julian days) as a continuous predictor variable. In preliminary analyses, we also included the presence of honeybee hives as an additional fixed predictor variable; however, this variable was not significant and did not explain the differences in honeybee visits in the fields ($P > 0.05$). Therefore, we included honeybee visitation instead in all models – except the model for honeybee visitation – as an additional predictor variable to test for any potential effect of honeybee competition (Thomson, 2004; Artz et al., 2011; Hudewenz and Klein, 2015). Moreover, in the models of fruit set, we also included the other variables describing pollinator visitation (i.e., wild pollinator visitation, pollinator-species richness and diversity) to assess whether these variables were directly related to fruit production. Lastly, in the model of pollinator-species richness, the number of flowers observed was included as a predictor variable, to exclude any bias related to differences in sampling effort. We used the distributions and link functions that best matched the structure of the data: 1) Zero-Inflated Poisson models (function glmmadmb) and log link function for wild pollinator visitation; 2) Negative binomial distribution and log link function for the analysis of honeybee visitation, to avoid biases related to data overdispersion; 3) Poisson and log link for the analysis of pollinator-species richness; 4) Gamma distribution and log link function for the model of pollinator diversity (Simpson's 1949); and 5) Binomial distribution and link logit for fruit set models. Prior to the models, we ran variation inflation factor (VIF) analyses to identify collinear predictor variables that should be removed from further analyses (Zuur et al., 2009). In all models, the diversity of wildflowers and the percentage of crop area in the buffer zones always showed VIF values larger than 3 and therefore, we included only flower richness and the percentage of natural habitat in further analyses. Pollinator-species richness and pollinator-species diversity were also collinear, as shown by VIF values; in this case, and as we were particularly interested in these two variables, we run models separately with pollinator-species richness and with pollinator-species diversity (both as responses and as predictors for fruit set models). Similarly, as the percentage of natural habitat at 1 km and 2km-buffer zones showed high collinearity, we conducted the models separately for each radius. The rest of the variables showed VIF values lower than 3 and therefore they were not collinear (Zuur et al., 2009). We used the automated model selection (function *dredge,* package MuMIn; Barton, 2014) to select the best models among the set of combinations of predictor variables. We compared the best models with 1km- vs. 2 km-buffer zones, and pollinator-species richness vs. diversity by means of AIC, to detect which predictor variables were the best in each case. Significance of variables is based on Likelihood Ratio Tests (LRT). Best models are given in the result section where predicted means are accompanied by their standard error. As an indication of goodness of fit, we also give for each model the Pearson's coefficient for the correlation between model predictions and observed data.

3. Results

3.1. Flower visitors

In total, we recorded 7733 insect visits to almond trees (2015: 4501; 2016: 3232), 89.69% of which were by honeybees, 4.51% by wild bees (11 species; being *Anthophora* species and *Bombus terrestris* the most frequent ones), 1.53% by hoverflies (5 species), 2.6% by other flies (15 species), and the rest 1.66% corresponded to beetles, butterflies and wasps (see Table A2 in the Appendix for insect species identified on almond fields).

3.2. Landscape and local characteristics on the abundance of pollinator visits

3.2.1. Flower visitation frequencies of wild pollinators

The number of wild-pollinator visits was significantly lower in 2015 than in 2016 (0.70 ± 0.02 vs. 0.90 ± 0.02 visits/500 flowers, respectively; Table 1A). Wild–pollinator visitation was positively related to flower richness (Table 1A; Fig. 2A) and honeybee visitation (Table 1A; Fig. 2B), whereas it significantly decreased with almond flower display (Table 1A; Fig. 2C). Although date also appears in the best model, its effect is non-significant (Table 1A). Pearson's coefficient for the correlation between model predictions and observed data was 0.44. Table 1A (Appendix) shows mean visitation rates by wild pollinators at each site each year.

3.2.2. Flower visitation frequencies of honeybees

Honeybee visitation was significantly higher in 2015 than in 2016 (6.99 ± 0.06 vs. 5.72 ± 0.06 visits/500 flowers, respectively;

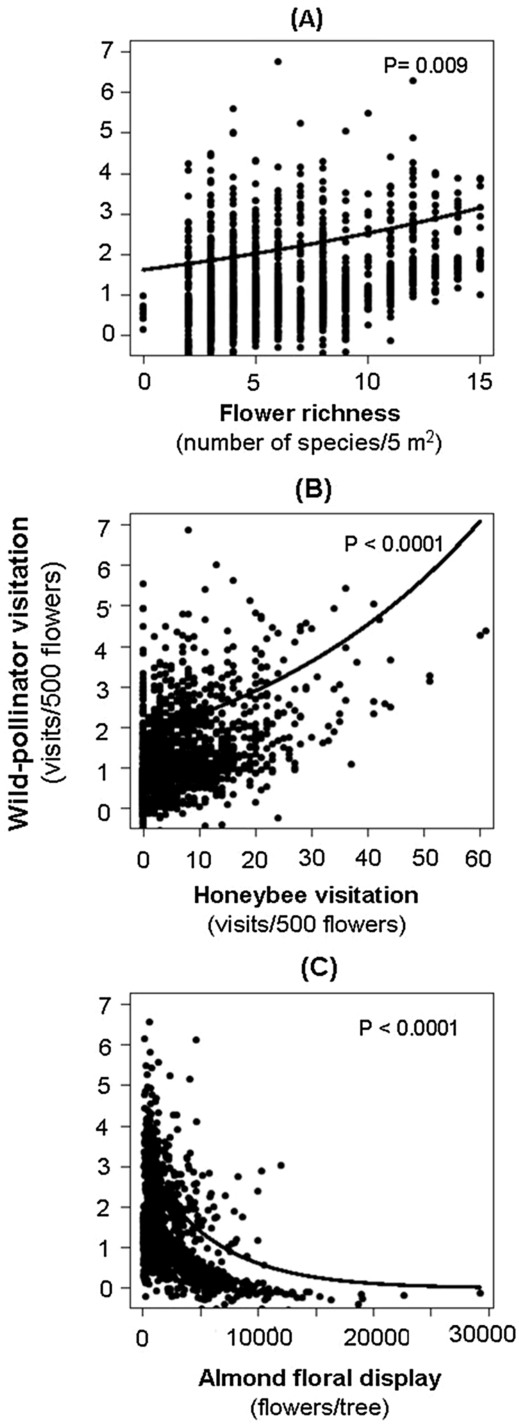

Fig. 2. Relationships between visits of wild pollinators and: (A) flower richness, (B) honeybee visitation, and (C) almond floral display. Lines represent the estimates of the best model and the circles represent partial residuals.

