

Spillover of managed honeybees from mass-flowering crops into natural habitats



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ABSTRACT

Mass-flowering crops (MFCs) and beekeeping are increasing across agroecosystems globally. Managed honeybees could spillover after the blooming of MFCs into nearby natural habitats, especially if hive numbers are associated with the cover of MFCs at the landscape scale. Nevertheless, this phenomenon has been largely overlooked despite the potential impacts of honeybees on local wildlife. We assessed this ‘MFC-beekeeping’ association and honeybee spillover into woodland patches in 17 fragmented landscapes in SW Spain with contrasting cover of orange groves as MFC. Hive densities were almost four times greater in landscapes with high cover of orange groves and, after the orange-tree bloom, mean honeybee densities were eight times higher in woodland patches within these landscapes, as compared to landscapes with no/low cover. Seemingly, this spillover was resource-mediated since it mirrored the temporal changes in flower cover at habitat and landscape scales. Our study demonstrates for the first time a consistent spillover of managed honeybees from a MFC into nearby natural habitats. These findings are a warning about the potential detrimental effects of magnified honeybee densities on local fauna and flora, especially on wild bees.

1. Introduction

The western honeybee (*Apis mellifera* L.) is probably the most abundant and widespread domesticated animal (Aizen and Harder, 2009; Garibaldi et al., 2013; Moritz et al., 2005). Despite regional episodes of colony losses (Neumann and Carreck, 2010), the global stock of honeybee hives has increased ~45% since the 1960's (Aizen and Harder, 2009). Outstandingly, in countries like China, Spain or Argentina, the stock has increased ~120%, ~250% and ~360%, respectively (Aizen and Harder, 2009). This global growth in hive numbers seems to have kept pace with human population growth and honey production (Aizen and Harder, 2009). Yet, honeybees are also increasingly reared for crop pollination (Aizen and Harder, 2009; Breeze et al., 2014; Garibaldi et al., 2013). In fact, the 23% expansion in global cultivated area between 1961 and 2006 mostly involved crops that are attractive for pollinators, including fruit/nut and biofuel crops (Aizen et al., 2008; Aizen and Harder, 2009; see also Breeze et al., 2014). Many of these crops are known as mass-flowering crops (MFCs), because they produce highly rewarding blooms that are only available for short time periods (Holzschuh et al., 2016; Westphal et al., 2003). During those periods, MFCs require ample pollination services, which are often favoured by the placement of managed honeybee hives (Breeze et al.,

2014; Cunningham et al., 2016; Garibaldi et al., 2013; Klein et al., 2012; Rucker et al., 2012). Despite the fact that managed honeybees and MFCs are presumably increasing in tandem across agroecosystems globally (e.g. Gaines-Day and Gratton, 2016; Klein et al., 2012), their combined impact on natural habitats and wildlife still remains largely unknown (Geslin et al., 2017; González-Varo et al., 2013; Holzschuh et al., 2016).

The cross-habitat spillover of organisms in agroecosystems is thought to play an important role in multiple ecological processes that are pivotal for community dynamics in natural habitats, such as predation, parasitism, seed dispersal or pollination (Blitzer et al., 2012; Driscoll et al., 2013; González et al., 2016; Macfadyen et al., 2015; Rand et al., 2006; Tschardt et al., 2012). Spillover from agricultural into natural habitats is expected to be acutely important after sudden changes or pulses in resource abundance in crop fields, typically associated with phenological events such as flowering, fruiting and harvesting (Blitzer et al., 2012; González et al., 2016; Rand et al., 2006; Vasseur et al., 2013). Within a landscape, honeybees can forage on the floral resources of contrasting habitat types, with a preference for highly rewarding flowering patches (Couvillon et al., 2014; Danner et al., 2016; Requier et al., 2015). Thus, honeybee spillover from MFCs into natural habitats is expected to occur after the blooming of MFCs,

