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Original Article

IMPACT OF HONEY BEE (*APIS MELLIFERA* L.) DENSITY ON WILD BEE FORAGING BEHAVIOUR

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A b s t r a c t

Honey bees are globally regarded as important crop pollinators and are also valued for their honey production. They have been introduced on an almost worldwide scale. During recent years, however, several studies argue their possible competition with unmanaged pollinators. Here we examine the possible effects of honey bees on the foraging behaviour of wild bees on *Cistus creticus* flowers in Northern Greece. We gradually introduced one, five, and eight honey-bee hives per site, each containing ca. 20,000 workers. The visitation frequency and visit duration of wild bees before and after the beehive introductions were measured by flower observation. While the visitation frequencies of wild bees were unaffected, the average time wild bees spent on *C. creticus* increased with the introduction of the honey-bee hives. Although competition between honey bees and wild bees is often expected, we did not find any clear evidence for significant effects even in honey-bee densities much higher than the European-wide average of 3.1 colonies/km^2.

Keywords: *Apis mellifera*, *Cistus creticus*, **competition, Mediterranean, native bees**

INTRODUCTION

Most plant species depend on animal pollination for their reproduction (Kremen et al., 2007). Plant-pollinator relationships are of great importance to ecosystem health (Costanza et al., 1997; Kearns, Inouye & Weser, 1998). During recent years, the biodiversity and number of native bees have been repeatedly reported to be in decline worldwide. The decline is mainly due to changes of agricultural activities such as changes in land use, modern agricultural practices, and pesticide use (Allen-Wardell et al., 1998; Potts et al., 2006; Kremen et al., 2007; Goulson et al., 2008; Brown & Paxton, 2009).

Pollinator efficiency, and therefore, pollination effectiveness, is strongly related to the compatibility between flowers and their pollinators. Honey bees (*Apis mellifera* L.) are extremely polylectic insects (Cane & Sipes, 2006) visiting and pollinating a variety of species (Crane, 1990; Free, 1993; Vaughton, 1992; Gross, 2001; Dupont et al., 2004). In addition, honey bees have been widely and successfully used as pollinators in crop systems (Free, 1993; Morse & Calderone, 2000; Artz, Hsu & Nault, 2011). Several studies, however, have shown that for certain plant species, honey bees are less efficient pollinators compared to wild flower visitors. The continued use of the honey bees and their possible competition with wild bees in natural areas might gradually affect both fauna and flora (Schaffer et al., 1983; Taylor & Whelan, 1988; Westerkamp, 1991; Vaughton, 1996; Gross & Mackay, 1998; Hansen, Olsen & Jones, 2002; Whelan, Ayre & Benyuon, 2009).

The potential impact of honey bees on wild bees has been discussed by several authors.

Competition between honey bees and wild bees is believed to affect the foraging behaviour of wild bees. Consequently the fecundity, abundance, and ultimately survival of the wild bees are thought to be affected. Some authors have shown a negative impact of honey bees on native bee foraging, reproduction, and populations (Pyke & Balzer, 1985; Sugden, Thorp & Buchmann, 1996; Kato et al., 1999; Goulson & Sparrow, 2009); whereas other researchers did not find such impacts (Butz Huryn, 1997; Horskins & Turner, 1999; Roubik & Wolda, 2001; Paini, Williams & Roberts, 2005). The various and contrasting results among the studies, or in some cases even among areas/seasons from the same study, may arise from multiple factors that may affect the relationship between honey bees and wild bees (i.e. floral resources, foraging behaviour, population density, fecundity). An additional causal factor might be because of the various methodologies applied to examine the potential effects of honey bees on wild bees (Aizen & Feinsinger, 1994; Roubik & Wolda, 2001; Thomson, 2004; Forup & Memmott, 2005; Shavit, Amots & Ne'eman, 2009; Gross, 2001). An indicated method to study the competition between honey bees and wild bees is the manipulation of hone-bee abundance by the introduction and/or removal of beehives (Schaffer et al., 1983; Thomson, 2004; Paini & Roberts, 2005; Paini, Williams & Roberts, 2005; Shavit, Amots & Ne'eman, 2009).

