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# Seasonal dynamics of competition between honey bees and wild bees in a protected Mediterranean scrubland

**Lise Ropars, Laurence Affre, Élisa Thébault and Benoît Geslin**

## Abstract

Due to the widespread use of pesticides and the lack of floral resources in many agricultural landscapes, beekeepers have moved numerous honey bee colonies in protected areas which could shelter an important diversity of wild bees. Here, we investigated the seasonal dynamics of the competition between honey bees and wild bees through a two-year study of plant–bee networks in a Mediterranean protected area. We recorded the visitation rates of four bee groups: honey bees, small wild bees, large wild bees and bumblebees. Our study reveals that the competition for floral resources induced by honey bees is especially strong during the early spring and then decreases along the season for all groups of wild bees. We observed a competitive exclusion of all groups of wild bees illustrated by an avoidance of well-flowered plant species in presence of honey bees. As a consequence, we detected a rewiring of large and small bee floral preferences linked to the presence of honey bees. In presence of honey bees, *Rosmarinus officinalis* and *Cistus albidus* were significantly less visited by large bees. This study underlines the need to mitigate the establishment of numerous honey bee colonies in protected areas as honey bees could strongly affect the foraging activity of wild bees.

Keywords: Apoidea, competition, floral resources, honey bee, plant–bee network, protected areas, wild bees

## Introduction

Pollination is one of the major ecosystem services that ensure human food supplies and the sexual reproduction of the vast majority of flowering plants. Almost 75% of crops and 87% of flowering plant species need to be animal-pollinated (Klein et al. 2007, Ollerton et al. 2011). On temperate latitudes, main animal pollinators are insects (Ollerton 2017). As flowering plants need pollinators to reproduce, conversely insect pollinators need to collect floral resources such as pollen or nectar to ensure their offspring and their population turnover (Roulston and Goodell 2011, Torné-Noguera et al. 2014, Hamblin et al. 2018). In the past few years, sharp declines of pollinator richness and abundances have been highlighted and well documented within several European countries (Potts et al.2010, Powney et al. 2019). Observed trends are multifactorial, mainly due to anthropogenic impacts on habitats including the use of pesticides, the introduction of species outside their native range and a decrease in the abundance and richness of flowering plant species (Bartomeus et al. 2013, Goulson et al. 2015, Hallmann et al. 2017, Ollerton 2017, Lister and Garcia 2018, Powney et al. 2019). To compensate for the global pollinator loss, awareness campaigns in favor of the western honey bee *Apis mellifera* have emerged, and have fostered beekeeping activities (Smith et al. 2016). From 1960 to nowadays, the number of honey bee colonies has increased globally (Aizen and Harder 2009) and within the Mediterranean Basin (Herrera 2020). In France, from 2012 to 2018, the national agricultural and seafood establishment recorded a 22.5% increase in the number of beekeepers and a 27% increase in the number of honey bee colonies (France AgriMer 2012, 2018). While habitats able to support large apiaries are decreasing (Otto et al. 2016), many beekeepers have installed their honey bee colonies within natural protected areas that present a large amount of floral resources and are preserved from pesticides.

To feed a colony and store honey for one year, the food requirements of a honey bee colony are estimated at several million visited flowers while the majority of solitary bees need uniquely the floral resources of a few hundred flowers to feed their brood (Müller et al. 2006, Cane and Tepedino 2017). As a consequence, massive introductions of honey bee colonies can lead to exploitative competition for floral resources between honey bees themselves (i.e. intraspecific competition) or between honey bees and wild bees (i.e. interspecific competition) (Geslin et al. 2017). By monopolizing the floral resources, honey bees could generate a modification in the behaviour of wild bees (Geslin et al. 2017, Mallinger et al. 2017). In cage experiments, red mason bees significantly decreased their number of visits on floral resources, their niche breadth and their reproduction when honey bees were present (Hudewenz and Klein 2015). In a protected area, Henry and Rodet (2018) reported that the individual foraging success of large wild bees was less important near honey bee colonies than farther away. A decrease in the availability of resources for wild bees can either lead to additional energy costs while foraging, a skewed sex ratio in favor of males, a smaller offspring or a population more vulnerable to parasites in the longer term (Cane and Tepedino 2017). Hence, the overabundance of honey bee colonies could negatively affect the reproductive success and the survival of wild bee populations. In case of intraspecific competition, a high density of honey bees could also reduce the net intake of bee workers and therefore the honey production (Henry and Rodet 2018).