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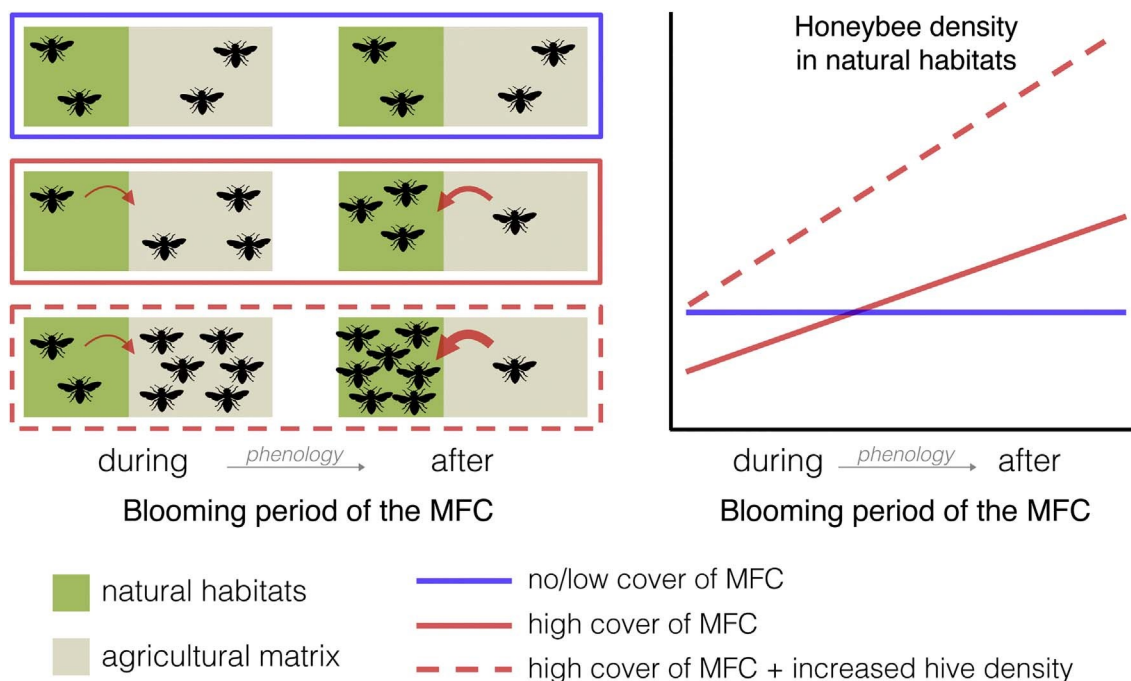


Fig. 1. *Left:* Hypothetical spatiotemporal patterns of honeybee densities in agricultural landscapes with contrasting cover of mass flowering crops (MFCs): ‘no/low’ cover (blue rectangle) and ‘high’ cover (red rectangles), differentiating between landscapes harbouring similar and increased densities of honeybee hives (continuous and dashed line, respectively). Note that honeybee densities at the landscape scale (here represented by four or eight bees) depend on hive density. Curved arrows denote cross-habitat spillover and arrow widths denote magnitude. *Right:* Expected honeybee densities in natural habitats during and after the blooming period of MFCs in the landscape types shown in the left panels. Note also that, while blooming, MFCs are also expected to attract honeybees from natural habitats (magnet effect), which would transiently reduce their densities in this period. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

owing to a sudden shortage of crop flowers (Blitzer et al., 2012; see also Montero-Castaño et al., 2016). Nevertheless, this phenomenon has received very little attention and has not yet been empirically demonstrated in honeybees (see Härtel and Steffan-Dewenter, 2014), despite their recognised impacts on native fauna and flora (Cane and Tepedino, 2017; Fürst et al., 2014; Goulson, 2003; Paine, 2004; Roubik, 1978; Torné-Noguera et al., 2016).

According to theoretical predictions of ‘cross-habitat spillover’ (Blitzer et al., 2012; Rand et al., 2006; Tschardt et al., 2012), we hypothesise that the temporal dynamics of honeybee densities in natural habitats depend on the presence/absence of a substantial cover of MFCs at the landscape scale (Fig. 1). In landscapes with no or low cover of MFCs, we predict honeybee densities in natural habitats to be roughly constant through the spring-flowering season (i.e. no spillover; Fig. 1), reflecting overlapping and/or prolonged flowering phenologies in different land-use types (e.g. Herrera, 1986; Olesen et al., 2008). In contrast, in landscapes with high cover of MFCs, we predict honeybee densities in natural habitats to suddenly increase after the end of the MFC bloom (i.e. a sizeable spillover; Fig. 1). In addition, we predict the magnitude of such spillover to be greater whenever hive densities are associated with the cover of MFCs (Fig. 1), which is indeed the most likely scenario, as explained above.