In the present study, we aimed to examine the impact of honey bees on wild bees. We gradually introduced 1, 5, and 8 honey-bee hives per site, each containing ca. 20,000 workers while recording wild and honey-bee foraging behaviour on *Cistus creticus* L. In particular, we observed the visitation frequencies and visit duration of bees before and during the presence of added hives, to explore possible competitive interactions potentially leading to changes in foraging behaviour.

MATERIALS AND METHODS

1 Study area and plant model

The study was conducted in Peristera, ca. 25 Km east of the town of Thessaloniki, North Greece (40.32°N, 23.09°E) during the years 2013 and 2014. Our experimental observations took place from May to June, i.e. the flowering period of *C. creticus*; our model plant. Besides being a common plant with a wide flowering period, this plant is visited by a wide range of insects, including both honey bees and wild bees (Petanidou, 1991). Each plant produces a large number of flowers, each one open for a day. The flower produces mostly pollen and provides a significant protein source for bees (Petanidou, 1991; Ortiz, 1994; Petanidou & Smets, 1995).

In order to establish how the density of honey bees affects the wild bee foraging behaviour, we selected a total of 12 study sites, 6 in each year. The sites were randomly distributed in the area to prevent possible autocorrelation and correlations with the landscape structure and the abiotic factors. The sites had similar vegetation profiles. The minimum distance between sites was 1.5–2 km. No managed beehives were observed within a radius of 3 km from each site.

2 Flowering plant composition and abundance

The vegetation in the study region is evergreen sclerophyllous scrub scattered with open patches of herbaceous plants and *C. creticus* bushes. To estimate the general resource availability for foraging bees, we recorded the species richness of flowering plants in each site. The flowering plant species were identified and recorded in 25 randomly selected patches (squares 1m x 1m) per site. In each square we counted the number of flowers per species.

3 Bee survey

3.1 Sampling

Before any treatment we recorded the wild bee species richness and abundance in each site. Each study site was sampled using a variable transect walk method (Westphal et al., 2008). For this method, the surveyors walked slowly among any potentially attractive resource patches and collected bees during a 120 min observational period. The time of day for sampling at successive transects was randomised for each site and took place between 8:30 and

14:30. The sampling occurred during the flight activity and suitable weather conditions for pollinators (minimum of 15°C, low wind, no rain, and dry vegetation). Temperature, wind speed, cloud coverage, and relative humidity (RH) were recorded daily using a mobile meteorological measuring device (Kestrel 3000 pocket weather meter, KestrelMeters.com). The bees were collected with a hand net for identification. All bees were identified to species wherever possible.

We subsequently established the average full body length (front to tip of the abdomen) of all collected bee species and assigned all collected specimens to three size groups (small-sized wild bees (SWB): ≤7.5 mm; medium-sized wild bees (MWB): >7.5 mm and ≤11.5 mm; large-sized bees (LWB): >11.5 mm) and honey bees (AM).

3.2 Foraging behaviour and focal plant species

The foraging behaviour of the four bee groups mentioned above was observed on wild *C. creticus* plants. This plant species is a common and widespread perennial in the Eastern Mediterranean. It is a species widely visited by bees (Brandt & Gottsberger, 1988; Bosch, 1992; Manetas & Petropoulou, 2000; Dimou et al., 2014). In each study site, nine patches were established as observation plots. Each observation patch consisted of a minimum of 100 *C. creticus* flowers, which were sufficiently densely distributed to allow the synchronous observation and monitoring of all visiting bees. The visitation to the flowers was surveyed twice, once in the morning (8:30 to 11:00) and once at noon (11:30 to 14:00), when the release and viability of *Cistus* pollen is highest (Aronne, 1999).