To reduce the competitive pressures, wild bees can avoid flowering patches visited concomitantly by honey bees (Goulson 2003) or modify their floral diet, thereby leading to interaction rewiring, changes in the visitation frequency of plant species and ultimately changes in the structure of pollination networks (Magrach et al. 2017, Valido et al. 2019). Magrach et al. (2017), through a network approach, showed that when honey bees shifted from depleted mass flowering crops to wild plants, it caused changes in the foraging behaviour of wild bees and concurred to a decrease in the reproductive success of associate wild plant species.

While several recent studies have shown the consequences of competition between managed honey bees and wild bees within plant–pollinator networks in agricultural, urban and natural landscapes (Magrach et al. 2017, Ropars et al. 2019, Valido et al. 2019, Garibaldi et al. 2021, Lázaro et al. 2021, Rasmussen et al. 2021), the temporal dimension of this competition and its relative impact on different groups of pollinators remains to be fully understood. Indeed, plant–pollinator networks have been recently emphasized to vary greatly over time (CaraDonna et al. 2017), which could strongly affect competition among honey bees, and between honey bees and other pollinator species. First, the strength of exploitative competition depends on the availability of floral resources, which is determined by plant phenology and plant species turnover across the flowering season (Timberlake et al. 2019). For example, within Mediterranean scrubland of the Garraf natural park (Spain), at the end of the spring season, due to the summer aridity, floral resources can become scarce suggesting that competition could be more intense between honey bees and wild bees (Flo et al. 2018). Secondly, exploitative competition could also be modulated by the phenology of bees. In natural areas, high abundances and richness of wild bee species are often concomitant with high abundances and richness of plant species (Stang et al. 2006). However, the presence and abundance of honey bee colonies massively depends on beekeeper activities, especially when beekeepers realize transhumance in accordance with mass blooming of highly rewarding plant species. Thus, the variation of competition between wild bees and honey bees and among honey bees thus needs to be investigated over an entire flowering season to understand when pollination networks are the most affected by honey bee management.

Through a two-year survey in 2017 and 2018, we examined the potential exploitative competition between honey bees and wild bees and among honey bees in a protected area along the spring season, and how it affects the foraging activity of wild bees at the scale of local flowering patches. Calanques National Park hosts about fifteen beekeepers with around 450 honey bee colonies. Beekeepers install their colonies in February during the bloom of *Rosmarinus officinalis*, *Thymus vulgaris* and *Cistus albidus* and remove their colonies in the beginning of May to do transhumance. We focused on the competition between honey bees and wild bees due to their shared diet from larval to adult stages. We thus expected that the competition for floral resources between honey bees and wild bees will be more important in the beginning of the spring season due to a high number of honey bee colonies and a low plant species diversity. We estimated the potential strength of competition among honey bee colonies and between honey bees and wild bees by analyzing plant–bee networks over time. We then explored the consequences of the competition induced by the presence of honey bees on the foraging activity of wild bees.

## Methods

### Study area and sample design

This study was conducted within Calanques National Park in the vicinity of Marseille (France, 43°13′27.55″N, 5°28′2.92″E). This National Park was created in 2012, and is characterized by a Mediterranean climate i.e. hot and dry summer, rainy autumn and mild winter. Calanques National Park is dominated by scrubland habitats mostly composed of bushes such as *Quercus coccifera*, and herbaceous nectariferous and polliniferous plants such as *Rosmarinus officinalis*, *Cistus albidus* and *Thymus vulgaris*.

To achieve our sampling protocol, we chose 17 sites (100 m2-circle-plots) distributed in a homogeneous habitat (scrubland) and harboring at least three individuals of *Cistus albidus* and *Rosmarinus officinalis* (Supporting information). This area is widely used by beekeepers to produce honey and the number of managed honey bee colonies within the park has been carefully inventoried using field observation and cartography analyses (Ropars et al. 2020b). In total, we counted 451 honey bee colonies in the Calanques National Park, which represents 5.3 honey bee colonies km¯2. The 17 sites were located at different distances from the closest apiaries (from 150 to 1300 m, with an average of 630 m) and encompassed the diversity of possible situations in the park area. Given the number of hives and the area of the park, it was not possible to choose a site without any influence of honey bees at the scale of the whole park, defining a maximum distance of 1300 m to the closest apiary. Finally, despite this National Park being located in the native area of *Apis mellifera*, we did not record any wild or feral colony in the vicinity of our study sites.