We tested these predictions in woodland patches located in 17 fragmented landscapes in SW Spain with contrasting cover of orange groves (*Citrus* spp.), a widespread MFC that has tripled its extent in the region since the 1990’s (Junta de Andalucía, 2016). As observed in other *Citrus* crops in South America (Chacoff and Aizen, 2006), orange groves in this region shelter huge honeybee densities during the blooming period, and honeybees are by far the most frequent visitor of orange flowers (97% of individual insects; Holzschuh et al., 2016). Virtually all honeybees in agricultural landscapes in Western Europe come from beekeeping activities (Breeze et al., 2014; Pirk et al., 2017). Importantly, honeybees also occur at high densities in the woodlands of the study region (Holzschuh et al., 2016), where they are the most frequent flower visitor of several wild plants (González-Varo et al.,

2009; González-Varo et al., 2016). To test our predictions, we (i) recorded honeybee hives within the study landscapes; (ii) sampled honeybee densities for two years in focal woodland patches during and after the orange-tree bloom; and (iii) assessed the temporal dynamics of flower cover in the main habitat types of the region and, thereby, at the landscape-scale.

2. Methods

2.1. Study region, landscape types and sampling design

The study was conducted during the springs (late March to mid May) of 2011, 2012 and 2013 in agricultural landscapes of Andalucía (SW Spain), in a region that extends over an area of ca. 140 km in longitude \times 30 km in latitude (Fig. S1). The climate is typically Mediterranean, with warm dry summers and cool humid winters. Mean annual precipitation is 525 mm and January and July temperatures average 11 °C and 26 °C, respectively (AEMET, 2015). The main traditional crops in this region are wind-pollinated olive groves (*Olea europaea* var. *europaea*) and cereal fields. The main crops visited by pollinators are mass-flowering orange groves (*Citrus* spp.) and non-mass-flowering berry fields (mainly strawberry *Fragaria* \times *ananassa* and raspberry *Rubus idaeus*). Natural habitats in the region are fragmented woodlands of stone pines (*Pinus pinea*) and Mediterranean oaks (*Quercus ilex* subsp. *ballota* and *Q. suber*), with an understory that is rich in insect-pollinated flowers (Aparicio, 2008; see also Table S3 in González-Varo et al., 2016), mainly in shrubs (Fig. S1).

We selected focal woodland patches (mean \pm sd = 3.6 \pm 2.0 ha, range = 1.0–7.5 ha) located in landscapes characterised by having either (i) no or low cover of orange groves (acting as ‘control’) or (ii) a high coverage (hereafter and for simplicity, ‘NO/LOW’ and ‘HIGH’ landscapes, respectively). Study landscapes comprised the area included within a 1-km buffer from the edge of the focal woodland patches (Fig. S1). This buffer distance is suitable because most honeybee foraging flights occur within this range (Couvillon et al., 2014),

especially in landscapes with MFCs (see Danner et al., 2016). We characterised the composition of the main land-use types within the study landscapes by digitising satellite orthophotos dating from 2011 in ArcMapTM 10.0 (© ESRI) and validating the land-use categories assigned to the polygons in the field.

In 2011, we initially selected 16 non-overlapping landscapes (inter-patch distances: 2–140 km), eight NO/LOW and eight HIGH. Four patches sampled in 2011 were discarded in 2012 because of severe local disturbances (fire and ploughing), and two new patches were selected to compensate this loss: one located within a previous landscape (130 m apart from the lost patch) and the other in an independent (i.e. non-overlapping) landscape (see details in Table S1). In total, we sampled 17 landscapes (8 NO/LOW and 9 HIGH): 16 in 2011 and 14 in 2012 (13 in both years). Mean cover of orange groves was 1.9% (range = 0–7.9%) in NO/LOW landscapes and 40.5% (range = 28.0–56.9%) in HIGH landscapes (Fig. S2). Conversely, mean cover of olive groves and cereal fields were, respectively, 24.0% and 20.8% in NO/LOW landscapes, but only 1.1% and 3.5% in HIGH landscapes (Fig. S2). Hence, olive groves and cereal fields dominated NO/LOW landscapes, whereas orange groves dominated HIGH landscapes. Importantly, both landscape types did not vary significantly in woodland cover (overall mean = 18.5%; range = 1.4–58.2%) nor in the cover of grasslands/pastures (overall mean = 13.1%; range = 1.9–22.4%) and berry fields (overall mean = 7.7%; range = 0–38.1%) (see details in Fig. S2). Together, these six main land-use types (i.e. orange groves, cereal fields, olive groves, woodlands, grasslands/pastures and berry fields) accounted for $85.1 \pm 9.1\%$ (mean \pm sd) of the area within the study landscapes (range = 69.2–97.3%), without significant differences between landscape types (Mann-Whitney U test: $P = 0.114$; see Fig. S2).

