Mass flowering crops in a patchy agricultural landscape can reduce bee abundance in adjacent shrublands

Ana Montero-Castaño[a,*], F. Javier Ortiz-Sánchez[b], Montserrat Vilà[c]

[a] Estación Biológica de Doñana (EBD-CSIC), Avda. Américo Vespucio s/n, Isla de la Cartuja, 41092 Sevilla, Spain
[b] Universidad de Almería, Grupo de Investigación "Transferencia de I+D en el Área de Recursos Naturales", Ctra. de Sacramento s/n, 04120 La Cañada, Almería, Spain
[c] Estación Biológica de Doñana (EBD-CSIC), Avda. Américo Vespucio s/n, Isla de la Cartuja, 41092 Sevilla, Spain

ARTICLE INFO

ABSTRACT

Pollinator spill-over among habitats can arise in order to fulfill the pollination function and whenever differences in floral offering change over time or space. Flowering crops offer pulsed and abundant floral resources (i.e., mass flowering crops) that might promote pollinator spill-over between cultivated and adjacent natural areas. We explored pollinator patterns in the mass flowering legume crop *Hedysarum coronarium* and its influence on the bee pollinator communities of adjacent shrublands in a heterogeneous and patchy agricultural landscape. We studied the temporal (i.e., during vs. after mass flowering in adjacent shrublands) and spatial (i.e., inside crops, adjacent and distant shrublands during mass flowering) functional pollinator spill-over. The honeybee was highly attracted to *Hedysarum* crops, yet its abundance and that of other bee species visiting native plants in adjacent shrublands did not differ during and after *Hedysarum* mass flowering. However, at the landscape scale, the honeybee and the other bee species were less abundant in shrublands adjacent to *Hedysarum* crops compared to distant ones; their visitation rates showing a similar trend.

These results show that some mass flowering crops can influence pollinator patterns in the surrounding landscape by competing for generalist pollinators with native plants. The characteristics of the crop species and the landscape can modulate and determine the role of mass flowering crops as competitors or supporters of wild pollinators for adjacent natural areas.

© 2016 Elsevier B.V. All rights reserved.

1. Introduction

There is growing concern about local and regional declines in pollinator species and the pollination services they provide (Bartomeus et al., 2013; Potts et al., 2010). Moreover, plant–pollinator interactions may be even more sensitive than the species themselves (Tylianakis et al., 2008), and factors driving the decline of pollinators might interact in non-additive ways (González-Varo et al., 2013).

More than 75% of the cultivated species depend on, or benefit from, animal mediated pollination (Klein et al., 2007), and the area devoted to pollinator-dependent crops is disproportionately growing (Aizen et al., 2008). In this context, during the last two decades, scientists have explored the role of remaining natural areas within agricultural landscapes as reservoirs of pollinators to provide pollination service to pollinator-dependent crops. Maintaining and restoring these areas in agricultural landscapes is one of the most commonly implemented agri-environment schemes. The underlying rationale is that remaining natural areas offer pollinators feeding resources and/or nesting sites not provided by the crop or not stable over time due to the inherent disturbance frequency (Westphal et al., 2003).

Pollinators move from one area to another in order to meet their feeding and/or nesting requirements. When such a movement results in the achievement of their functions (e.g., pollination), it is called functional spill-over (hereafter, spill-over) (Blitzer et al., 2012). Spill-over can occur whenever the offer of required floral resources differs between habitats; therefore, it can occur in both directions. However, only recently has the spill-over of pollinators

from entomophilous mass flowering crops (MFCs, hereafter) to natural habitats received the attention of scientists and managers (Blitzer et al., 2012; Holzschuh et al., 2011). MFCs, despite offering only pulsed floral rewards, could compensate for food resource limitation during periodic intervals, and help in maintaining and enhancing pollinator communities in agricultural landscapes (Westphal et al., 2003), as long as nesting sites and other feeding areas are also available within the foraging ranges of pollinators. Thus, those natural areas that offer alternative resources and that are close to MFCs could benefit from a pollinator spill-over from MFCs. That is, the MFC could exert a magnet effect (Johnson et al., 2003; Molina-Montenegro et al., 2008) over close natural areas. This magnet effect would more likely occur in heterogeneous agricultural landscapes (Blitzer et al., 2012).

In addition to spill-over between habitats with different resource offer at a given period of time (i.e., spatial spill-over), differences in resource offer between habitats can also arise at different moments in time (i.e., temporal spill-over). For instance, the high floral rewards of a MFC compared to its surrounding habitats can be reverted after the MFC flowering peak (Hanley et al., 2011).

Here we study the effect of the highly rewarding *Hedysarum coronarium* L. MFC on the pollinator community in adjacent shrublands in a patchy and heterogeneous Mediterranean agricultural landscape. We specifically focus on the bee pollinator community because this MFC is mainly bee-pollinated (the honeybee, *Apis mellifera* L., accounting for more than the 80% of its visits; Montero-Castaño et al., 2014). We address the following questions: (a) Does the MFC affect the bee community visiting plant species in adjacent shrublands through a temporal bee spill-over during and after mass flowering? (b) Is there a spatial bee spill-over from the MFC to adjacent shrublands during mass flowering? (c) Is the role of the honeybee (the main pollinator of the MFC) different from that of the other bee species, for both the temporal and spatial spill-over?

We expect the MFC to attract a large number of bees and to exert a magnet effect on adjacent shrublands. That is, increasing the abundance of bees in adjacent shrublands compared to shrublands away from MFCs (i.e., spatial spill-over). Additionally, after mass flowering, bees may spill-over from the MFC to adjacent shrublands (i.e., temporal spill-over). We expect both temporal and spatial spill-over to be largely mediated by the honeybee, as it is the main pollinator of the MFC.

2. Materials and methods

2.1. Crop species

The MFC species studied was *H. coronarium* L. (Fabaceae; hereafter *Hedysarum*). *Hedysarum* is a short-lived N-fixing perennial (Bullitta et al., 2000; Sulas et al., 2000) that can reach a height of 1.5 m (Bustamante et al., 1998; Montes Pérez, 2016). Its inflorescences are racemes with up to 30 pink flowers rich in pollen and nectar that bloom during April and May. Its flowers are self-compatible, although they need to be tripped, and have high out-crossing rates (Louati-Namouchi et al., 2000; Yagoubi and Chriki, 2000). Bees are the primary pollinators of *Hedysarum* with the honeybee being the most abundant (Louati-Namouchi et al., 2000; Montero-Castaño et al., 2014; Satta et al., 2000).