### Plant–bee network surveys

In 2017 and 2018, we conducted a survey of plant–bee networks (honey bees and wild bees) in the 17 sites of 100 m2. For both years, the networks were sampled from March to June (hereafter the pollinating season), which corresponds to the main flowering period of the Mediterranean scrubland (Flo et al. 2018).

In each site, each week, to maximize the record of bee visitation rates, we first determined three most flowered patches of 1 m2 through a visual observation where observe plant–bee interactions. We recorded the number of visits of each bee group on each plant species present in 1 m square for 5 min per patch in 2017 and 10 min per patch in 2018. These records allowed us to calculate the visitation rate of each bee groups at the flowering patch scale by plant species. A session consisted of the sum of observations of all plant–bee interactions on the three 1m2 patches observed by week, by plant species (i.e. for the same plant species, maximum 15 min per site in 2017 and 30 min per site in 2018) corresponding to the plant–bee network at each site, each week. Each site was visited nine times in 2017 (2–3 times per month – corresponding to 9 sessions). Due to meteorological conditions with more frequent rainfalls each site could only be visited five times in 2018 (1–2 times per month – corresponding to 5 sessions) so we increased observation time per session the second year to improve the sampling effort. To sample the 17 sites each week, observations were realized during 2 or 3 consecutive days between 8:00 and 18:00, when weather conditions were favorable (no windy or rainy days). From one week to another, sites were surveyed alternatively in morning or afternoon to account for variations of the pollinator's activity. Overall, we thus sampled 1100 plants in our 1 m2 well flowered patches within the 17 sites across the 14 weeks (which represents for each site the nine sampling weeks in 2017 and the five sampling weeks in 2018).

We chose to work on the visitation rate of morphological groups of bees. This is a widely used methodology in plant–pollinator network analysis (Geslin et al. 2013, Pardee et al. 2019, Daniels et al. 2020, Theodorou et al. 2020, Zaninotto et al. 2020), which allows to assess variations in the visitation rate on the basis of a large number of interactions and without killing the observed bees. Our study sites are located in a bee biodiversity rich area (Petanidou et al. 2008, Nielsen et al. 2011, Popic et al. 2013, Ropars et al. 2020a, Orr et al. 2021) which is susceptible to present many rare pollination events (e.g. a bee species sampled once on a plant species). Due to the likely high number of rare events in our case (one bee species visiting a plant species one time), a species-based network would not allow to model variations of a visitation rate or change in the diet of most species without an extremely high sampling effort (Bartomeus 2013). Here, we classified bees in four morphological groups based on their size and easily distinctive criteria: a) small bees with body size approximately ≤ 10–12 mm (mostly *Andrena*, *Hylaeus* and *Lasioglossum* genera), b) large bees (body size > 12 mm; mostly *Anthophora*, *Eucera*, *Rhodanthidium* and *Xylocopa* genera), honey bees and bumblebees (Ropars et al. 2019, 2020b). We chose this limit between small and large bees because it approximately corresponds the mean body size of honey bees worker size (12 mm), (Bosch et al. 1997, Albrecht et al. 2007, Henry and Rodet 2018).

For each week at each site, all flowering plants visited by bees were identified to the species level corresponding to the visited plant richness within the three most flowered patches. To estimate the abundance of floral resources available to bees in each site, the covering of each plant species within 100 m2 was estimated following a slightly modified Braun– Blanquet coefficients ranking from 1 to 5 (with 1 = 1–10% of plant covering; 2 = 10–25%; 3 = 25–50%; 4 = 50–75% and 5 = 75–100%) (Van Der Maarel 1975). Plant richness and covering in each site was then added in our statistical models.

We built the global plant–bee network over both year and descriptive parameter such as the mean shared partner by bee groups and plant species, connectance, nestedness and modularity were calculated with *networklevel()* and *computeModules()* functions of bipartite package respectively (Dormann et al. 2009).

## Statistical analyses

### *Potential competition*

We built plant–bee networks at the week scale by combining for each sampling session all the observations from the 17 sites, which results in a total of 14 plant–bee networks (i.e. 9 networks in 2017 and 5 in 2018). These 14 plant–bee networks are thus distributed throughout a pollination season from March to June.

To assess the potential exploitative competition between bees, we used the Müller's index that allows to estimate the indirect effect of one bee group on another one via all their shared interaction partners in a network (Müller et al. 1999, Simba et al. 2018). In our case, this index is equal to 0 when a bee group (including honey bees for intraspecific competition) shares no plant with honey bees and it is close to 1 when a bee group depends only on plants highly visited by honey bees. The Muller's index is thus a calculation of a potential indirect competition between groups of bees. To calculate this index, we used the function *PAC()* available in the bipartite package of R ver. 3.6 (Dormann et al. 2009, <www.r-project.org>).