2.2. Density of honeybee hives within the landscapes

The presence of wild honeybee colonies in the study region is virtually null, as in most Europe (Pirk et al., 2017). In spring 2012, we counted the number of managed honeybee hives within the study landscapes (i.e. 1-km buffer around our focal woodland patches). We first asked local people about the location of hives. Then, we visited these locations to count the number of hives and georeference the clusters. We finally conducted intensive on-the-ground searches within all study landscapes in order to seek possible hives not reported by local people (notably, many hives had an unregistered status). To obtain hive densities (i.e. ' n_{hives} per km²'; Steffan-Dewenter and Tscharnkte, 2000), the number of hives was divided by the area within each study landscape. Areas varied slightly among landscapes (mean \pm sd = 4.0 ± 0.3 km²) because the 1-km buffer was established from the edge of focal patches (see e.g. in Fig. S1). All the beehives recorded remained in the same location throughout the study period; thus, beekeepers of the study region did not move their colonies during – at least – a 3-months period.

2.3. Honeybee density and flower cover in natural habitats

In springs 2011 and 2012, we sampled honeybees in the focal woodland patches during and after the orange-tree bloom (late March to early April, and late April to early May, respectively; hereafter, '*during*' and '*after*'); we did not sample the '*before*' period because of the almost complete lack of flowers in woodlands prior to mid March. The flowering peak in the studied woodlands spans between March and May (González-Varo et al., 2016). Hence, when flowering had ceased in the MFC in the *after* period, woodlands were still in their flowering peak. Flower-visiting honeybees were recorded by a slowly-walking observer (J.P. González-Varo) within two fixed belt transects (1 m \times 150 m during 15 min) randomly located in each woodland patch, aiming to cover a random representation of local flower assemblages. We conducted two survey rounds per sampling period (i.e. two transects \times two

rounds in the *during* and *after* periods = four transects per period), accounting for a total of eight transects per woodland patch and year (see details and a few exceptions in Table S1). Overall, 226 transects were conducted. Within the same transects, and just after finishing honeybee sampling, we counted the number of floral units (individual flowers or inflorescences, such as spikes or capitula) of each flowering species. We then calculated the flower cover within each transect as: Flower cover (%) = $\sum_{i=1}^n (n_i \times a_i \times 100/a_t)$; where n_i and a_i are the number of floral units and the average area (m²) of a single floral unit of species i , respectively, and a_t is the transect area (i.e. 150 m²). Honeybee densities and flower covers were averaged over the two transects and the two survey rounds per period, resulting in one data point per period, site and year (see also Holzschuh et al., 2016).

2.4. Temporal changes in landscape-scale flower cover

In order to assess the temporal changes in flower resources in both landscape types (i.e. NO/LOW and HIGH), we quantified flower cover in the six major land-use types within the study landscapes (i.e. orange groves, cereal fields, olive groves, woodlands, grasslands/pastures and berry fields) both *during* and *after* the orange-tree bloom. In woodlands and orange groves, flower cover was calculated as explained above, from counts of floral units within the same belt transects (1 m \times 150 m, two per land use type) used to sample honeybees in 2011 and 2012 (see Holzschuh et al., 2016 for sampling details at orange groves). In 2012 and 2013, we also conducted flower counts within 1 m \times 100 m or 1 m \times 150 m belt transects placed in cereal fields, olive groves, grasslands/pastures and berry fields of different study landscapes, *during* and *after* the orange-tree bloom. Because we placed two transects per site in woodlands and orange groves, and sampled some sites in different years (unlike in cereal fields, olive groves, grasslands/pastures or berry fields), we averaged data per period and site by averaging first over the two transects and the two survey rounds per site and period, and then by averaging over the two years (see details in Table S2). Resulting data on flower cover consisted of one data point per period and site (mean = 11.5 sites per land-use type: $n = 9$ –17 *during* and 7–17 *after*; see details in Table S2).

