



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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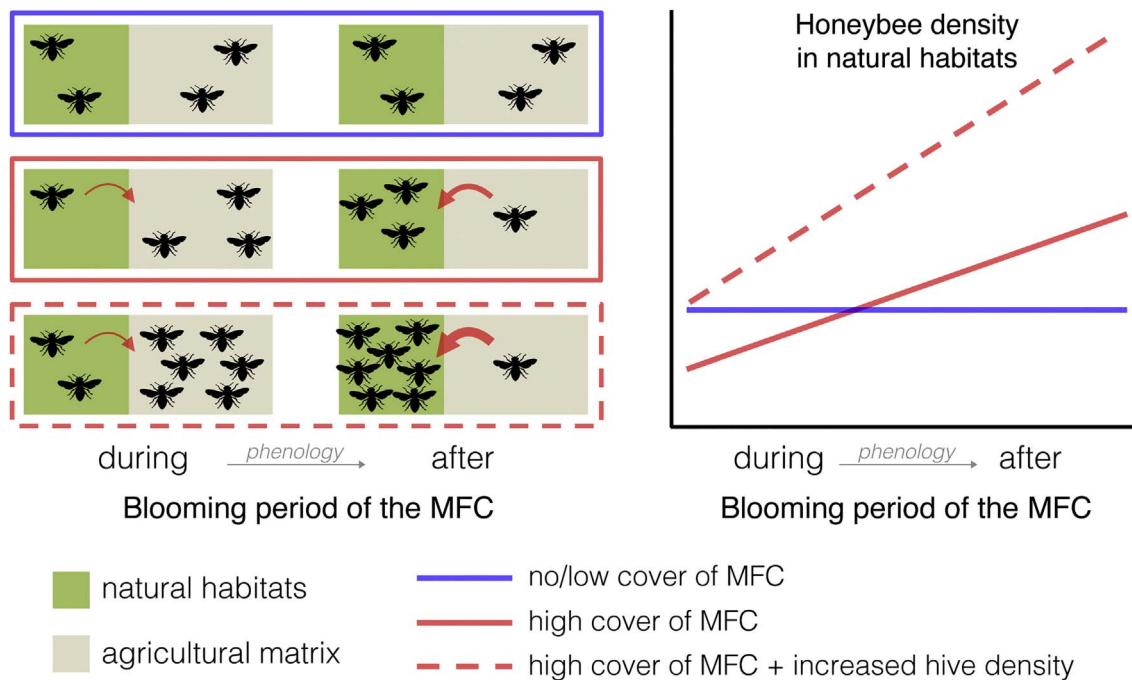


Fig. 1. *Left:* Hypothetical spatiotemporal patterns of honeybee densities in agricultural landscapes with contrasting cover of mass flowering crops (MFCs): ‘no/low’ cover (blue rectangle) and ‘high’ cover (red rectangles), differentiating between landscapes harbouring similar and increased densities 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 1990s (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),

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