Müller's indexes were calculated based on visitation rates of the four bee groups: small bees, large bees, honey bees, bumblebees. To evaluate the variation of honey bee exploitative competition across the spring period, we built a linear model with honey bees' Müller index as response variable and the calendar number of the week, years of sampling, the wild bee groups and their interactions as fixed effects. p-values for each bee group were obtained through lstrends using the *summary()* function (package lsmeans – Lenth 2016).

### *Avoidance of honey bees by wild bees at one-meter flowering patch scale*

To evaluate whether the presence of the wild bee groups was affected at a fine spatial scale, we analysed whether wild bee presence on a given plant individual during a timed-observation in one square meter depended on the presence of honey bees on the same plant individual for the same timed-observation. To do so, we transformed the visitation rate of each bee groups by their absence–presence on each plant individual (i.e. 0 for absence and 1 for presence). The dataset contained all observations performed on plant individuals which received at least one visit of bees, corresponding to 201, 5-min observations in 2017 and 128 10-min observations in 2018 (329 plant sampled for both years). Then, we fitted generalized linear mixed models with presence/absence of each wild bee groups as response variable and honey bee presence/absence as factor, week, year, plant covering at site scale and visited plant species richness at session scale as fixed effects; sites as random variable; following a binomial structure. An offset was added to this model, corresponding to the logarithm of the observation period to account for differences in sampling duration between the two years. These complete models were then simplified according to the lowest Akaike information criterion (AIC) using vgam package (Yee 2015). We only present the results of simplified models for each bee groups, estimates and standard errors were obtained with the *summary()* function.

### *Visitation shifts between flowering species at the week scale*

We questioned if wild bees modified their visitation rates (i.e. number of visits per plant species) with the presence of honey bees. We only considered observations performed on plant species which received at least one visit of bees. The number of visits was cumulated on the three well-flowered patches per site per week corresponding to the plant–bee network at a given site in a given week. Data corresponded to a total of 214 plant sampled at week scale. For each bee group, we built a generalized linear mixed model with Poisson distribution error using the visit number of each wild bee group as response variable and a) honey bee presence/absence as factor, the plant classes and their interactions, c) plant cover and visited plant richness and d) year as fixed effects. We completed this model with an offset corresponding to the logarithm of the observation period to account for differences in sampling duration by plant species. Finally, the number of plants sampled was also added as random effect to account for over-dispersion. Site and week variables, which had been included in the complete models as random effects in the first instance, had a variance close to or equal to 0, so we decided not to include them in simplified models. Complete models were then simplified according to the lowest Akaike information criterion (AIC) using vgam package (Yee 2015) (Supporting information).

We classified the plant species by the number of times we sampled them throughout the two years. We grouped all plant species recorded fewer than 10 times together. Finally, plant species were a) *Rosmarinus officinalis* (sampled 96 times), b) *Cistus albidus* (sampled 42 times), c) *Cistus monspeliensis* (sampled 15 times), d) *Thymus vulgaris* (sampled 13 times) and e) other species (corresponding to 21 plant species sampled fewer than 10 times and to 9% of total visitations – Supporting information). We finally performed pairwise Tukey comparisons on each model with the lowest AIC to examine the changes of wild bee visitation rates on each plant with or without honey bees using the package lsmeans (Lenth 2016). In the following, D indicates the difference between the visitation rate with or without honey bees, with $D > 0$ corresponding to a higher number of visits to the given plant when honey bees are present.

## Results

### Plant–bee network surveys

From late February to early June in 2017 and 2018, we recorded 7754 visits performed by the four bee groups on 25 plant species. *Apis mellifera* realized 80.7% of the visits following by small bees, large bees and bumblebees (respectively 8.2, 6.4 and 4.7% – Supporting information). The entire network contained 55 links. Small bees contributed to the global network by being involved in 19 links, large bees 16 links, *Apis mellifera* 13 links and bumblebees realized 7 links. We estimated sampling completeness following Jordano (2016) using vegan, biodiversityR packages in R software. By considering cumulative interactions across the pollination seasons over the two years, we detected from 22% to 68% of the links depending on the bee group considered according to the Chao index (Supporting information). In average, bee groups visited 7.66 plant species according to the mean number of shared partners. The modularity, nestedness and connectance of the entire network were estimated at 0.09, 22.11 and 0.55 respectively. Twelve plant species (*Biscutella laevigata*, *Centranthus ruber*, *Coris monspeliensis*, *Crepis sancta*, *Echium vulgare*, *Fumana ericoides*, *Iris lutescens*, *Lactuca perenis*, *Lonicera implexa*, *Potentilla hirta*, *Ruta angustifolia*, *Sinapis alba*) were only visited by wild bees whereas only one species (*Rhamnus alaternus*) was visited by honey bees only (Fig. 1). In average, plant species were visited by 1.3 bee group according to the mean number of shared partners.