We estimated the average flower cover within each landscape, based on data from the six main land-use types, which accounted on average for 85.1% of landscape cover. We first multiplied (i.e. weighted) the mean flower cover of each of the six land-use types (separately, in periods *during* and *after*) by the fraction of the landscape they covered (i.e. cover expressed as proportion). Then, we summed the result, which represents the average flower cover at the landscape scale in periods *during* and *after*.

2.5. Statistical analyses

All statistical analysis were performed using R (version 3.2.3). We used a non-parametric Mann-Whitney U test to assess differences between NO/LOW and HIGH landscapes in the density of honeybee hives. We used a linear mixed-effects model (LMM) with a normal error distribution in the package *lme4* (v. 1.1–12) to test differences between landscape types in honeybee densities at woodland patches, and to test temporal honeybee spillover, which would be evidenced by a significant 'landscape type \times period' interaction. The response variable was the average honeybee density per woodland patch, period and year, expressed as $n_{\text{honeybees}}$ per 100 m². Values were transformed as $\log_{10}(x + 1)$ to meet the normality and homoscedasticity assumptions of LMMs. Predictors included landscape type (i.e. NO/LOW or HIGH), period (*during* and *after* the orange-tree bloom) and their interaction, as well as local flower cover as a co-variable in order to control for differences in flower resources among woodland patches. We included 'landscape identity' in the LMM as a random factor to account for the non-independence of landscapes that were re-sampled in different years (13 out of 17). F and P values were calculated using Satterthwaite's approximations to determine denominator degrees of freedom in package

lmerTest (v. 2.0–32). We also built an additional LMM incorporating woodland cover in the landscape as co-variable. Model fit was evaluated according to the Akaike Information Criterion for small sample sizes (AICc) (Burnham et al., 2011) and marginal R^2 values ($R^2_{LMM(m)}$), that is, the variance explained by the fixed effects variables; Nakagawa et al., 2013).

Finally, we used a generalised linear model (GLM) with a Gamma distribution and a log-link to analyse differences between landscape types in temporal changes of flower cover. We chose the Gamma distribution because of the right-skewed distribution of the response variable (landscape-scale flower cover), which did not resemble a normal distribution even after log-transformations. Predictors included the landscape type (i.e. NO/LOW or HIGH), period (*during* and *after*) and their interaction.

3. Results

Despite a huge variability within each landscape type, the density of honeybee hives was on average 3.7 times greater in HIGH than in NO/LOW landscapes (mean = 20.0 and 5.4 hives per km², respectively; Mann-Whitney *U* test: $P = 0.028$; Fig. 2a). Matching such differences, honeybee densities were significantly greater in woodland patches located in HIGH than in NO/LOW landscapes (see LMM results in Table 1). Overall back-transformed mean honeybee density (i.e. periods pooled) was 3.6 times greater at patches in HIGH (22.7 bees per 100 m²) than in NO/LOW landscapes (6.3 bees per 100 m²), a magnitude that closely resembled that found in hive density (3.7-fold; see above). Owing to contrasting temporal dynamics, such density differences between landscape types varied hugely between periods (*during* and *after*; see Fig. 2b), as supported by the significant ‘landscape type × period’ interaction (see Table 1). Mean honeybee density in woodland patches within NO/LOW landscapes decreased 2.5 times from *during* to *after* periods, yet such decrease was not significant as shown by the overlap in the 95% CI (Fig. 2b). Conversely, mean density increased 2 times in patches within HIGH landscapes, and such increase was significant as revealed by the non-overlapping 95% CIs (Fig. 2b). As a result of these opposing trends, differences between landscape types in honeybee densities at woodland patches were small and non-significant *during* but very large and significant *after* (1.6 times and 8.3 times greater in HIGH landscapes, respectively; see 95% CIs in Fig. 2b).