2.2. Study sites

We conducted our study in Menorca (Balearic Islands, Spain), where *Hedysarum* was introduced between the end of the 18th and the beginning of the 19th centuries (Ortells and Campos, 1983). Since 1860 it has been used in a traditional cyclical agro-farming system (Bustamante et al., 2007) which consists of growing crops of *Hedysarum* for two consecutive years, followed by cereal cropping in the third year, and leaving the land fallow during the fourth year (Bustamante et al., 2007). To some extent, this traditional system is still present in the extensive and heterogeneous agricultural landscape of the island, but the area devoted to it has been reduced by 97% in the last three decades due to land use intensification (Bustamante et al., 2000; Díaz-Ambrona Medrano et al., 2014). Currently, the public administration is attempting to restrain this trend by subsidizing *Hedysarum* crops.

Hedysarum is the only spring MFC on the island. Most *Hedysarum* crops are harvested during the flowering peak, when the balance between plant yield and its nutritional value is greatest (Bustamante et al., 2005), in order to provide feed for cattle during the summer.

In 2009, to explore whether there was a temporal bee spill-over between *Hedysarum* crops and adjacent shrublands, we selected four Mediterranean shrublands adjacent to *Hedysarum* crops (≤10 m apart), which were studied during and after mass flowering (i.e., after crops were harvested during the flowering peak). The distance among study shrublands ranged from 500 m to 12.01 km.

Table 1
Location, area and flower density of each study shrubland or *Hedysarum* MFC. The land uses of the 500 m radius surrounding landscape of each study shrubland are also given. Landscape characterization was based on the land-use cover map (Carreras et al., 2007).

Site	Treatment	Year	Latitude	Longitude	Area (m²)	Flower density (flowers/m²)	% Land-uses 500 m landscape			
							MFC	Other crops	Natural areas	Non-natural areas[*]
Binicalaf	Adjacent	2009	39°52′14.81″N	4°10′2.49″E	2940.30	54.65	0.49	34.82	55.17	9.14
	MFC		39°52′16.99″N	4°10′1.25″E	3844.45	208.75				
Binixabó	Adjacent	2009	39°56′12.04″N	4°6′57.23″E	873.54	11.43	0.43	47.03	47.95	4.48
	MFC		39°56′12.82″N	4°6′56.60″E	3379.52	216.88				
Mila1	Adjacent	2009	39°55′29.35″N	4°15′12.05″E	151.53	283.78	4.47	58.60	34.46	2.45
	MFC		39°55′28.61″N	4°15′15.34″E	15542.47	1038.37				
Mila2	Adjacent	2009	39°55′40.88″N	4°15′21.39″E	15837.37	145.05	4.59	55.36	35.89	2.14
	MFC		39°55′39.50″N	4°15′16.90″E	20522.74	1295.31				
Albufera	Distant	2010	39°56′27.50″N	4°15′21.11″E	29742.80	215.63	0.00	4.37	82.03	9.81
Binigurdó	Adjacent	2010	39°59′56.09″N	4°6′2.40″E	2707.70	24.28	0.29	60.54	36.48	2.35
	MFC		39°59′54.93″N	4°6′0.63″E	2240.15	494.51				
Favaraix	Distant	2010	39°58′26.19″N	4°13′39.69″E	13745.07	110.86	0.00	61.86	34.14	2.25
Molí	Adjacent	2010	39°59′50.42″N	4°5′34.13″E	455.82	38.45	1.46	79.30	13.65	5.52
	MFC		39°59′48.71″N	4°5′35.22″E	11487.12	308.52				
Mongofre	Adjacent	2010	39°59′3.85″N	4°13′18.29″E	3090.83	42.43	2.68	63.94	32.98	0.00
	MFC		39°59′3.14″N	4°13′17.40″E	21065.59	589.37				
Palafanguer	Adjacent	2010	39°55′35.74″N	4°14′15.21″E	132.95	323.35	0.78	44.23	54.09	0.88
	MFC		39°55′34.61″N	4°14′15.38″E	6110.35	307.50				

[*] Human settlements and infrastructures.

Although honeybees and bumblebees can fly distances greater than 500 m (Greenleaf et al., 2007; Osborne et al., 2008), pollinators do not usually travel very far when rewards are available in the vicinity (Greenleaf et al., 2007; Johnson et al., 2003; Wolf and Moritz, 2008). Moreover, due to the heterogeneity of the Minorcan agricultural landscape, we considered 500 m to be a sufficient minimum distance to assure shrubland independence.

In 2010, in order to investigate whether there was a spatial bee spill-over at the landscape scale, we selected four *Hedysarum* crops (inside, hereafter) and six Mediterranean shrublands, four adjacent to the selected *Hedysarum* crops (i.e., ≤10 m apart; adjacent, hereafter) and two without *Hedysarum* crops in the surrounding 500 m radius landscape (distant, hereafter). The distance among study shrublands ranged from 690 m to 15.27 km.

For the two study years, the area of MFCs ranged from 2240 to 21066 m^2 with a mean flower density of 557.40 ± 142.85 flowers/m^2. Study shrublands had an area that ranged from 133 to 29743 m^2 (Table 1). They were early successional shrublands of *Quercus ilex* L. and *Olea europaea* L. subsp. *sylvestris* Brot. (Carreras et al., 2007) with a rich herbaceous understory. The flowering community slightly differed among study shrublands but was mainly composed by Leguminosae and Compositae species. The species that overlapped their flowering peak with *Hedysarum* and that contributed the most to the total abundance of floral units (hereafter flowers, according to Dicks et al., 2002) were all legumes, either *Calicotome infesta* (C. Presl) Guss., *Lotus angustissimus* L., *Lotus ornithopodioides* L. and/or *Trifolium campestre* Schreb. There were no honeybee hives within any of the 500 m radius surrounding landscapes (landowners' *personal communication*).

Adjacent and distant shrublands in our 2010 study had similar flowering plant species richness (0.46 ± 0.04 and 0.43 ± 0.03 species/m^2, respectively; $t = -0.067$, *p*-value = 0.950), similar total flower density (100.12 ± 24.49 and 163.24 ± 30.95 flowers/m^2, respectively; $t = 0.616$, *p*-value = 0.571) and showed a proportional similarity index of 0.37 (see below for vegetation surveys and index calculation details).