In order to study the potential competition of honey bees with wild bees, we gradually increased the honey-bee population by introducing 1, 5, and 8 honey-bee hives per site. Each hive contained about 20,000 workers. While introducing the bees, we measured visitation to *C. creticus* in the absence of beehives, and before and after each introduction. We allowed 3-4 days of acclimatisation after the introduction of the hives before resuming the observations. The total experiment lasted about two weeks in each site to minimise temporal changes in the composition and abundance of plant and bee species. To minimise the effect of uncontrolled factors, we haphazardly changed the observation patches with each introduction.

Visitation rate: We observed the individual visits to flowers of all bees in each patch of *C. creticus*, in 10 minute sessions and recorded the results separately for each of the four groups of bees (AM, SWB, MWB, LWB). We only recorded a visit when the observed bee landed and made a "legitimate visit" to the flower, coming into contact with the sexual organs of the flower and thereby potentially contributing to pollination. For each observation patch, we also counted the number of available open flowers to estimate the visitation frequencies (number of visits per flower).

Visit duration: In each of the nine observation patches we followed each visiting bee and measured the total time of the forage bout (i.e. time between the arrival on and departure from a flower).

4 Data analysis

We used a mixed linear modelling (package nlme) approach with the site as a random factor and flower species richness and the number of beehives as categorical, fixed factors to analyse the impact of honey-bee hives on the foraging behaviour (response variables: visitation rate and visit duration) of wild bees of three size classes, all wild bees combined, and honey bees. For the analyses we combined all observations within a day (morning and noon). We used the Tukey HSD test (package lsmeans) to disentangle differences between bee groups. All statistical analyses were performed using the R software (R core team 2012). The data were checked for heteroscedasticity. Different letters above bars of graphs indicate significant differences between bee groups. Mean values are followed by their SE.

RESULTS

1 Co-flowering species

We found a total of 48 plant species (22 families) co-flowering with *C. creticus*. The most abundant families in regards to the number of species were Caryophyllaceae, Asteraceae, and Fabaceae; and regarding population were Fabaceae, Lamiaceae, and Caryophyllaceae.

2 Bee diversity

A total of 97 bees belonging to 28 species were collected while visiting *C. creticus* in our study areas. The most abundant families were Andrenidae, Halictidae, and Megachilidae (Tab. 1).

3 Foraging behaviour

Visitation rate: A total of 3,460 visits were recorded carried out by honey bees (449 visits), small-sized wild bees (1,268), medium-sized wild bees (1,670) and large-sized wild bees (73). The bees were recorded on a total of 27,417 *C. creticus* flowers. In both years, the medium and small-sized wild bees were the most commonly observed wild bees accounting for

Table 1.
Bee families and species recorded in the study areas.

Family	Genus	Subgenus	Species
Andrenidae	*Andrena*	*Chlorandrena*	*clypella*
Andrenidae	*Andrena*	*Brachyandrena*	*colletiformis*
Andrenidae	*Andrena*	*Zonandrena*	*flavipes*
Andrenidae	*Andrena*	*Charitandrena*	*hattorfiana*
Andrenidae	*Andrena*	*Poliandrena*	*kriechbaumeri*
Andrenidae	*Andrena*	*Melandrena*	*limata*
Andrenidae	*Andrena*	*Melandrena*	*morio*
Andrenidae	*Panurgus*	*Panurgus*	*calcaratus*
Apidae	*Apis*	*Apis*	*mellifera*
Apidae	*Ceratina*	*Ceratina*	*cucurbitina*
Apidae	*Eucera*	-	*spec. 1*
Colletidae	*Hylaeus*	*Abrupta*	*cornutus*
Colletidae	*Hylaeus*	*Prosopis*	*meridionalis*
Colletidae	*Hylaeus*		*spec. 1*
Halictidae	*Halictus*	*Halictus*	*brunnescens*
Halictidae	*Halictus*	*Hexataenites*	*scabiosae*
Halictidae	*Halictus*	*Hexataenites*	*sexcinctus*
Halictidae	*Halictus*	*Seladonia*	*subauratus*
Halictidae	*Lasioglossum*	*Evylaeus*	*leucopus aff.*
Halictidae	*Lasioglossum*	*Evylaeus (pauperatum-group)*	*pauperatum*
Halictidae	*Lasioglossum*	*Evylaeus (pauperatum-group)*	*pygmaeum*
Halictidae	*Lasioglossum*		*spec.*
Megachilidae	*Anthidiellum*	*Anthidiellum*	*strigatum*
Megachilidae	*Hoplitis*	*Anthocopa*	*dalmatica*
Megachilidae	*Megachile*	*Chalicodoma*	*parietina*
Megachilidae	*Osmia*	*Osmia*	*nigrohirta*
Megachilidae	*Osmia*	-	*spec. 1*
Melittidae	*Dasypoda*	*Heterodasypoda*	*pyrotrichia*