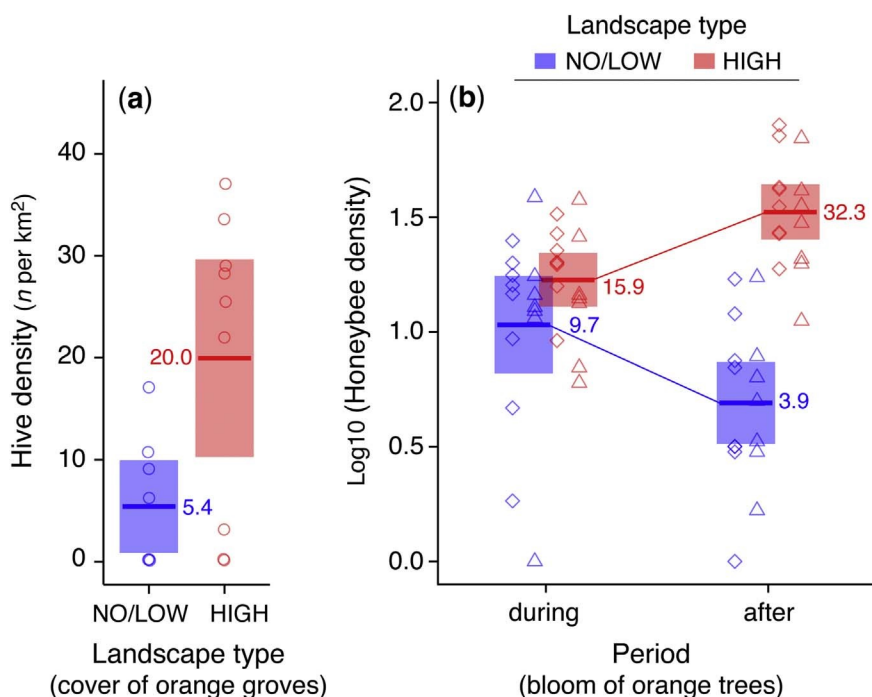


Fig. 2. Differences between landscapes with ‘NO/LOW’ ($n = 8$) and ‘HIGH’ ($n = 9$) cover of orange groves in (a) hive density at the landscape-scale (2012 data; open circles are observed densities); and (b) honeybee density in focal woodland patches *during* and *after* the orange-tree bloom (open diamonds and triangles are 2011 and 2012 data, respectively). Horizontal lines denote means and shaded areas denote 95% CI. Coloured numbers denote means in (a) and back-transformed means (i.e. $n_{\text{honeybees}}$ per 100 m²) in (b).

Table 1
Results of the linear mixed-effect model (AICc = 49.6; $R^2_{LMM(m)} = 0.498$) relating densities of honeybees in woodland patches to the predictors ‘Landscape type’ (‘NO/LOW’ and ‘HIGH’ cover of orange groves), ‘Period’ (*during* and *after* the bloom of orange trees) and local ‘Flower cover’.

Variables	df	F	P
Landscape type	1, 15.1	18.13	< 0.001
Period	1, 41.6	0.08	0.773
Landscape type × Period	1, 42.4	14.56	< 0.001
Flower cover	1, 51.7	4.79	0.033

Honeybee densities did not vary between periods when not accounting for the landscape type (see Table 1). Finally, honeybee densities were positively and significantly related to the local flower cover within the woodland patches (estimate ± se = 0.111 ± 0.051). Overall, the fixed factors included in this model accounted for ~50% of the variance observed in honeybee densities ($R^2_{LMM(m)} = 0.498$). LMM incorporating woodland cover had inadequate support ($\Delta AICc = 10.4$) and this co-variable had non-significant effects (estimate = 0.005 ± 0.004, $P = 0.257$).

Landscape-scale flower cover differed significantly between NO/LOW and HIGH landscapes ($F_{1,31} = 10.34$, $P \ll 0.001$) and between periods ($F_{1,32} = 15.01$, $P \ll 0.001$), but, chiefly, the temporal changes varied significantly between both landscape types (‘landscape type × period’ interaction: $F_{1,30} = 2.66$, $P \ll 0.001$). Remarkably, this model accounted for ~95% of the variance in landscape-scale flower cover ($R^2_{GLM} = 0.947$). Although there was a general decrease in flower cover from *during* to *after* periods, the decrease was moderate within NO/LOW landscapes (2 times lower) but very abrupt within HIGH landscapes (14 times lower) (see Fig. 3a). This was mainly caused by a decrease of two orders of magnitude in mean flower cover in orange groves (from 25.1% *during* to 0.3% *after*; see Fig. 3b). In contrast, in the other land-use types, mean flower cover was always ≤ 2.6%, differences between periods were smaller, and temporal trends included decreases, stability and increases in flower cover (Fig. 2b; see details in Fig. S3).