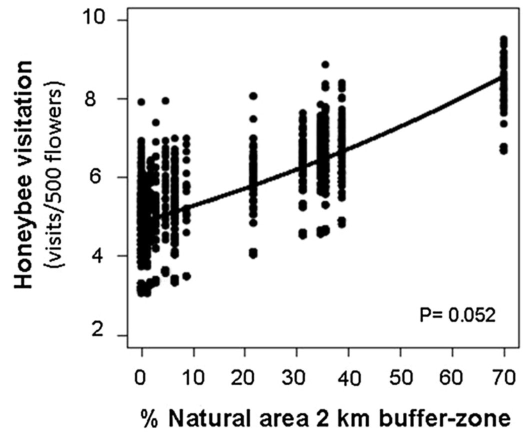

Fig. 3. Relationship between visits of honeybees and the percentage of natural area surrounding the almond fields (radius 2 km). Line represents the estimate of the best model and the circles represent partial residuals.

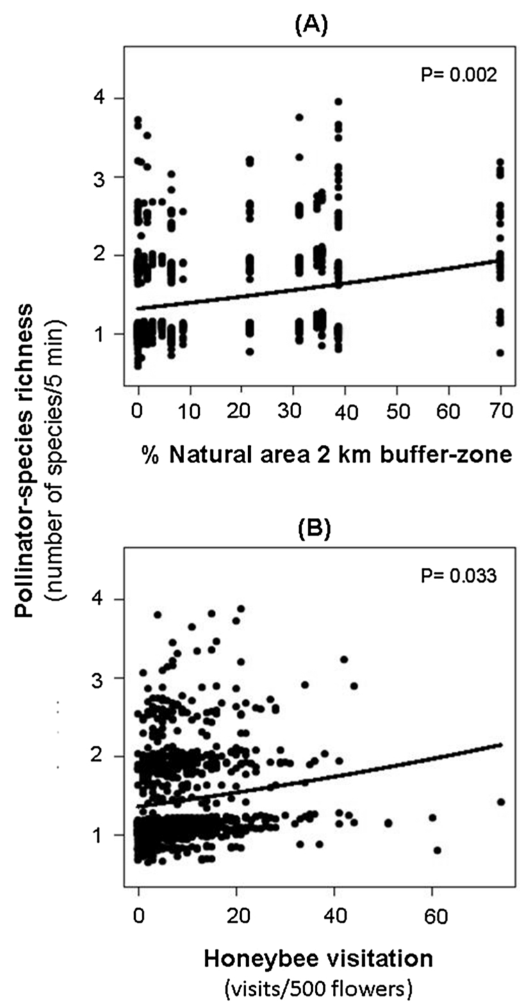

Fig. 4. Relationships between pollinator-species richness and: (A) the percentage of natural area surrounding the almond fields (radius 2 km), and (B) honeybee visitation. The line represents the estimate of the best model and the circles represent partial residuals.

Table 1B), and it was positively related to the percentage of natural habitat surrounding the fields in the 2 km buffer zone (Table 1B; Fig. 3A). Pearson's coefficient for the correlation between model predictions and observed data was 0.25. Table A3 (Appendix) shows mean visitation rates by honeybees at each site each year.

3.3. Landscape and local characteristics on the diversity of pollinator visits

3.3.1. Pollinator-species richness

After controlling for the number of flowers observed, we found that pollinator-species richness was positively related to the percentage of natural area surrounding the fields (Table 1C; Fig. 4A) and to honeybee visitation (Table 1C; Fig. 4B). Pearson's coefficient for the correlation between model predictions and observed data was 0.33. Table A3 (Appendix) shows mean pollinator-species richness per census at each