an average of 84.9% of all bee visits (medium-sized: 48.3%, small-sized: 36.6%); while honey bees constituted only 13%.
We found no statistically significant effect of the number of beehives on the visitation rates by any of the tested bee groups (Tab. 2). Yet, there was a general trend of decreased visitation rates with increased bee hive numbers in all groups apart from the small-sized bees (Fig. 1).
Visit duration: In total, we recorded 5,026 bee visit durations carried out by honey bees (1,608 visits), small-sized wild bees (1,302), medium-sized wild bees (2,040), and large-sized wild bees (76). Statistically significant differences were found regarding the visit duration among the different types of bees (p <0.001). In general, small-sized bees spent more time foraging than bees of other sizes. Specifically, the average time that small-sized bees spent on a *C. creticus* flower (69.0 ± 70.3 sec) was higher than that of the medium-sized bees (11.6 ± 13.3 sec), large-sized bees (9.7 ± 11.7 sec), and honey bees (6.8 ± 3.9 sec) (Fig. 2).

Table 2.
Effect of the number of bee hives on the visitation rate of wild bees in *Cistus creticus* flowers.

Response variable	Effects	df	χ^2	p
Honey bee mean visit duration	Colonies	3	ns	ns
	Flower species richness	1	ns	ns
Mean visit duration of all wild bees	Colonies	3	14.117	0.003
	Honey bee mean visit duration	1	ns	ns
	Flower species richness	1	ns	ns
Small-sized bee mean visit duration	Colonies	3	ns	ns
	Honey bee mean visit duration	1	ns	ns
	Flower species richness	1	ns	ns
Medium-sized bee mean visit duration	Colonies	3	ns	ns
	Honey bee mean visit duration	1	ns	ns
	Flower species richness	1	ns	ns
Large-sized bee mean visit duration	Colonies	3	ns	ns
	Honey bee mean visit duration	1	ns	ns
	Flower species richness	1	ns	ns

The number of honey-bee hives had no statistically significant effect on the visit duration by any single bee group (Tab. 3). There was, however, a significant effect of honey-bee hives on the visitation duration of all wild bees combined (p=0.003). We observed a gradual increase in visit duration with the use of an increased number of beehives with the exception of the addition of 8 beehives, which led to a small drop in visit duration compared to the 5 beehive treatment. Statistically, the 5 beehive treatment was different from all other treatments (Fig. 2).