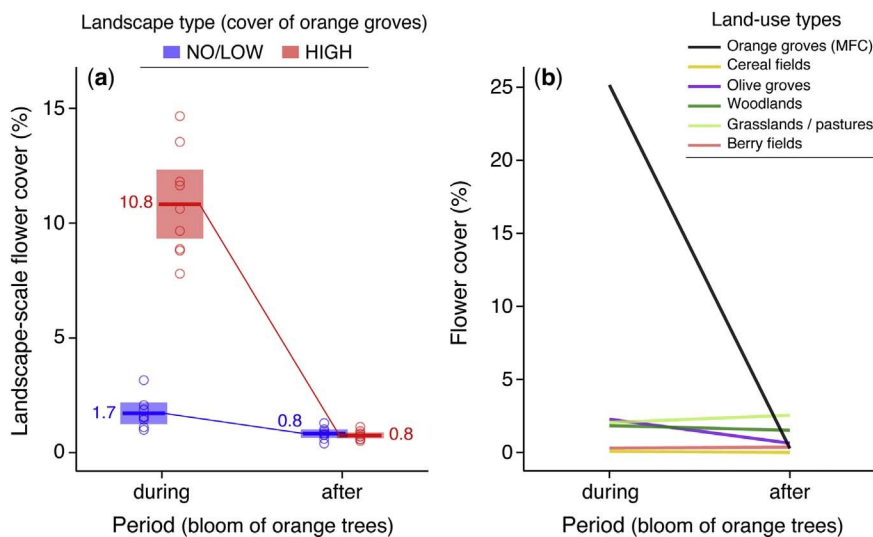


Fig. 3. (a) Differences between landscapes with 'NO/LOW' ($n = 8$) and 'HIGH' ($n = 9$) cover of orange groves in landscape-scale flower cover *during* and *after* the orange-tree bloom; open circles are estimates per landscape; horizontal lines and coloured numbers denote means, whereas shaded areas denote 95% CI. (b) Temporal trends in mean flower cover (i.e. *during* and *after*) in the six main land-use types within the study landscapes.

4. Discussion

We found strong empirical evidence of honeybee spillover from mass-flowering crops (MFCs) into natural habitats. Hive densities were greater in landscapes with high cover of orange groves, which led to higher densities of honeybees in woodland patches within these landscapes. When blooming, orange groves acted as a magnet for honeybees, diluting – in relative terms – their densities in nearby woodland patches. Yet a sizeable honeybee spillover from orange groves into woodlands occurred after crop bloom. Seemingly, this spillover was resource-mediated, since it happened at the same time as a sudden shortage in flower cover in orange groves. These findings support empirically and for the first time several predictions of the 'cross-habitat spillover' theory that have not yet been tested in managed honeybees (Tschamtké et al., 2012). Honeybee spillover into natural habitats is likely to be a common phenomenon in agroecosystems worldwide (see Holzschuh et al., 2016). Moreover, the spillover is expected to be particularly predictable when the hives are not transported immediately after crop bloom and when the MFCs are perennial, therefore, not subject to rotation (e.g. oranges, almonds, mangoes, apples, pears and many others; Garibaldi et al., 2013).

We found a positive association between the density of honeybee hives and the cover of orange groves. This finding supports the idea that beekeeping and MFCs are not spreading through agroecosystems independently, but in tandem. Surprisingly, there is almost no empirical evidence relating the extent of MFCs and hive densities at the landscape scale. In our study system, the association between hives and orange groves is based on the production of monofloral *Citrus* honey (Serrano et al., 2004), rather than on pollination services. Yet, in many other cases, beekeepers aim both to produce honey and provide pollination services to crops (see Cane and Tepedino, 2017; Rucker et al., 2012). Recently, Holzschuh et al. (2016) have shown across six European countries that, during the bloom of three different MFCs (oilseed rape, orange and sunflower), honeybee densities in (semi-) natural habitats are consistently higher in landscapes with higher MFC cover. From this result and the present study, we can infer now that hive densities were associated with the cover of MFCs across countries and crop types, especially because, while blooming, MFCs are expected to attract honeybees rather than to spill them over into natural habitats (Blitzer et al., 2012; Rand et al., 2006) (see also below).