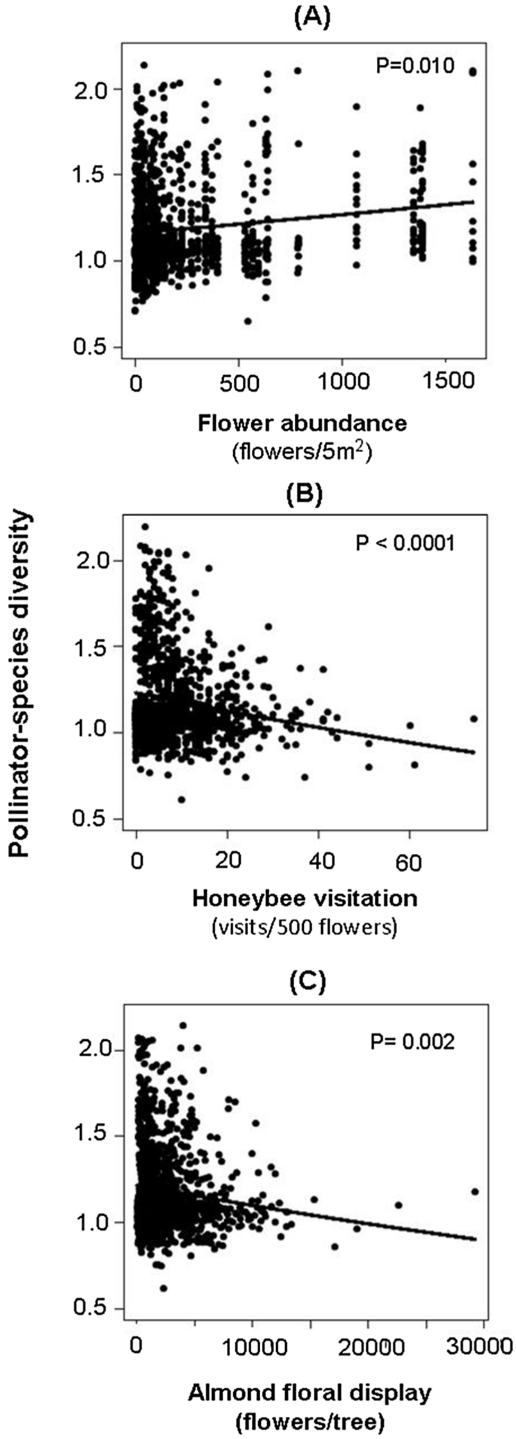

Fig. 5. Relationships between pollinator-species diversity and: (A) flower abundance, (B) honeybee visitation, and (C) almond floral display. The line represents the estimate of the best model and the circles represent partial residuals.

site each year.

3.3.2. Pollinator-species diversity

Pollinator-species diversity increased with flower abundance in the fields (Table 1D; Fig. 5A), whereas it decreased with honeybee visitation (Table 1D; Fig. 5B) and almond floral display (Table 1D; Fig. 5C). Both the percentage of natural habitat in the 2 km buffer zone and date appeared in the best models, but none of them had a significant effect (Table 1D). Pearson's coefficient for the correlation between model predictions and observed data was 0.47. Table A3 (Appendix) shows mean pollinator-species diversity per census at each site each year.

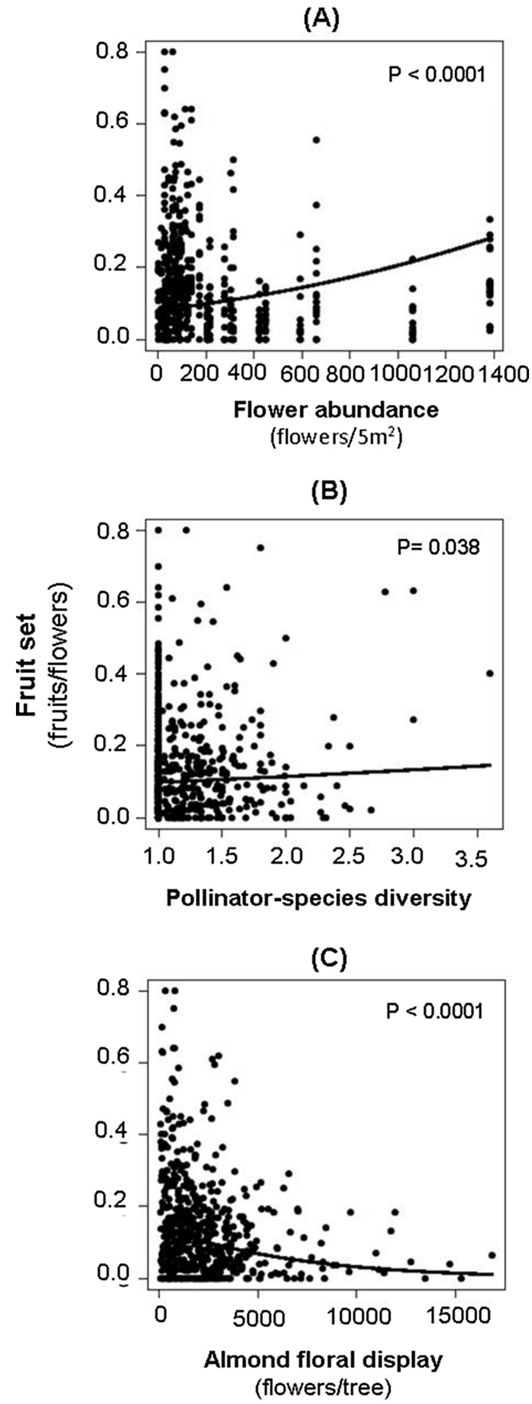

Fig. 6. Relationships between fruit set and: (A) flower abundance, (B) pollinator-species diversity, and (C) almond flower display. The line represents the estimate of the best model and the circles represent fruit set values.

3.4. Landscape and local characteristics on the fruit set

There was a large variation in fruit set values, ranging from 0 to 0.8 fruit/flower depending on the individual and year. Fruit set was slightly lower in 2016, but differences were only marginally non-significant (0.14 ± 0.02 vs. 0.13 ± 0.02 fruits/flowers, respectively; Table 1E). It significantly increased with flower abundance in the fields (Table 1E; Fig. 6A) and with pollinator-species diversity (Table 1E; Fig. 6B). On the contrary, fruit set decreased with almond floral display (Table 1E; Fig. 6C). The percentage of natural habitat in the 1 km buffer zone appeared in the best model, but its effect was non-significant (Table 1E). An alternative model that included the percentage of natural habitat in the 2 km buffer zone (instead of in the 1 km buffer zone) did not differ from the best model presented here either in the variables selected, their significance, or in its AIC value ($\Delta AIC < 2$). Pearson's coefficient for the correlation between model predictions and observed data was 0.86. Table A3 (Appendix) shows mean fruit set at each site each year.