2.3. Pollination censuses

We conducted pollination censuses during the flowering peak of *Hedysarum* (from 30th April to 25th May and from 28th April to 24th May in 2009 and 2010, respectively) on sunny, warm ($\geq 17\,°C$) and non-windy days, from 10 am to 6 pm. In both years weather conditions fell within the average ranges for these months in the study area (Agencia Estatal de Meteorología (AEMET), 2015).

Unidentified bee pollinator species in the field were caught and sorted into distinct morphospecies for later identification by specialists. Voucher specimens are deposited at Doñana Biological Station (EBD-CSIC).

2.3.1. Temporal bee spill-over

In 2009, in each adjacent shrubland we surveyed two or three target plant species out of seven: *Asphodelus aestivus* Brot., *Cistus albidus* L., *Daucus carota* L., *Galactites tomentosa* Moench, *Hypochoeris achyrophorus* L., *Oxalis pes-caprae* L. and *Urospermum dalechampii* (L.) Scop. ex F. W. Schmidt (Supplementary material, Appendix A). They all shared pollinators with *Hedysarum* and were in their flowering peak during the study period. Moreover, we selected target plant species with low-restrictive flower morphologies because we expected them to attain higher visitation rates than those with more restrictive flower morphologies (Córdoba and Cocucci, 2011).

For each target species we conducted focal censuses that lasted 15 min during which we noted the number and identity of bee pollinators and counted the number of open flowers of the observed target plants. A visitor was considered a pollinator when it entered a flower and touched its reproductive structures.

Censuses were taken daily for 13 days and on average were conducted 3.50 ± 1.35 days before and after crop harvesting. The order of observation of each site, plant species and individual was randomly established. We conducted a total of 134 focal censuses (33.5 h), including 66 during and 68 after *Hedysarum* mass flowering. Each plant species was observed an average of 1.84 ± 0.09 h and 1.89 ± 0.08 h during and after mass flowering, respectively. For statistical analyses, data for each target plant species was pooled.

2.3.2. Spatial bee spill-over

In 2010, during the mass flowering, we conducted bee censuses in the adjacent and distant shrublands by walking along 20 m long and 1 m width parallel transects, for a duration of 10 min. During those 10 min, we noted the identity number and visits of bees and the identity of the plants visited.

In each shrubland we marked between three and 17 parallel transects, depending on the area of the shrubland. In total, we marked 36 and 16 parallel transects in adjacent and distant shrublands, respectively. Each transect was walked an average 5.35 ± 0.35 times (0.89 ± 0.06 h), ranging from two to 11 times. Overall, we conducted a total of 278 transect walks (46.33 h): 164 (27.33 h) in adjacent and 114 (19.00 h) in distant shrublands, respectively.

The sampling order of shrublands and of transects within shrublands was randomly established. We sampled shrublands until we found no new plant-bee pollination interaction after six or more transect walks according to rarefaction curves (Supplementary material, Appendix B), which we considered a good compromise between sampling effort and data accuracy. For statistical analyses, data for each study shrubland or crop was pooled.

To account for the abundance and richness of flowers in the shrublands, quadrats (0.4×0.4 m) were laid at every meter along each transect in the shrublands. All plant species were identified and all open flowers were counted. In total we observed 46 plant species belonging to 34 genera and 17 families: 38 species in adjacent shrublands and 24 in distant ones.

Simultaneously, we conducted censuses in the four *Hedysarum* crops (i.e., inside) following the same methodology as in the shrublands. We marked a total of 21 transects (three to seven transects per crop). Each transect was walked an average of 5.24 ± 0.39 times (0.87 ± 0.07 h) accounting for a total of 18.33 h of crop sampling. Quadrats were also laid every meter along each transect inside the crops to account for the abundance of *Hedysarum* flowers.

2.4. Data analyses

We explored the similarity of bee communities, in terms of their identity and relative abundance across time (during vs. after mass flowering, in 2009), and across space (inside, adjacent and distant, in 2010) with the proportional similarity index (PS; Hurlbert, 1978). PS was calculated as: $PS = \Sigma_{i=1}^{n} \min(p_{ia}, p_{ib})$ where for n species p_{ia} is the relative abundance of species i at time a (i.e., during or after *Hedysarum* mass flowering) or at distance a (i.e., inside, adjacent or distant to *Hedysarum* crops) and p_{ib} is the relative abundance of species i at time or distance b. PS values range from 0 (no overlap between species composition) to 1 (complete overlap).

To explore the temporal and spatial spill-over, we built generalized mixed models with bee species richness and abundance per target plant species (in 2009) or per study

shrubland or crop (in 2010) as response variables. In 2010, bee visitation rate and plant-bee pollination interaction richness were also explored as response variables.

2.4.1. Temporal bee spill-over

In 2009, for the response variable bee richness, time (during vs. after mass flowering) was included as a fixed factor in the model. For the response variable bee abundance, pollinator group (honeybee vs. other bees) and its interaction with time were also included as fixed factors. In both models target plant species nested in study shrubland was included as a random factor. The logarithm of the flowers under observation and the logarithm of the hours of observation of each target plant species were included as offsets. Poisson was used as the error distribution family. Post hoc comparisons were conducted by building contrast matrices.

We also explored whether the effect of time and pollinator group in these response variables differed for each target plant species and site by conducting Wilcoxon tests (Supplementary material, Appendix C).

2.4.2. Spatial bee spill-over

In 2010, for the response variable bee species richness, distance (inside, adjacent and distant) was included as a fixed factor in the model and study site as a random factor. For the response variables bee abundance and visitation rate, pollinator group (honeybee vs. other bees) and its interaction with distance were also included as fixed factors and study site as a random factor. In the three models, the logarithm of the number of 10 min transect walks conducted in each shrubland or crop was included as offset. Poisson was used as the error distribution family. Post hoc comparisons were conducted by building contrast matrices.

We are aware that the number of replicates is unbalanced among treatments with distant shrublands underrepresented. To account for this limitation, we repeated the analyses by randomly excluding two MFC and two adjacent shrublands while keeping the geographical spatial distribution of the study sites. The results obtained did not qualitatively differ from those including all study sites (Supplementary material, Appendix D).

Additionally, we explored whether the richness of plant-bee pollination interactions differed between adjacent and distant shrublands by conducting Wilcoxon tests.

All analyses were conducted in R (R Development Core Team, 2014). We used the library *nlme* for building the generalized mixed models and the library *multcomp* for building the post hoc comparisons. Mean ± SE values are given throughout the text unless otherwise specified.