Honeybee densities in woodland patches mirrored hive densities at the landscape scale (periods pooled), as both were on average four times higher in landscapes with a high orange-grove cover. According to our predictions, we found a sizeable spillover of managed honeybees into woodlands after the blooming of orange groves. The MFC first

acted as a magnet (see Blitzer et al., 2012), transiently attracting the bulk of the (hive-mediated) greater honeybee densities in HIGH landscapes. Owing to this magnet effect, during blooming, honeybee densities were roughly similar between woodland patches in both landscape types (NO/LOW and HIGH). This, along with the huge densities of honeybees reported in orange groves (see Fig. S1 in Holzschuh et al., 2016), demonstrates that, while blooming, MFCs can retain to some extent the hive-mediated surplus of honeybees at the landscape scale.

However, the magnet effect turned into a massive spillover effect after blooming, resulting in honeybee densities in woodland patches within HIGH landscapes that, on average, were twice as high as those observed during bloom. This temporal density change is remarkable not only in magnitude, but also in sign because in woodland patches within NO/LOW landscapes honeybee densities decreased from *during* to *after* periods. Two complementary processes, operating at the habitat and landscape scale, respectively, can explain this density decrease. On the one hand, from *during* to *after* periods, flower cover decreased in woodlands but increased in other land-use types. Hence, a preference by foraging honeybees for flower-rich habitats could explain the observed density decrease in woodland patches (see Couvillon et al., 2014). On the other hand, flower cover also decreased from *during* to *after* periods at the landscape scale. This could dilute honeybee densities at the landscape scale – and thus in woodland patches – because foraging flights are longer in flower-poor landscapes (see Danner et al., 2016). Temporal changes in resource availability were remarkably different in HIGH landscapes, where the end of the orange-tree bloom led to a massive decrease in landscape-scale flower cover. Consequently, after the ca. 3–4 weeks from *during* to *after* periods, hordes of honeybees that were predominantly foraging in orange groves moved to nearby habitats, provoking a sizeable spillover into woodland patches that was evidenced by a sudden density increase. Our findings align with the theoretical predictions of cross-habitat (resource-mediated) spillover of mobile organisms from managed into natural habitats (Blitzer et al., 2012; Rand et al., 2006; Tschamtké et al., 2012).

As a result of these opposing temporal changes, after crop bloom, honeybee densities were on average eight times higher in woodland patches within landscapes with a high cover of orange groves. This difference is more than twice the difference found in hive density at the landscape scale, which suggests synergistic effects between MFCs and beekeeping on honeybee spillover (see González-Varo et al., 2013). Magnified honeybee densities in natural habitats can have multiple impacts on local fauna and flora. Wild pollinators can suffer from the increased competition with honeybees for floral resources (Dupont et al., 2004; Goulson, 2003; Moritz et al., 2005; Roubik, 1978; Torné-Noguera et al., 2016). Wild bees are expected to be particularly

sensitive because pollen represents the protein source with which they feed their broods (Cane and Tepedino, 2017; Michener, 2007; Paini, 2004). For instance, Cane and Tepedino (2017) have recently estimated that a healthy honeybee hive can gather as much pollen as could produce ~33,000 progeny of an average solitary bee on one month. Hordes of honeybees foraging in natural habitats can also increase pathogen transition to wild pollinators via shared flowers (Fürst et al., 2014). Furthermore, honeybees can also affect the reproduction of wild plants by disrupting their mating patterns. Honeybees usually forage by visiting more flowers from the same individual and during longer time periods than wild bees of similar size (see Dupont et al., 2004), particularly in plants that bear large numbers of flowers. Such behaviour promotes self-pollination (England et al., 2001), which can reduce both fecundity (Valido et al., 2011) and plant progeny performance (González-Varo et al., 2010).

Understanding how landscape characteristics moderate the distribution of organisms and the ecological processes they mediate is critical for mitigating the environmental changes affecting agroecosystems globally (Tscharntke et al., 2012). We demonstrate here that landscape composition determines the spillover of managed honeybees from MFCs into natural habitats after crop bloom. Furthermore, we shed some light on the mechanisms driving the occurrence and magnitude of honeybee spillover; namely, temporal changes in flower cover at the local and landscape scales, and increased beekeeping at the landscape scale. Our study is a warning about the potential detrimental effects of magnified honeybee densities in natural habitats on local fauna and flora, especially on wild bees, an issue that deserves further research. Hence, this study provides baseline information for conservation managers to make decisions about where and when the location of managed hives should be restricted.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at <http://dx.doi.org/10.1016/j.biocon.2017.06.018>.

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