4. Discussion

The large majority (c. 90%) of insect visits to almond flowers were made by honeybees, though a wide assemblage of other species also consume the flower resources of this species. Interestingly, both pollinator-species richness and frequency of honeybee visits increased with the percentage of natural areas surrounding the fields. At the field level, the flower community in each almond field positively influenced almond production, both directly and indirectly by favouring the diversity of wild-pollinators. A greater diversity of pollinators directly increased fruit production, but such diversity was negatively related to honeybee abundance. Hence, through its negative effects on pollinator diversity, a high density of honeybees might result in the decrease of almond production.

4.1. Wild pollinator visitation in almond trees

A total of 31 species of wild pollinators, including wild bees, beetles, butterflies, hoverflies, flies and wasps, visit the flowers of almond trees besides honeybees. This result agrees with previous studies in other parts of the world that show an important presence of honeybees in almond tree fields (e.g., Klein et al., 2012; Brittain et al., 2013b), but also a high diversity of other wild pollinators (Ortiz-Sánchez and Tianut, 1993; Mandelik and Roll, 2009) which often conduct 20–30% of pollinator visits to almond trees (Klein et al., 2012; Norfolk et al., 2016). Consistent with such studies, we found that the principal wild pollinator groups visiting the crop were bees, followed by flies (Ortiz-Sánchez and Tianut, 1993; Klein et al., 2012; Norfolk et al., 2016). Despite their relative lower quantitative importance, these wild insects might be of particular relevance, as they might be more effective pollinators than honeybees, as it has been reported for many crops (Sadeh et al., 2007; Garibaldi et al., 2013; Zhang et al., 2015).

In intensively cultivated areas, honeybee colonies are commonly rented in large numbers by concerned almond growers to maintain sufficient pollination (Vargas and Romero, 1987; Delaplane and Mayer, 2000). We expected the abundance of honeybees to have a negative effect on the abundance of wild pollinators, as high local densities of managed honeybees could favor the competition between honeybees and native pollinators (Goulson, 2003, 2004) and given that several studies have shown negative correlations between flower visitation by honeybees and wild bees (Thomson, 2004; Artz et al., 2011; Hudewenz and Klein, 2015). On the contrary, we found positive relationships between honeybee visitation and wild-pollinator visitation, and pollinator-species richness. It is possible that we have not detected such a negative effect because the abundance of honeybees was not high enough to produce a negative effect on wild pollinators, as suggested by Goras et al. (2016). Alternatively, this result may reflect similar preferences for foraging in natural and diverse habitats. Despite this, we found that the diversity of wild pollinators (measured as Simpson's diversity index), which directly affects fruit production, decreased with the dominance of honeybees.

4.2. Landscape and local characteristics on wild pollinator visitation

Our study shows that the percentage of natural area surrounding the fields increased both pollinator-species richness and honeybee visitation. Several studies have shown that pollinator visitation and richness (Ricketts et al., 2008; Garibaldi et al., 2011; Klein et al., 2012; Bravo-Monroy et al., 2015; Motzke et al., 2016) as well as their spatial and temporal stability (Garibaldi et al., 2011; Bravo-Monroy et al., 2015) increase as the distance of crops to natural or semi-natural areas decreases, or the amount of natural habitat in the surrounding landscape increases. In addition, in previous studies on almond trees, Mandelik and Roll (2009) showed that wild bee visits in almond trees from Israel increased in the edges between crop fields and natural habitats, while Klein et al. (2012) reported increases of wild bee visitation frequencies associated to an increase in natural habitat surrounding the fields. Natural or semi-natural areas within agricultural landscapes often provide habitat for wild pollinator species, as they increase the availability of natural resources on which they depend, such as flowers to forage (Steffan-Dewenter and Tscharntke, 2001; Potts et al., 2003), and nesting (Potts et al., 2005; Williams et al., 2010) and oviposition sites (Johst et al., 2006). Interestingly, whereas we found that honeybee visitation rates were more affected than wild bees' visitation rates by the surrounding landscape, Klein et al. (2012) reported the opposite, probably due to large differences in pollinator composition between the two studies.

As expected, the flower community in almond fields increased the abundance and diversity of flower visitors. A high abundance and diversity of available flowers on the ground usually increase the attractiveness for wild pollinators (Scheper et al., 2015) and are important to ensure resources throughout the season, as it has been shown for honeybees (Requier et al., 2015). Positive relationships between flower cover or vegetation strips and wild pollinators have been documented for several crops (e.g., Nayak et al., 2015; Campbell et al., 2017; but see Holzschuh et al., 2012), including almond trees (Mandelik and Roll, 2009; Klein et al., 2012; Saunders et al., 2013; Norfolk et al., 2016). In this study, we found different effects of flower abundance and richness on the pollinators. First, flower richness was positively related to the overall wild pollinator visitation frequencies. This finding is concordant with other studies on almond trees reporting that the richness of vegetation cover increases the abundance of native bees (Saunders et al., 2013) or pollinators in general (Norfolk et al., 2016). Second, we found that flower abundance in the fields increased the diversity of wild-pollinators, an important variable that positively influenced fruit production. Interestingly, while wild pollinator visitation was considerably affected by the local flower communities in our almond fields, the frequency of honeybees was not, being more affected by the landscape context. This result is contrary to that reported by Földesi et al. (2016) for apple orchards, as in their case groundcover vegetation supported honeybees while wild pollinators were more related to the surrounding landscape. Future research might benefit from the evaluation of the interactions between landscape and local features (e.g. Kennedy et al., 2013) and other variables not considered here, as the varieties or the age of almond trees, which could also affect pollinator foraging.

Lastly, we found a negative effect of almond floral display on per flower wild bee visitation, but not on per flower honeybee visitation. Although larger floral displays may attract more pollinators (Makino et al., 2007; Woods et al., 2012; Földesi et al., 2016), if wild visitation is low, as it is the case in our study sites, the increase in the number of flowers cannot be associated to a similar increase in the number of wild pollinator visits and, instead, the number of wild visitors relative to the number of flowers might decrease (Totland and Matthews, 1998; Ebeling et al., 2008). Taken together, similar visitation rates of honeybees and decreased visitation per flower by wild pollinator leads to lower pollinator-species diversity in larger floral displays. This dominance of honeybees is what might led to pollinator-species diversity decreases with the number of almond flowers in the trees.