3. Results

Pooling the 2009 and 2010 data, we observed a total of 25 bee species belonging to 16 genera, all of them considered native in the study area. Nine species visited *Hedysarum* crops while 23 species visited plants in shrublands (19 in adjacent and 14 in distant ones). All bee species that visited *Hedysarum* were shared with shrubland plants except two, *Bombus terrestris* L. and *Eucera numida* Lepeletier, which were exclusive to *Hedysarum* MFC (Table 2).

3.1. Temporal bee spill-over

In adjacent shrublands there were not significant differences in bee species richness in target plant species during and after *Hedysarum* mass flowering (during = 0.028 ± 0.008 and after = 0.035 ± 0.014 species/flower/h, Table 3). Despite that, the composition and relative abundance of the species partially differed during and after mass flowering, as indicated by the proportional similarity index PS = 0.65.

Table 2
Bee pollinator species observed during 2009 and 2010 with indication of whether they were observed inside *Hedysarum* MFCs and/or in adjacent or distant shrublands.

Species	Family	MFC	Shrublands	
			Adjacent	Distant
Andrena flavipes	Andrenidae		X	
Andrena nigroolivacea	Andrenidae		X	X
Andrena ovatula	Andrenidae	X	X	
Andrena parviceps	Andrenidae		X	
Andrena tenuistriata	Andrenidae		X	
Anthophora plumipes	Apidae		X	
Apis mellifera	Apidae	X	X	X
Bombus terrestris	Apidae	X		
Ceratina cucurbitina	Anthophoridae		X	X
Ceratina dallatorreana	Anthophoridae		X	
Chalicodoma sicula	Megachilidae	X		X
Eucera numida	Apidae	X		
Eucera oraniensis	Apidae	X	X	X
Halictus gemmeus	Halictidae		X	X
Halictus scabiosae	Halictidae		X	X
Hoplitis praestans	Megachilidae			X
Hoplosmia ligurica	Megachilidae			X
Hylaeus clypearis	Megachilidae		X	
Hymenoptera *sp.1*	–			X
Lasioglossum sp.1	Halictidae		X	X
Lasioglossum sp.2	Halictidae			X
Megachile pilidens	Megachilidae	X	X	
Osmia caerulescens	Megachilidae	X	X	X
Osmia niveata	Megachilidae		X	
Rhodanthidium septemdentatum	Megachilidae	X	X	X
Scoliidae *sp.1*	Scoliidae		X	

Honeybee abundance did not differ between during and after mass flowering, and neither did the combined abundance of all other bee species (Fig. 1 and Table 3).

When analyzing each target plant species in each site separately, the trend was not consistent. For example, after mass flowering, honeybee abundance marginally decreased in one target plant species (*A. aestivus*) while in other two target plant species (*C. albidus* and *G. tomentosa* in the *Binicalaf* site) the abundance of other bees increased (Fig. C.2). *Hedysarum* mass flowering also affected bee species richness in three target plant species. In *C. albidus* and *G. tomentosa* at the *Mila1* site, bee species richness increased after mass flowering while in *G. tomentosa* at the *Binicalaf* site it decreased.

3.2. Spatial bee spill-over

Bee species richness did not differ with distance to *Hedysarum* crops (0.128 ± 0.033, 0.201 ± 0.075 and 0.150 ± 0.017 species/transect, for inside, adjacent and distant sites, respectively; Table 4). However, composition and relative abundance of the species partially differed across distances as indicated by the proportional similarity indexes. The similarity in bee communities was the highest between adjacent and distant shrublands (PS = 0.58), in which the honeybee and the wild bee *Eucera oraniensis* Lepeletier were the most abundant species (Fig. 2). Meanwhile, the bee community in *Hedysarum* crops was largely dominated by the honeybee but lacked *E. oraniensis*. The similarity of *Hedysarum* crop with adjacent (PS = 0.30) and distant (PS = 0.36) shrublands was low (Fig. 2). When the bee pollinator communities of *Hedysarum* crops and adjacent shrublands were pooled together, the similarity with distant shrublands was PS = 0.62.

Distance to *Hedysarum* crops affected bee abundance, and the effect differed between pollinator groups (Fig. 3a and Table 4). The abundance of honeybees and other bees was almost two times higher in distant than in adjacent shrublands. Inside *Hedysarum* crops, the two pollinator groups showed different trends. The

Table 3
Effect of *Hedysarum* mass flowering time (i.e., during vs. after) on bee pollinator species richness and abundance in shrublands adjacent to *Hedysarum* MFCs. The effect on abundance is explored for the honeybee and other bee species separately.

Response variable	N	Group	Contrast	Estimate	SE	Z	p-value
Richness	18	–	After vs. During	0.366	0.402	0.911	0.362
Abundance	36	Honeybee	After vs. During	−0.225	0.459	−0.491	0.858
		Other bees	After vs. During	0.105	0.205	0.509	0.848
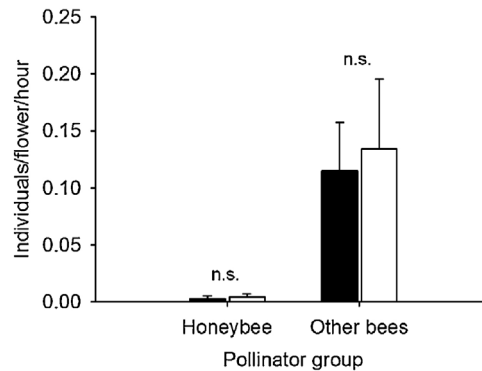
Fig. 1. Temporal spill-over. Mean + SE abundance of the honeybee and other bee species in plants in shrublands adjacent to *Hedysarum* MFCs during (black) and after (bold) mass flowering.

abundance of the honeybee was one order of magnitude higher than in shrublands, while the abundance of other bee species was lower than in distant shrublands and did not differ from that in adjacent shrublands (Fig. 3a and Table 4). When excluding *E. oraniensis* from the analysis, differences in the abundance of other bees were not significant among distances (Table 4).

Visitation rates showed the same trends as abundance of bees (Fig. 3b and Table 4). There were no significant differences in plant-bee pollination interaction richness between adjacent and distant shrublands (0.304 ± 0.053 and 0.303 ± 0.086 interactions/transect, respectively; $N = 6$, $W = 4$, p-value = 1). The most frequently observed interactions in both types of shrublands were between *G. tomentosa* and honeybees (20.37%) and *E. oraniensis* (30.73%).