The species richness of flowering plant increased across the season, with only two species flowering in early March (*Rosmarinus officinalis* and *Ulex parviflorus*) to 12 species in the last week of May (*Aphyllantes monspeliensis*, *Biscutella laevigata*, *Cistus albidus*, *Cistus monpeliensis*, *Coris monspeliensis*, *Coronilla juncea*, *Crepis sancta*, *Echium vulgare*, *Lonicera implexa*, *Ruta angustifolia*, *Sinapis alba*, *Teucrium polium* – Supporting information).

### Temporal variation of exploitative competition

We found that intraspecific competition among honey bees stayed high (i.e. close to 1) and did not vary over the pollinating season (honey bees: slope = −0.005 ± 0.01, $p > 0.05$). By construction, the sum of the competitive effects received by a bee group through the network is equal to 1 with the Muller index. This means that most of the potential competition sustained by honey bees is intraspecific. We also found that the potential effect of competition by honey bees on each wild bee group significantly decreases along the pollinating season (Anova test $p < 0.001$; large bees: slope = −0.066 ± 0.01, $p < 0.001$; small bees: slope = −0.070 ± 0.01, $p < 0.001$; bumblebees: slope = −0.071 ± 0.01, $p < 0.001$) but it does not differ among wild bee groups (Fig. 2). These results suggested that plant species were highly shared in the beginning of the pollinating season between honey bees and wild bee groups and less shared in the end of the pollinating season.

### Avoidance of honey bees by wild bees at one-meter flowering patch scale

We found that the potential competition revealed in the previous section resulted in an exclusion of wild bee groups by the presence of honey bees. This exclusion was consistent for all wild bee groups. The presence of small bees was negatively impacted by the presence of honey bees on the same flowering patch and increased across the pollinating season (Table 1). The presence of large bees was negatively impacted by the presence of honey bees, decreased across the pollinating season and differed marginally across years. Finally, the presence of bumblebees was also negatively impacted by the presence of honey bee on the same flowering patch and differed across years.