4.3. Local and landscape characteristics and wild pollinators on almond production

We expected the percentage of natural habitat in the surrounding landscape to affect almond production, as several studies have shown that pollination services in agricultural landscapes increase with the proximity to natural habitats or the percentage of natural habitat in the landscape (Greenleaf and Kremen, 2006; Ricketts et al., 2008; Garibaldi et al., 2011), and a previous study on almond trees in California showed increases in wild bee visitation frequencies and fruit set associated to an increase in natural habitat surrounding the fields (Klein et al., 2012). In our models, although the percentage of natural habitat significantly affected honeybee visitation and pollinator-species richness and was one of the variables retained in the final model, it did not significantly affect almond fruit set.

On the contrary, local flower abundance in the fields positively influenced almond production, both directly and indirectly by increasing the diversity of wild pollinators. This is interesting, as landscape effects often overcome those at the more local scale (Kremen et al., 2002; Carvalheiro et al., 2010). We found first a direct link between flower abundance in the fields and fruit set. Similar results have been found in almond orchards of Egypt (Norfolk et al., 2016) and in other crops (Motzke et al., 2016), whereas other studies both in almond orchards ('habitat strips', Klein et al., 2012) and other crops (Holzschuh et al., 2012, Campbell et al., 2017) showed no effect of the local flower community on crop yield. Some of these differences might be due to the type of local vegetation considered, as habitat strips could be, in some cases, relatively poor habitats in terms of food resources (Klein et al., 2012). From the management perspective, these results are important because in Mallorca it is common practice to mow wild flowers within orchards in order to prevent competition for pollinators, whereas our study indicates that maintaining the wildflower groundcover might favor almond production.

Our results show a positive effect of pollinator-species diversity on almond production, while no significant relationship between honeybee visitation and fruit set. Moreover, the effects of pollinator diversity on fruit set were stronger than those of pollinator richness. This is not a surprising finding if we consider that 89.69% of visits are conducted by honeybees: the appearance of new species might not translate on effects on fruit set if they are not minimally abundant. Other studies have found fruit set to be related to wild pollinator visitation and not to honeybee visitation (Holzschuh et al., 2012; Klein et al., 2012; Földesi et al., 2016; Norfolk et al., 2016; Campbell et al., 2017). In addition, larger importance of pollinator diversity than of wild pollinator abundances on crop production has been reported in almond trees (Klein et al., 2012), coffee (Klein et al., 2003), pumpkins (Hoehn et al., 2008), and apple orchards (Földesi et al., 2016; Campbell et al., 2017). Wild bees are often more effective pollinators than honeybees (Vicens and Bosch, 2000; Thomson and Goodell, 2001; Sadeh et al., 2007; Garibaldi et al., 2013; Zhang et al., 2015), and in particular in almond trees, non-*Apis* bees have been found to pollinate them more efficiently than honeybees on per flower basis (Bosch and Blas, 1994). In addition, pollination diversity in crops can help buffer pollination services to environmental changes like wind speed (Tuell and Isaacs, 2010; Brittain et al., 2013b) and temperature (Tuell and Isaacs, 2010; Papanikolaou et al., 2016). Moreover, increased pollinator diversity can synergistically increase pollination service through species interactions that alter the behavior and result in increased pollination efficiency (Greenleaf and Kremen, 2006; Brittain et al., 2013a).

Finally, the negative relationship between almond floral display and fruit set may be due to the use of a measure of fruit production relative to the number of flowers. Such negative relationships are expected when there is pollinator saturation, i.e., if the number of flowers increases faster than the number of wild pollinator visits (Ohashi and Yahara, 2002; Mitchell et al., 2004). This idea of pollinator saturation would be further supported by the also negative relationships found between floral display and wild pollinator visitation and pollinator richness. Alternatively, decreasing fruit set as floral display increases could be related to resource availability instead of pollinator saturation. Trees normally over-produce flowers but then they abort fruits based on resource availability (Harder and Johnson, 2009). Indeed, pruning branches in crops is a common practice to increase productivity, because it can ensure better use of growth sources, such as light, mineral nutrition, photosynthesis products, and water (Long, 2007; Macit et al., 2017). However, future studies are necessary to test these hypotheses.

5. Conclusions

Increased natural habitat for pollinators both at the landscape and field level favored wild pollinator visits and almond production. Further studies should analyze additional effects of local and landscape characteristics on the stability of almond pollination and production, as well as their impact on almond quality. This study encourages establishing a series of management strategies, such as maintaining natural habitats surrounding the fields and preserving the local flowering communities within the fields to enhance wild pollinators as a natural resource for almond trees, and to increase production in a sustainable manner.

Acknowledgements

We are very grateful to Andreu Joan, from the 'Conselleria de Medi Ambient, Agricultura i Pesca' of the Regional Government of the Balearic Islands, and to Alejandro Aristondo, from the Cooperative 'Productors Mallorquins de Fruits Secs S.A.T', for all the information they have provided, and for their invaluable cooperation during the process of field selection. We are indebted to all the owners of almond tree fields that allowed us to work in their properties. We thank also Manuel Hidalgo, Manuel Igual, and María Martín for their help in the field. Miguel González Calleja and Charina Cañas, from the Geographical Information Service of IMEDEA, estimated the landscape parameters and provided the map. This project was financed by the Spanish Association of Terrestrial Ecology (AEET). During part of the writing of this manuscript, DA was funded by a Javier Benedí Introduction to Research fellowship, financed by the Mediterranean Institute for Advanced Studies (UIB-CSIC), whereas AL was supported by a postdoctoral contract co-funded by the Regional Government of the Balearic Islands and the European Social Fund 2014-2020.

Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at https://doi.org/10.1016/j.agee.2018.05.004.

References

Aizen, M.A., Harder, L.D., 2009. The global stock of domesticated honey bees is growing slower than agricultural demand for pollination. Curr. Biol. 19, 915–918.
Anderson, G.J., Bernardello, G., Stuessy, T.F., Crawford, D.J., 2001. Breeding system and pollination of selected plants endemic to Juan Fernandez Islands. Am. J. Bot. 88, 220–233.
Artz, D.R., Hsu, C.L., Nault, B.A., 2011. Influence of honey bee, *Apis mellifera*, hives and field size on foraging activity of native bee species in pumpkin fields. Environ. Entomol. 40, 1144–1158.
Artz, D.R., Allan, M.J., Wardell, G.I., Pitts-Singer, T.L., 2013. Nesting site density and distribution affect *Osmia lignaria* (Hymenoptera: Megachilidae) reproductive success and almond yield in a commercial orchard. Insect Conserv. Divers. 6, 715–724.
Barrett, S.C.H., 1996. The reproductive biology and genetics of island plants. Philos. Trans. R. Soc. B 351, 725–733.
Barton, K., 2014. MuMIn: Multi-Model Inference. R Package Version 1.10.0. (Retrieved May 14, 2014, from http://cran.r-project.org/package=MuMIn).
Biesmeijer, J.C., Roberts, S.P.M., Reemer, M., Ohlemüller, R., Edwards, M., Peeters, T., Kunin, W.E., 2006. Parallel declines in pollinators and insect-pollinated plants in Britain and the Netherlands. Science 313, 351–354.
Bosch, J., Blas, M., 1994. Foraging behaviour and pollination efficiency of *Osmia cornuta* and *Apis mellifera* on almond (Hymenoptera, Megachilidae and Apidae). Appl. Entomol. Zool. 29, 1–9.
Bravo-Monroy, L., Tzanopoulos, J., Potts, S.G., 2015. Ecological and social drivers of