4. Discussion

4.1. No temporal bee spill-over from Hedysarum MFCs to adjacent shrublands

Contrary to what we expected, we did not observe a temporal spill-over of honeybees from the MFC to adjacent shrublands after *Hedysarum* mass flowering. During mass flowering, the floral offer of MFCs seems to cover all the requirements of the honeybee so that the crops monopolize their visits. However, after mass flowering, due to their large foraging ranges (Greenleaf et al., 2007; Osborne et al., 2008), capacity to locate highly rewarding resources at greater distances (Cresswell and Osborne, 2004) and developed

Table 4
Effect of distance to *Hedysarum* MFCs (i.e., inside, adjacent and distant) on bee pollinator species richness, abundance, visitation rate and on plant-bee pollination interactions richness. The effect on abundance is explored for the honeybee and other bee species separately and for other bees when excluding from the analysis the wild bee *Eucera oraniensis*. Significance levels: *p < 0.05, **p < 0.01, ***p < 0.001.

| Response variable	N	Pollinator group	Contrast	Estimate	SE	Z	p-value	
Richness	10	–	Distant vs. Adjacent	0.152	0.326	0.467	0.887	
			Inside vs. Adjacent	−0.080	0.353	−0.227	0.972	
			Inside vs. Distant	−0.233	0.368	−0.631	0.803	
Abundance	20	Honeybee	Distant vs. Adjacent	1.000	0.336	2.976	0.015	*
			Inside vs. Adjacent	3.887	0.167	23.301	<0.001	***
			Inside vs. Distant	2.887	0.294	9.808	<0.001	***
		Other bees	Distant vs. Adjacent	0.635	0.299	2.122	0.148	
			Inside vs. Adjacent	−0.339	0.170	−1.995	0.194	
			Inside vs. Distant	−3.861	0.196	−19.708	<0.001	***
	10	Other bees excluding *E. oraniensis*	Distant vs. Adjacent	−0.254	0.386	−0.659	0.778	
			Inside vs. Adjacent	0.107	0.184	0.580	0.824	
			Inside vs. Distant	0.361	0.390	0.925	0.612	
Visitation rate	20	Honeybee	Distant vs. Adjacent	0.913	0.267	3.425	0.003	**
			Inside vs. Adjacent	3.315	0.088	37.656	<0.001	***
			Inside vs. Distant	2.401	0.253	9.487	<0.001	***
		Other bees	Distant vs. Adjacent	1.050	0.259	4.056	<0.001	***
			Inside vs. Adjacent	−0.052	0.109	−0.479	0.982	
			Inside vs. Distant	−3.503	0.115	−30.375	<0.001	***
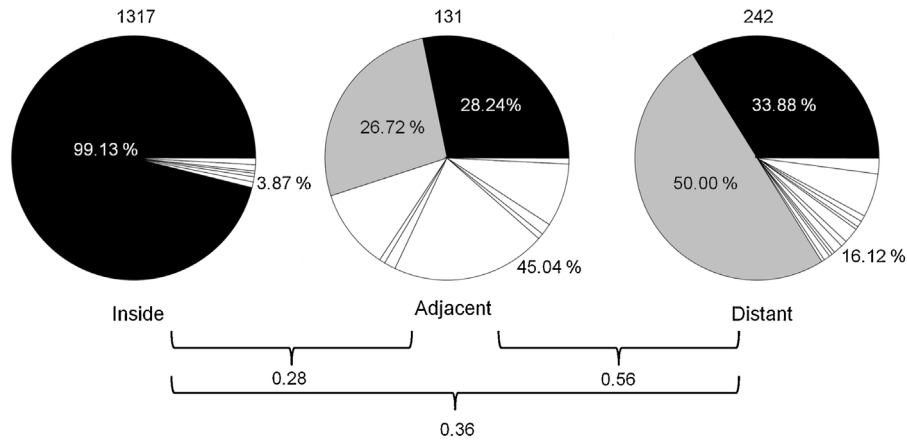
Fig. 2. Pollinator communities similarity. Percentage of bee species inside, adjacent and distant to *Hedysarum* MFCs. The honeybee is represented in black, the wild bee *Eucera oraniensis* in grey and the rest of species in white. Total number of individuals observed in each habitat type is given above each pie chart. Below brackets values for the proportional similarity index (PS) are given.

communication skills (Steffan-Dewenter and Kuhn, 2003), honeybees might move to other still unharvested MFCs or to other highly rewarding plant communities within their foraging ranges, such as old-fields (Gathmann et al., 1994). For instance, in our study system, communities with abundant *G. tomentosa* might be highly attractive to the honeybee. Therefore, the temporal spill-over effect mediated by honeybees in patchy and heterogeneous agricultural landscapes might be spatially diluted.

A temporal spill-over of other bees from MFC to adjacent areas was also not observed. We did not expect the other bee species to be strongly attracted to *Hedysarum* crops as prior studies have shown that most *Hedysarum* visits in cultivated and naturalized populations are made by the honeybee (Montero-Castaño et al., 2014; Satta et al., 2000). The pollinator survey conducted in 2010 inside *Hedysarum* crops also supported this observation, as

the other bee species represented only 3.87% of the total visitors. Thus, even if a temporal spill-over of a particular bee species could occur, it would be difficult to detect it due to their low abundance. In our study system, this was the case for *Megachile pilidens* Alfken and *Osmia caerulescens* L. Despite that the phenologies of these species overlapped with the flowering peak of *Hedysarum* (they were observed visiting *Hedysarum* crops); in adjacent shrublands they were only observed after mass flowering. Therefore, the lack of a significant general pollinator temporal spill-over is due to both non-significant trends for most of target plant species, and to significant but opposed trends that nullify each other for few target plant species.