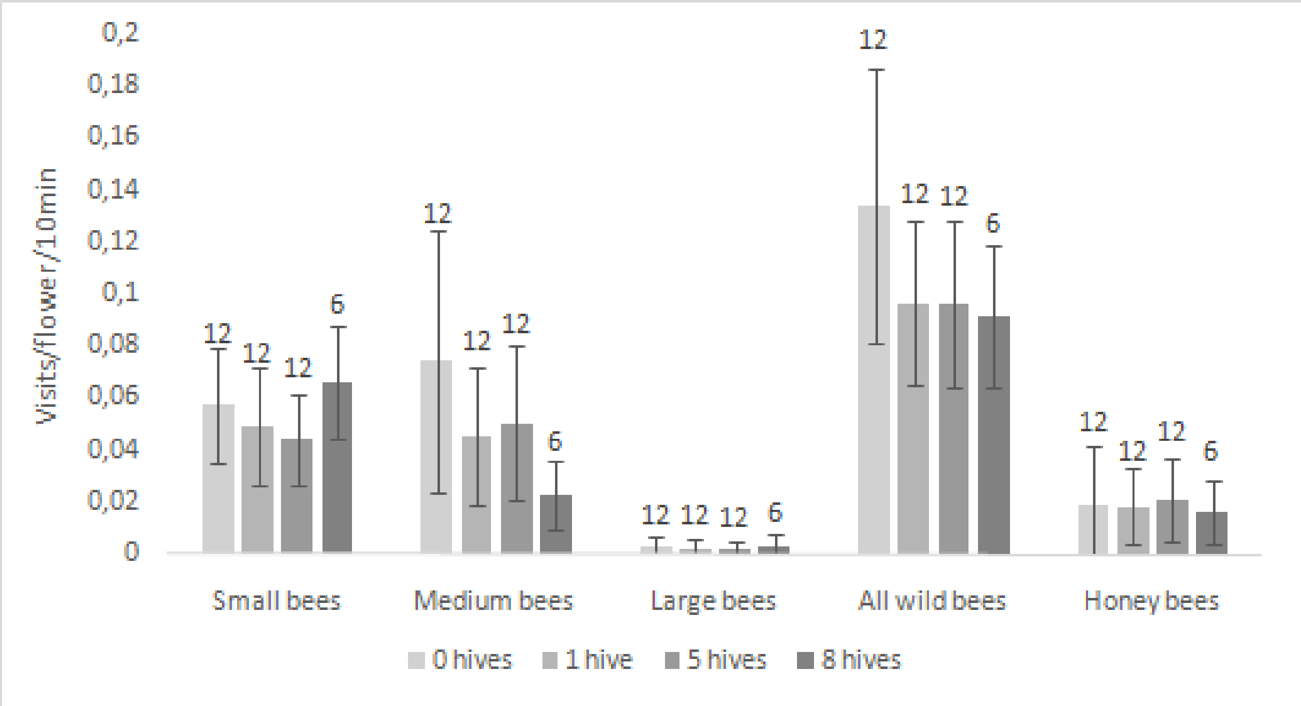

Figure 1.
Effect of the number of bee hives on the visitation rate of wild bees in Cistus creticus flowers. There was no statistically significant effect of honey-bee hives on visitation rates. Numbers above the bars indicate the sample size (number of sites the respective result is based on).

DISCUSSION

In the last few decades, several researchers have studied the competitive effects of managed honey bees on native bees with conflicting results (Sugden, Thorp & Buchmann, 1996; Butz Huryn, 1997; Kato et al., 1999; Paini, 2004; Paini, Williams & Roberts, 2005; Goulson & Sparrow, 2009). The great majority of the studies were carried out in areas where honey bees were introduced relatively recently (Wils, Lyons & Bell, 1990; Schwarz, Gross & Kukuk, 1991; Bailey, 1994; Roubik, 1996; Paton, 1999; Gross, 2001; Goulson, Stout & Kells, 2002; Paini & Roberts, 2005; Inoue, Yokoyama & Washitani, 2008). There are a comparatively small number of studies from Europe and even fewer from the Mediterranean area, where there is a long history of beekeeping (Pechhacker & Zeillinger, 1994; Ingolf & Tscharnkte, 2000; Dupont et al., 2004; Shavit, Amots & Ne'eman, 2009; Hudewenz & Klein, 2013).

In this study, we gradually increased the number of honey-bee hives and observed the bee foraging behaviour in the same sites before and after the introduction of the hives. We recorded several wild bee species of the genera *Andrena, Hylaeus, Halictus, Lasioglossum,* and *Osmia,* which include a number of species considered as polylectic (Westrich, 1996). In general, polylectic bees might be more affected by competition with honey bees due to similar foraging preferences (Schaffer et al., 1979, 1983; Roubik, 1978; 1980). Still, we found no clear evidence of competition between wild bees and honey bees regarding their foraging behaviour on *Cistus* flowers.