coffee pollination in Santander, Colombia. Agric. Ecosyst. Environ. 211, 145–154.
Brittain, C., Williams, N., Kremen, C., Klein, A.M., 2013a. Synergistic effects of non-Apis bees and honey bees for pollination services. Proc. R. Soc. Lond. B Biol. Sci. 280, 20122767.
Brittain, C., Kremen, C., Klein, A.M., 2013b. Biodiversity buffers pollination from changes in environmental conditions. Glob. Chang. Biol. 19, 540–547.
Brittain, C., Kremen, C., Garber, A., Klein, A.M., 2014. Pollination and plant resources change the nutritional quality of almonds for human health. PLoS One 9, e90082.
Burkle, L.A., Marlin, J.C., Knight, T.M., 2013. Plant-pollinator interactions over 120 years: loss of species, co-occurrence, and function. Science 339, 1611–1615.
Campbell, A.J., Wilby, A., Sutton, P., Wäckers, F.L., 2017. Do sown flower strips boost wild pollinator abundance and pollination services in a spring-flowering crop? A case study from UK cider apple orchards. Agric. Ecosyst. Environ. 239, 20–29.
Carvalheiro, L.G., Seymour, C.L., Veldtman, R., Nicolson, S.W., 2010. Pollination services decline with distance from natural habitat even in biodiversity-rich areas. J. Appl. Ecol. 47, 810–820.
Carvalheiro, L.G., Veldtman, R., Shenkute, A.G., Tesfay, G.B., Pirk, C.W.W., Donaldson, J.S., Nicolson, S.W., 2011. Natural and within-farmland biodiversity enhances crop productivity. Ecol. Lett. 14, 251–259.
Certal, A.C., Almeida, R.B., Bošković, R., Oliveira, M.M., Feijó, J.A., 2002. Structural and molecular analysis of self-incompatibility in almond (*Prunus dulcis*). Sex Plant Reprod. 15, 13–20.
Dag, A., Zipori, I., Pleser, Y., 2006. Using bumblebees to improve almond pollination by the honeybee. J. Apic. Res. 45, 215–216.
Delaplane, K.S., Mayer, D.F., 2000. Crop Pollination by Bees. CABI Publishing, New York.
Ebeling, A., Klein, A.M., Schumacher, J., Weisser, W.W., Tscharntke, T., 2008. How does plant richness affect pollinator richness and temporal stability of flower visits? Oikos 117, 1808–1815.
Földesi, R., Kovács-Hostyánszki, A., Kőrösi, Á., Somay, L., Elek, Z., Markó, V., Sárospataki, M., Bakos, R., Varga, Á., Nyisztor, K., Báldi, A., 2016. Relationships between wild bees, hoverflies and pollination success in apple orchards with different landscape contexts. Agric. For. Entomol. 18, 68–75.
FAO, 2010. Food and Agriculture Organization of the United Nations, Statistical Databases. (Available at http://www.fao.org).
Fenster, C.B., Armbruster, W.S., Wilson, P., Dudash, M.R., Thomson, J.D., 2004. Pollination syndromes and floral specialization. Annu. Rev. Ecol. Evol. Syst. 35, 375–403.
Gallai, N., Salles, J.M., Settele, J., Vaissière, B.E., 2009. Economic valuation of the vulnerability of world agriculture confronted with pollinator decline. Ecol. Econ. 68, 810–821.
Garibaldi, L.A., Steffan-Dewenter, I., Kremen, C., Morales, J.M., Bommarco, R., Cunningham, S.A., et al., 2011. Stability of pollination services decreases with isolation from natural areas despite honey bee visits. Ecol. Lett. 14, 1062–1072.
Garibaldi, L.A., Steffan-Dewenter, I., Winfree, R., Aizen, M.A., Bommarco, R., Cunningham, S.A., Klein, A.M., 2013. Wild pollinators enhance fruit set of crops regardless of honey bee abundance. Science 339, 1608–1611.
Gary, N.E., Witherell, P.C., Marston, J.M., 1976. The inter-and intra-orchard distribution of honeybees during almond pollination. J. Apic. Res. 15, 43–50.
Goras, G., Tananaki, C., Dimou, M., Tscheulin, T., Petanidou, T., Thrasyvoulou, A., 2016. Impact of honeybee (*Apis mellifera* L.) density on wild bee foraging behaviour. J. Apic. Sci. 60, 49–62.
Goulson, D., 2003. Effects of introduced bees on native ecosystems. Annu. Rev. Ecol. Evol. Syst. 34, 1–26.
Goulson, D., 2004. Keeping bees in their place: impacts of bees outside their native range. Bee World 85, 45–46.
Greenleaf, S.S., Kremen, C., 2006. Wild bees enhance honey bees' pollination of hybrid sunflower. Proc. Natl. Acad. Sci. U. S. A. 103, 13890–13895.
Gurevitch, J., Scheiner, S.M., Fox, G.A., 2006. Community properties and mechanisms. The Ecology of Plants, 2nd edn. Sinauer, Sunderland, pp. 215–216.
Harder, L.D., Johnson, S.D., 2009. Darwin's beautiful contrivances: evolutionary and functional evidence for floral adaptation. Phytol. 183 (3), 530–545.
Hoehn, P., Tscharntke, T., Tylianakis, J.M., Steffan-Dewent, I., 2008. Functional group diversity of bee pollinators increases crop yield. Proc. R. Soc. Lond. B. Biol. Sci. 275, 2283.
Holzschuh, A., Dudenhöffer, J.H., Tscharntke, T., 2012. Landscapes with wild bee habitats enhance pollination, fruit set and yield of sweet cherry. Biol. Conserv. 153, 101–107.
Hudewenz, A., Klein, A.M., 2015. Red mason bees cannot compete with honey bees for floral resources in a cage experiment. Ecol. Evol. 5, 5049–5056.
IGN (Instituto Geográfico Nacional), 2010. Metodología de Producción de la Base de Datos CLC-Change 2000–2006 enero. Madrid. (Available online: http://centrodedescargas.cnig.es/CentroDescargas/).
Johst, K., Drechsler, M., Thomas, J., Settele, J., 2006. Influence of mowing on the persistence of two endangered large blue butterfly species. J. Appl. Ecol. 43, 333–342.
Kennedy, C.M., Lonsdorf, E., Neel, M.C., Williams, N.M., Ricketts, T.H., Winfree, R., Bommarco, R., 2013. A global quantitative synthesis of local and landscape effects on wild bee pollinators in agroecosystems. Ecol. Lett. 16, 584–599.
Klein, A., Steffan-Dewenter, I., Tscharntke, T., 2003. Pollination of *Coffea canephora* in relation to local and regional agroforestry management. J. Appl. Ecol. 40, 837–845.
Klein, A.M., Vaissiere, B.E., Cane, J.H., Steffan-Dewenter, I., Cunningham, S.A., Kremen, C., Tscharntke, T., 2007. Importance of pollinators in changing landscapes for world crops. Proc. R. Soc. Lond. B. Biol. Sci. 274, 303–313.
Klein, A.M., Brittain, C., Hendrix, S.D., Thorp, R., Williams, N., Kremen, C., 2012. Wild pollination services to California almond rely on semi-natural habitat. J. Appl. Ecol. 49, 723–732.
Kremen, C., Williams, N.M., Thorp, R.W., 2002. Crop pollination from native bees at risk from agricultural intensification. Proc. Natl. Acad. Sci. U. S. A. 99, 16812–16816.
Long, L.E., 2007. Four Simple Steps to Pruning Cherry Trees on Gisela and Other Productive Rootstocks. Oregon State University Extension Service, Covallis, Or.