In addition, other bee species able to access the restrictive flowers of *Hedysarum* are medium to large-sized ones (Córdoba and Cocucci, 2011) with medium-large foraging ranges (Greenleaf
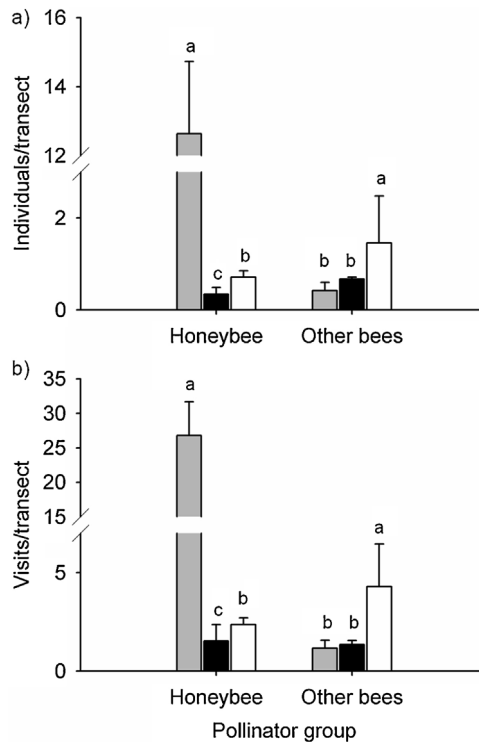

Fig. 3. Spatial spill-over. Mean + SE (a) abundance and (b) visitation rate of the honeybee and other bee species inside (grey), adjacent (black) and distant (bold) to *Hedysarum* MFCs. Different letters above bars represent significant differences within pollinator groups.

et al., 2007), so that their potential temporal spill-over could also be spatially diluted. Nonetheless, we would expect this spatial dilution to occur at shorter distances than in the case of the honeybee because maximum foraging distances for wild bees, which are mostly solitary central place foragers, fall below the ones described for honeybees (Gathmann and Tscharntke, 2002; Steffan-Dewenter and Kuhn, 2003; Steffan-Dewenter and Kuhn, 2003).

4.2. No spatial spill-over from Hedysarum MFCs to adjacent shrublands but the reverse

We did not observe a spatial spill-over from the MFC to adjacent shrublands neither of honeybees nor of other bee species. However, the explanation for this result differs between the two pollinator groups.

The honeybee preferentially selected *Hedysarum* crops and did not spill-over to adjacent shrublands. Pollinators, seek to optimize their floral rewards intake (Armbruster and Herzig, 1984) and might benefit greatly from MFCs, where the relative abundance and quality of available floral resources are usually high (Dietzsch et al., 2011). This behavior is amplified if they have an intensive foraging behavior with short flying distances between consecutive flower visits, as is the case of the honeybee (Gross, 2001). In fact, the predominance of the honeybee in MFCs is not exclusive to *Hedysarum* crops as in many parts of the world crop pollination relies on this single species (Winfree et al., 2007).

In the case of the other bee species, they did not highly select *Hedysarum* MFCs and, consequently, they did not significantly spill-over to adjacent shrublands. We suggest three non-exclusive explanations for the pool of other bee species not highly selecting the MFC. First, flower constancy at the individual level might be more highly associated with social pollinators like the honeybee (Leonhardt and Blüthgen, 2012) than with solitary bees. Therefore, monospecific areas like MFCs do not fulfill the individual requirements of solitary bees. Second, other bee species could be excluded from MFCs due to competition with the honeybee for the use of floral resources (Paini, 2004; Roubik, 1983) or by physical disturbance (Gross and Mackay 1998). Floral resources would not be expected to be limiting in MFCs. However, interspecific competition depends on the relative abundance of interacting species (Steffan-Dewenter and Tscharntke, 2000), and we cannot disregard the possibility of competition to arise due to the high abundance of honeybees inside crops.

Third, other factors co-varying with the presence of MFCs (for instance, some agricultural practices like the use of pesticides), could lead to the avoidance of MFCs by bee species.

Nevertheless, despite that the pool of other bee species did not highly select *Hedysarum* MFCs, it did not avoid them either, as indicated by the similar abundance inside crops and in adjacent shrublands for the pool of other bee species. That is, some particular species might spill-over from MFCs to adjacent shrublands. Most wild bees are central placed foragers (Cresswell et al., 2000) and due to their more restrictive foraging ranges compared to honeybees, their spill-over occurs at smaller spatial scales. However, due to the low abundance of other bee species, we could not conduct analyses for particular species separately to elucidate such specific responses.

Finally, some bee species did not profit from the resources offered by *Hedysarum*. Moreover, they seemed to prefer landscapes without *Hedysarum* MFCs. That was the case for *E. oraniensis,* whose relative abundance was twofold in distant shrublands than in adjacent ones, and in fact, it was the main responsible for the higher bee abundance in distant shrublands compared with adjacent ones. In general, medium to large-sized bees (Greenleaf et al., 2007) are able to perceive their landscapes at larger spatial scales (Steffan-Dewenter et al., 2002). Therefore, regardless of the reason for their not exploiting a particular crop species, these bees can chose landscapes without such MFCs and with high concentrations of their preferred required resources (e.g., nesting sites, food) (Tscharntke et al., 2012).

Our approach allowed us to detect a spatial bee spill-over, not from *Hedysarum* MFC to adjacent natural habitats, but rather the reverse. As *Hedysarum* crops are part of a cyclical agro-farming system (Bustamante et al., 2007) and are grown a maximum of two consecutive years in the same field, their negative effect in the abundance of bee pollinators in adjacent areas could be buffered in the long term. Therefore, we would not expect the observed spill-over to alter the demography of neither pollinator populations nor of the entomophilous wild plants in adjacent shrublands. However, at larger spatial scales than the one considered here, *Hedysarum* MFCs could have an indirect positive effect on the abundance of wild bees in natural areas. If honeybee hives are spread across the Minorcan landscape and *Hedysarum* MFCs attract honeybees not only from adjacent but also from distant shrublands, MFCs could be reducing the abundance of honeybees in natural areas at a large spatial scale. As this species can outcompete wild pollinators (Gross and Mackay, 1998; Paini, 2004; Roubik, 1983), these latter could profit from the decrease of honeybee abundance and increase their visitation rates, as we have observed at smaller spatial scales (Montero-Castaño and Vilà, *unpublished result*). At such large spatial scale, the rotation of crops might not dilute the effect on pollinators and entomophilous wild plants. It would have been very interesting, though not feasible, to test this hypothesis by manipulating the presence and absence of honeybee hives at larger spatial scales like Valido et al. (2014) did.

In addition, and though the study years were representative of the average weather conditions for the study area (Agencia Estatal de Meteorología (AEMET), 2015), pollinator communities show a high interannual variability (Williams et al., 2001). Thus, a long term study would be necessary to elucidate whether the observed pattern is maintained in the long-term or if *Hedysarum* crops support and enhance the abundance of generalist pollinators and provide a benefit through greater pollinator service overall (Holzschuh et al., 2011; Mitchell et al., 2009).