Similar results of absence or weak competitive effects have been reported in several studies conducted in Europe. For instance, in Austria, Pechhacker & Zeillinger (1994) studied the abundance of nesting from solitary bees at different distances from one large apiary and they did not find evidence of competitive effects. Similarly, in Germany, Ingolf & Tscharntke (2000) studied the possible honey-bee effects on species richness and abundance of flower-visiting wild bees, ground-nesting wild bees and trap-nesting wild bees. They found no negative relationship between the densities of honey-bee colonies and abundance or species

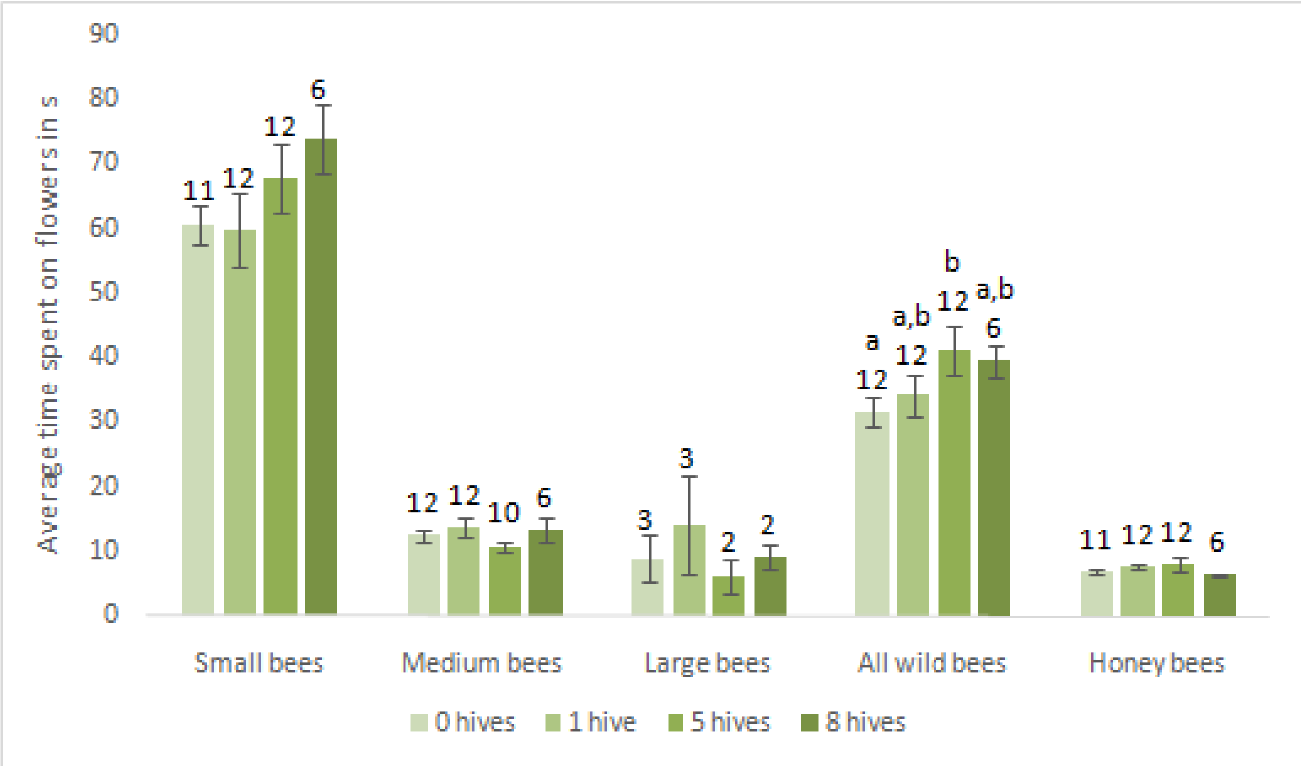

Figure 2.
Effect of the number of bee hives on the visit duration of wild bees in Cistus creticus flowers. Numbers above the bars indicate the sample size (number of sites the respective result is based on). Different letters above bars indicate statistically significant differences.

richness of wild bees. Dupont et al. (2004), recording the impact of honey bees on native pollination interactions of *Echium wildpretii* in the Canary Islands, also did not clearly show competitive behaviour between honey bees and native bees. Studying the competition between honey bees and native solitary bees in Israel by observing their foraging behaviour, Shavit, Amots & Ne'eman (2009) found conflicting results among different species, floral resources, and years. These researchers could provide only partial evidence for competition between these bees. Finally, weak effects of competition between honey bees and wild bees were reported by Hudewenz & Klein (2013) in Germany when they observed the visitation rate on flowers of *Calluna vulgaris*; while no such evidence was found regarding overall reproductive success.