Márquez, J., Bosch, J., Vicens, N., 1994. Pollens collected by wild and managed populations of the potential orchard pollinator *Osmia cornuta* (Latr.)(Hym., Megachilidae). J. Appl. Entomol. 117, 353–359.
Macit, I., Lang, G.A., Demirsoy, H., 2017. Bud management affects fruit wood, growth, and precocity of cherry trees. Turk. J. Agric. For. 41, 42–49.
Makino, T.T., Ohashi, K., Sakai, S., 2007. How do floral display size and the density of surrounding flowers influence the likelihood of bumble bee revisitation to a plant? Funct. Ecol. 21, 87–95.
Mandelik, Y., Roll, U., 2009. Diversity patterns of wild bees in almond orchards and their surrounding landscape. Isr. J. Plant Sci. 57, 185–191.
Mitchell, R.J., Karron, J.D., Holmquist, K.G., Bell, J.M., 2004. The influence of *Mimulus ringens* floral display size on pollinator visitation patterns. Funct. Ecol. 18, 116–124.
Morandin, L.A., Winston, M.L., 2005. Pollinators provide incentive to preserve natural land in agrosystems. Agric. Ecosyst. Environ. 116, 289–292.
Motzke, I., Klein, A.M., Saleh, S., Wanger, T.C., Tscharntke, T., 2016. Habitat management on multiple spatial scales can enhance bee pollination and crop yield in tropical homegardens. Agric. Ecosyst. Environ. 223, 144–151.
Nayak, G.K., Roberts, S.P., Garratt, M., Breeze, T.D., Tscheulin, T., Harrison-Cripps, J., Potts, S.G., 2015. Interactive effect of floral abundance and semi-natural habitats on pollinators in field beans (*Vicia faba*). Agric. Ecosyst. Environ. 199, 58–66.
Norfolk, O., Eichhorn, M.P., Gilbert, F., 2016. Flowering ground vegetation benefits wild pollinators and fruit set of almond within arid smallholder orchards. Insect Conserv. Divers. 9, 236–243.
Ohashi, K., Yahara, T., 2002. Visit larger displays but probe proportionally fewer flowers: counterintuitive behaviour of nectarcollecting bumble bees achieves an ideal free distribution. Funct. Ecol. 16, 492–503.
Ortiz-Sánchez, F.J., Tianut, A., 1993. Composición y variación latitudinal de la fauna de polinizadores potenciales del almendro, *Prunus dulcis* (Mill.), en la provincia de Granada (sur de Espaóa). Bol. Sanid. Veg. Plagas. 19, 491–502.
Papanikolaou, A.D., Kühn, I., Frenzel, M., Schweiger, O., 2016. Semi-natural habitats mitigate the effects of temperature rise on wild bees. J. Appl. Ecol. 54, 527–536.
Potts, S.G., Vulliamy, B., Dafni, A., Ne'eman, G., Willmer, P., 2003. Linking bees and flowers: how do floral communities structure pollinator communities? Ecology 84, 2628–2642.
Potts, S.G., Vulliamy, B., Roberts, S., O'Toole, C., Dafni, A., Ne'eman, G., Willmer, P., 2005. Role of nesting resources in organising diverse bee communities in a Mediterranean landscape. Ecol. Entomol. 30, 78–85.
Potts, S.G., Biesmeijer, J.C., Kremen, C., Neumann, P., Schweiger, O., Kunin, W.E., 2010. Global pollinator declines: trends, impacts and drivers. Trends Ecol. Evol. 25, 345–353.
R Core Team, 2014. R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria. http://www.R-project.org/.
Requier, F., Odoux, J.F., Tamic, T., Moreau, N., Henry, M., Decourtye, A., Bretagnolle, V., 2015. Honey bee diet in intensive farmland habitats reveals an unexpectedly high flower richness and a major role of weeds. Ecol. Appl. 25, 881–890.
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? Ecol. Lett. 11, 499–515.
Sadeh, A., Shmida, A., Keasar, T., 2007. The carpenter bee *Xylocopa pubescens* as an agricultural pollinator in greenhouses. Apidologie 38, 508–517.
Saunders, M.E., Luck, G.W., Mayfield, M.M., 2013. Almond orchards with living ground cover host more wild insect pollinators. J. Insect Conserv. 17, 1011–1025.
Scheper, J., Bommarco, R., Holzschuh, A., Potts, S.G., Riedinger, V., Roberts, S.P.M., Rundlöf, M., Smith, H.G., Steffan-Dewenter, I., Wickens, J.B., Wickens, V.J., Kleinj, D., 2015. Local and landscape-level floral resources explain effects of wildflower strips on wild bees across four European countries. J. Appl. Ecol. 52, 1165–1175.
Simpson, E.H., 1949. Measurement of diversity. Nature 163, 688.
Steffan-Dewenter, I., Tscharntke, T., 2001. Succession of bee communities on fallows. Ecography 24, 83–93.
Steffan-Dewenter, I., Münzenberg, U., Bürger, C., Thies, C., Tscharntke, T., 2002. Scale-dependent effects of landscape context on three pollinator guilds. Ecology 83, 1421–1432.
Thomson, D., 2004. Competitive interactions between the invasive European honey bee and native bumble bees. Ecology 85, 458–470.
Thomson, J.D., Goodell, K., 2001. Pollen removal and deposition by honeybee and bumblebee visitors to apple and almond flowers. J. Appl. Ecol. 38, 1032–1044.
Tombesi, S., Lampinen, B., Metcalf, S., DeJong, T., 2016. Yield in almond is related more to the abundance of flowers than the relative number of flowers that set fruit. Calif. Agric. 71, 68–74.
Totland, Ø., Matthews, I., 1998. Determinants of pollinator activity and flower preference in the early spring blooming *Crocus vernus*. Acta Oecol. 19, 155–165.
Tuell, J.K., Isaacs, R., 2010. Weather during bloom affects pollination and yield of highbush blueberry. J. Econ. Entomol. 103, 557–562.
Vargas, M.J., Romero, M.A., 1987. Mejora del almendro en Cataluña. Frutic. Prof. 11, 93–98.
Vicens, N., Bosch, J., 2000. Pollinating efficacy of *Osmia cornuta* and *Apis mellifera* (Hymenoptera: Megachilidae, Apidae) on 'red Delicious' apple. Environ. Entomol. 29, 235–240.
Williams, N.M., Crone, E.E., T'ai, H.R., Minckley, R.L., Packer, L., Potts, S.G., 2010. Ecological and life-history traits predict bee species responses to environmental disturbances. Biol. Conserv. 143, 2280–2291.
Winfree, R., Williams, N.M., Dushoff, J., Kremen, C., 2007. Native bees provide insurance

against ongoing honey bee losses. Ecol. Lett. 10, 1105–1113.
Woods, T.M., Jonas, J.L., Ferguson, C.J., 2012. The invasive *Lespedeza cuneata* attracts more insect pollinators than native congeners in tallgrass prairie with variable impacts. Biol. Invasions 14, 1045–1059.
Zhang, H., Huang, J., Williams, P.H., Vaissière, B.E., Zhou, Z., Gai, Q., Dong, J., An, J., 2015. Managed bumblebees outperform honeybees in increasing peach fruit set in China: different limiting processes with different pollinators. PLoS One 10, e0121143.
Zuur, A., Ieno, E.N., Walker, N., Saveliev, A.A., Smith, G.M., 2009. Mixed Effects Models and Extensions in Ecology with R. Springer Science and Business Media.