Finally, the extrapolation of our results to other MFCs should be done cautiously and taking into account the particular characteristics of our study crop species, specially its restrictive flower morphology and its high attractiveness to honeybees. For instance, *Hedysarum* MFC can only directly compete for or share with natural areas those pollinators able to access its floral rewards (Córdoba and Cocucci, 2011). Meanwhile, other MFCs with non-restrictive flower morphologies, such as sunflower (*Helianthus annuus* L.) and oilseed rape (*Brassica napus* L.), might compete for or share with natural areas a broader array of pollinators including bees, butterflies, flies and beetles (Bommarco et al., 2012) potentially showing larger spill-over effects on one direction or another.

4.3. Conclusions

In the studied agricultural landscape in Menorca the presence of *Hedysarum* MFCs decreased pollinator abundance in adjacent shrublands by monopolizing the visits of the honeybee, and by attracting some wild bees away from the surrounding natural areas. Thus, the proposed role of MFCs as supporters and sources of wild pollinators for surrounding natural areas should be cautiously analyzed for each particular system. Factors such as the flower morphology (i.e., restrictive or easy access to floral resources) of the crop species, the presence of honeybees and their preference for the crop species and the landscape configuration, might modulate and determine the role of MFCs as supporters and sources of wild pollinators for surrounding natural areas.

Acknowledgements

Supplementary data

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.agee.2016.02.019.

References

Agencia Estatal de Meteorología (AEMET), 2015. http://www.aemet.es/es/serviciosclimaticos/datosclimatologicos/valoresclimatologicos (accessed: 21.10.15.).

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

Armbruster, W.S., Herzig, A.L., 1984. Partitioning and sharing of pollinators by four sympatric species of *Dalechampia* (Euphorbiaceae) in Panama. Ann. Mo. Bot. Gard. 71, 1–16.

Bartomeus, I., Ascher, J.S., Gibbs, J., Danforth, B.N., Wagner, D.L., Hedtke, S.M., Winfree, R., 2013. Historical changes in northeastern US bee pollinators related to shared ecological traits. Proc. Natl. Acad. Sci. U. S. A. 110, 4656–4660.

Blitzer, E.J., Dormann, C.F., Holzschuh, A., Klein, A.M., Rand, T.A., Tscharntke, T., 2012. Spillover of functionally important organisms between managed and natural habitats. Agric. Ecosyst. Environ. 146, 34–43.

Bommarco, R., Marini, L., Vaissière, B.E., 2012. Insect pollination enhances seed yield, quality, and market value in oilseed rape. Oecologia 169, 1025–1032.

Bullitta, S., Saba, P., Bullitta, P., 2000. Seed production and its components in Sardinian germplasm of *Hedysarum coronarium* L. and *H. spinosissimum* L. In: Sulas, L. (Ed.), Legumes for Mediterranean Forage Crops, Pastures and Alternative Uses = Légumineuses Pour Cultures Fourragères, Pâturages et Autres Usages En Région Méditerranéenne. CIHEAM-IAMZ, Zaragoza, pp. 355–358.

Bustamante, J., Allés, A., Espadas, M., Muñoz, J., 1998. El cultivo de la zulla en Menorca (IA): la siembra. Consell Insular de Menorca, Maó, Menorca.

Bustamante, J., Allés, A., Espadas, M., Muñoz, J., 2000. Zulla 1er año. Consell Insular de Menorca, Maó, Menorca.

Bustamante, J., Allés, A., Espadas, M., de Olives, J.R., Rovira, J., 2005. Valoración bromatológica de zullares de más de un año. Consell Insular de Menorca, Maó, Menorca.

Bustamante, J., Allés, A., Espadas, M., 2007. Alternativa de tres hojas o sementers. Consell Insular de Menorca, Maó, Menorca.

Carreras, D., Pons, C., Canals, A., 2007. Cartografia digital de l'ocupació del territori de Menorca—2002. Consell Insular de Menorca, Maó, Menorca.

Córdoba, S.A., Cocucci, A.A., 2011. Flower power: its association with bee power and floral functional morphology in papilionate legumes. Ann. Bot. 108, 919–931.

Cresswell, J.E., Osborne, J.L., 2004. The effect of patch size and separation on bumblebee foraging in oilseed rape: implications for gene flow. J. Appl. Ecol. 41, 539–546.

Cresswell, J.E., Osborne, J.L., Goulson, D., 2000. An economic model of the limits to foraging range in central place foragers with numerical solutions for bumblebees. Ecol. Entomol. 25, 249–255.

Díaz-Ambrona Medrano, A., Seoane Spielgelberg, P., López Pérez, J.J., 2014. Anuario de estadística 2013, Ministerio de Agricultura Alimentación y Medio AmbienteMadrid

Dicks, L.V., Corbet, S.A., Pywell, R.F., 2002. Compartmentalization in plant-insect flower visitor webs. J. Anim. Ecol. 71, 32–43.

Dietzsch, A.C., Stanley, D.A., Stout, J.C., 2011. Relative abundance of an invasive alien plant affects native pollination processes. Oecologia 167, 469–479.

Gathmann, A., Tscharntke, T., 2002. Foraging ranges of solitary bees. J. Anim. Ecol. 71, 757–764.

Gathmann, A., Greiler, H.J., Tscharntke, T., 1994. Trap-nesting bees and wasps colonizing set-aside fields: succession and body size, management by cutting and sowing. Oecologia 98, 8–14.

González-Varo, J.P., Biesmeijer, J.C., Bommarco, R., Potts, S.G., Schweiger, O., Smith, H.G., Steffan-Dewenter, I., Szentgyorgyi, H., Woyciechowski, M., Vilà, M., 2013. Combined effects of global change pressures on animal-mediated pollination. Trends Ecol. Evol. 28, 524–530.

Greenleaf, S.S., Williams, N.M., Winfree, R., Kremen, C., 2007. Bee foraging ranges and their relationship to body size. Oecologia 153, 589–596.

Gross, C.L., 2001. The effect of introduced honeybees on native bee visitation and fruit-set in *Dillwynia juniperina* (Fabaceae) in a fragmented ecosystem. Biol. Conserv. 102, 89–95.

Gross, C.L., Mackay, D., 1998. Honeybees reduce fitness in the pioneer shrub *Melastoma affine* (Melastomataceae). Biol. Conserv. 86, 169–178.