On the other hand, Goulson, Stout & Kells (2002), exploring the competitive foraging behaviour of bumblebees and honey bees to native bees in Tasmania, found that sites where honey bees were absent supported greater numbers of native bees than sites where honey bees occurred. Additionally, Paini & Robetrs (2005) in a two-year study reported that honey bees significantly affected the fecundity of the solitary native bee *Hylaeus alcyoneus* located in Western Australia.

Most studies which showed clear evidence of competition between honey bees and wild bees concerned non-European countries where honey bees were recently introduced (Paini, 2004). This is not surprising as honey bees are native to Europe and are likely to have evolved with other native bees to reduce niche overlap and limit competition (Paini, 2004). Although wild or feral swarms of honey bees might be rare in nature today (Moritz, Härtel & Neumann, 2005), apiculture is widespread in the area; and honey bees have been managed for thousands of years in the Mediterranean area (Crane, 1990). According to FAO (2015), in the last few decades, the beehive population in Greece ranged approximately from 1,000,000 to 1,340,000 beehives, reaching the largest concentration of hives per area worldwide. The large density of honey bees in Greece can be expected to heavily reduce floral resource availability for wild bees through competition, and therefore, affect them negatively. Although there are no comparable data about the wild bee populations in Greece from the past, the present study provides some evidence that the long history of honey bees and beekeeping in the area seems to have led to the development of mechanisms that allow their coexistence.

In our study sites, we found no significant change in the *C. creticus* flower visitation rate by wild bees or honeybees even when we raised the number of bee hives and thereby honey bees in each area, by up to eight hives. The Mediterranean region is characterized by a massive spring flowering production (Bosch, Retana & Cerda, 1997; Potts et al., 2003) that may minimize the competition between honey bees and native bees in spring. Thus, the availability of food sources in our study sites might have decreased any possible impacts of the honey bees on wild native bees. However, the competition between the honey bees and native bees can be more severe when the floral resources are limited in an area (Ingolf & Tscharntke, 2000).

We also observed that after the introduction of five hives of honey bees in the area, the medium and large-sized wild bees spent less time on *C. creticus* flowers while the small-sized wild bees spent more time on the flowers. Even though there was no statistically significant difference on the visit duration for each group, there was a slight trend of differentiation, probably because of the different bee body sizes. An increase in the number of honey bees in an area has been proven to depress the availability of nectar and pollen (Wills, Lyons & Bell, 1990; Horskins & Turner, 1999). This may explain why different sized wild bees react to this pressure. The energetic cost of foraging is approximately proportional to the weight (Greenleaf et al., 2007). Larger bees need more food, thus, under pressure and low food availability, they spend less time in each flower in order to collect the pollen and nectar they need. On the other hand, small-sized bees such as *Hylaeus* would spend more energy to find another source of pollen. Such bees prefer to spend more time on a single flower and collect the biggest amount of food they can.

Conclusions

In conclusion, although competition between honey bees and wild bees is often expected, we did not find any clear evidence for significant effects even in honey bee densities much higher than the European-wide average of 3.1 colonies/km^2. The impact of honey bees to native bees on a native pollination system may vary between regions and habitat types. So far, no study has unambiguously shown significant negative effects of honey bees on wild bees in Europe. This may, at least in part, be due to the fact that honey bees are native to Europe and are likely to have evolved with other native bees to reduce niche overlap and limit competition. However, more long-term studies would be necessary to assess the impact of honey bees at the population level of native flower visitors over time, and to evaluate the relative importance of factors influencing the population dynamics.

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