Hanley, M.E., Franco, M., Dean, C.E., Franklin, E.L., Harris, H.R., Haynes, A.G., Rapson, S.R., Rowse, G., Thomas, K.C., Waterhouse, B.R., Knight, M.E., 2011. Increased bumblebee abundance along the margins of a mass flowering crop: evidence for pollinator spill-over. Oikos 120, 1618–1624.

Holzschuh, A., Dormann, C.F., Tscharntke, T., Steffan-Dewenter, I., 2011. Expansion of mass-flowering crops leads to transient pollinator dilution and reduced wild plant pollination. Proc. R. Soc. B: Biol. Sci. 278, 3444–3451.

Hurlbert, S.H., 1978. Measurement of niche overlap and some relatives. Ecology 59, 67–77.

Johnson, S.D., Peter, C.I., Nilsson, L.A., Agren, J., 2003. Pollination success in a deceptive orchid is enhanced by co-occurring rewarding magnet plants. Ecology 84, 2919–2927.

Klein, A.M., Vaissière, 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. B: Biol. Sci. 274, 303–313.

Leonhardt, S.D., Blüthgen, N., 2012. The same, but different: pollen foraging in honeybee and bumblebee colonies. Apidologie 43, 449–464.

Louati-Namouchi, I., Louati, M., Chriki, A., 2000. Mating system and multiple paternity in *Hedysarum coronarium* L. (Fabaceae). Agronomie 20, 655–663.

Mitchell, R.J., Flanagan, R.J., Brown, B.J., Waser, N.M., Karron, J.D., 2009. New frontiers in competition for pollination. Ann. Bot. 103, 1403–1413.

Molina-Montenegro, M.A., Badano, E.I., Cavieres, L.A., 2008. Positive interactions among plant species for pollinator service: assessing the magnet species concept with invasive species. Oikos 117, 1833–1839.

Montero-Castaño, A., Vilà, M., Ortiz-Sánchez, F.J., 2014. Pollination ecology of a plant in its native and introduced areas. Acta Oecol. 56, 1–9.

Montes Pérez, T., 1993/94. La zulla. Nuevas áreas de cultivo. Su problemática Pastagens Forrag. 15, 173–187.

Ortells, V., Campos, X., 1983. Els anglicismes de Menorca. Editorial Moll, Palma de Mallorca.

Osborne, J.L., Martin, A.P., Carreck, N.L., Swain, J.L., Knight, M.E., Goulson, D., Hale, R. J., Sanderson, R.A., 2008. Bumblebee flight distances in relation to the forage landscape. J. Anim. Ecol. 77, 406–415.

Paini, D.R., 2004. Impact of the introduced honey bee (*Apis mellifera*) (Hymenoptera: Apidae) on native bees: a review. Aust. Ecol. 29, 399–407.

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 Development Core Team, 2014. R: A Language and Environment for Statistical Computing. R Development Core Team.

Roubik, D.W., 1983. Experimental community studies: time-series tests of competition between African and Neotropical bees. Ecology 64, 971–978.

Satta, A., Acciaro, M., Floris, I., Lentini, A., Sulas, L., 2000. Insect pollination of sulla (*Hedysarum coronarium* L.) and its effect on seed production in a Mediterranean environment. In: Sulas, L. (Ed.), Legumes for Mediterranean Forage Crops, Pastures and Alternative Uses. CIHEAM-IAMZ, Zaragoza, pp. 373–377.

Steffan-Dewenter, I., Tscharntke, T., 2000. Resource overlap and possible competition between honey bees and wild bees in central Europe. Oecologia 122, 288–296.

Steffan-Dewenter, I., Kuhn, A., 2003. Honeybee foraging in differentially structured landscapes. Proc. Biol. Sci. 270, 569–575.

Steffan-Dewenter, I., Munzenberg, U., Burger, C., Thies, C., Tscharntke, T., 2002. Scale-dependent effects of landscape context on three pollinator guilds. Ecology 83, 1421–1432.

Sulas, L., Stangoni, A.P., Re, G.A., Ledda, L., 2000. Growing cycle of *Hedysarum coronarium* L. (sulla): relationship between plant density, stem length, forage yield and phytomass partitioning. In: Sulas, L. (Ed.), Legumes for Mediterranean Forage Crops, Pastures and Alternative Uses. CIHEAM-IAMZ, Zaragoza, pp. 147–151.

Tscharntke, T., Tylianakis, J.M., Rand, T.A., Didham, R.K., Fahrig, L., Batary, P., Bengtsson, J., Clough, Y., Crist, T.O., Dormann, C.F., Ewers, R.M., Frund, J., Holt, R. D., Holzschuh, A., Klein, A.M., Kleijn, D., Kremen, C., Landis, D.A., Laurance, W., Lindenmayer, D., Scherber, C., Sodhi, N., Steffan-Dewenter, I., Thies, C., van der Putten, W.H., Westphal, C., 2012. Landscape moderation of biodiversity patterns and processes—eight hypotheses. Biol. Rev. 87, 661–685.

Tylianakis, J.M., Didham, R.K., Bascompte, J., Wardle, D.A., 2008. Global change and species interactions in terrestrial ecosystems. Ecol. Lett. 11, 1351–1363.

Valido, A., Rodríguez-Rodríguez, M.C., Jordano, P., 2014. Impacto de la introducción de la abeja doméstica (*Apis mellifera*, Apidae) en el Parque Nacional del Teide (Tenerife, Islas Canarias). Ecosistemas 23, 58–66.

Westphal, C., Steffan-Dewenter, I., Tscharntke, T., 2003. Mass flowering crops enhance pollinator densities at a landscape scale. Ecol. Lett. 6, 961–965.

Williams, N.M., Minckley, R.L., Silveira, F.A., 2001. Variation in native bee faunas and its implications for detecting community changes. Conserv. Ecol. 5. http://www.consecol.org/vol5/iss1/art7/.

Winfree, R., Williams, N.M., Dushoff, J., Kremen, C., 2007. Native bees provide insurance against ongoing honey bee losses. Ecol. Lett. 10, 1105–1113.

Wolf, S., Moritz, R.F.A., 2008. Foraging distance in *Bombus terrestris* L. (Hymenoptera: Apidae). Apidologie 39, 419–427.

Yagoubi, N., Chriki, A., 2000. Estimation of mating system parameters in *Hedysarum coronarium* L. (Leguminoseae, Fabaceae). Agronomie 20, 933–942.