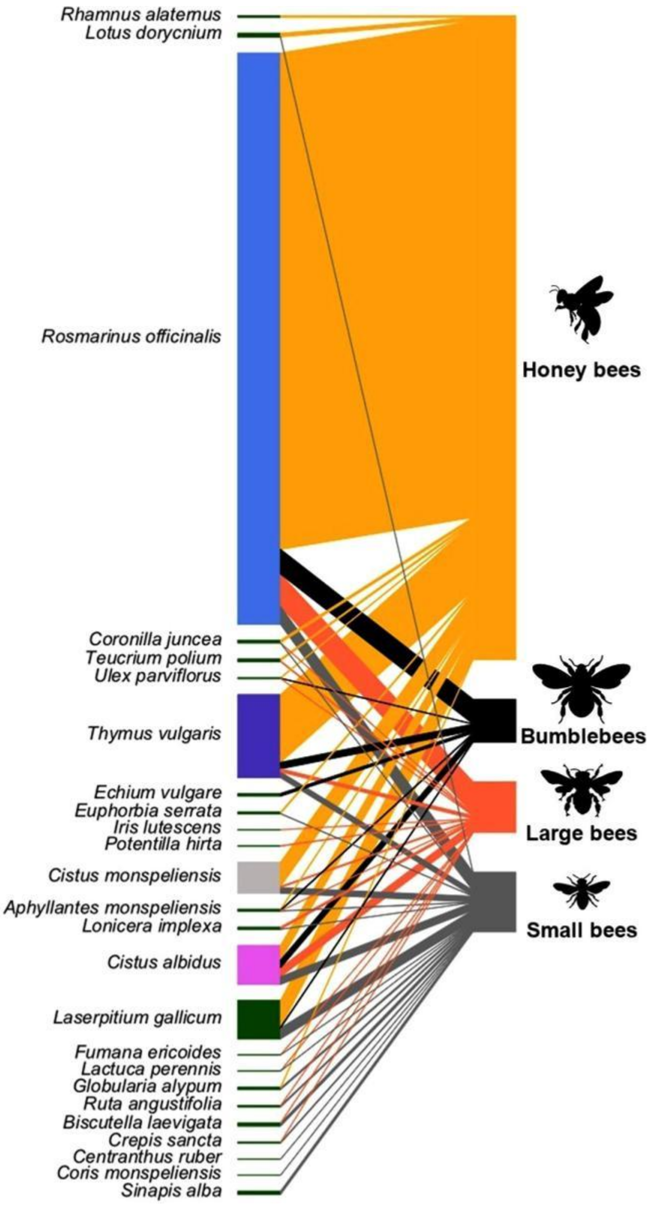

Figure 1. Interaction network between bee groups and plant species in Calanques National Park. Honey bees are highlighted in yellow, bumblebees in black, large bees in orange and small bees in grey. *Rosmarinus officinalis* is highlighted in blue, *T. vulgaris* in violet, *C. monspeliensis* in light grey, *C. albidus* in pink and the other plant species in dark green. Width of interactions is proportional to the number of visits performed on each plant species.

### Shifts in the visitation rates between flowering species at session scale

The number of visits of small and large wild bees were affected by the honey bee presence. This result shows that the visit number of each wild bee group was different with or without honey bees. Precisely, small bees foraged significantly less in presence of honey bee on other plant species (Δ = −3.26 ± 1.18 – $p = 0.006$). However, small bees did not significantly change their number of visits in presence of honey bees on *Rosmarinus officinalis*, *Thymus vulgaris*, *Cistus albidus* and *Cistus monspeliensis* (Fig. 3A). Considering large bees, their number of visits on *Rosmarinus officinalis* and *Cistus albidus* were negatively influenced by honey bee presence (Δ = −1.99 ± 0.56 – $p < 0.001$; Δ = −3.59 ± 1.18 – $p = 0.003$ respectively). In the presence of honey bees, we also did not observe any visit of large bees on *Thymus vulgaris* and on the category 'other plant species' in the presence of honey bees (Fig. 3B). The presence of honey bees did not induce significant changes on the visit number of large bees on *Cistus monspeliensis*.

Finally, the presence of honey bees did not induce significant changes on bumblebee visits on *Rosmarinus officinalis*, *Thymus vulgaris* and *Cistus albidus*. However, we did not observe any visit of bumblebees in presence of honey bees on the category 'other plant species'.

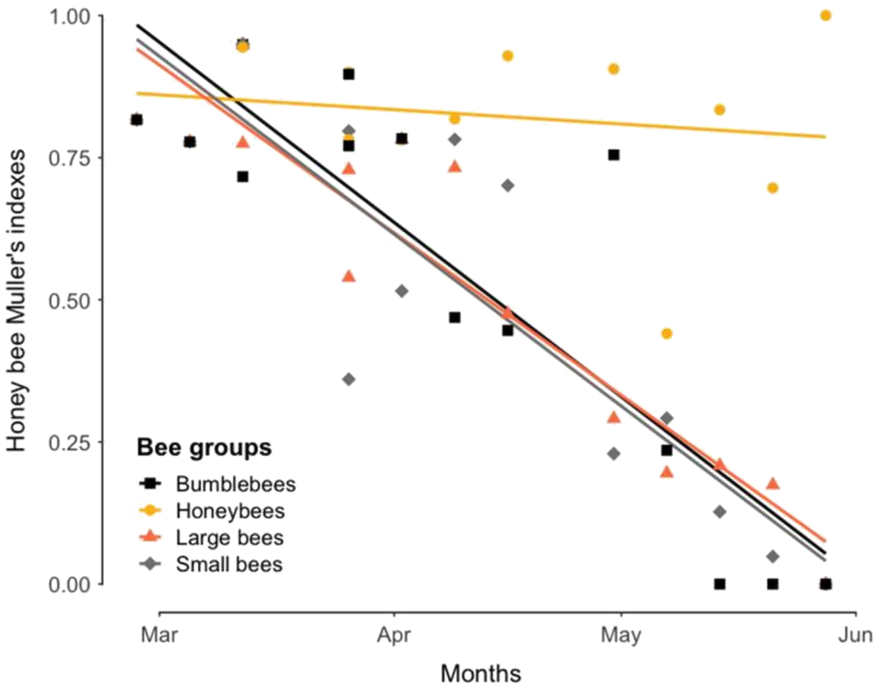

Figure 2. Muller's index of potential competition of honey bees on each bee groups along the spring flowering season.

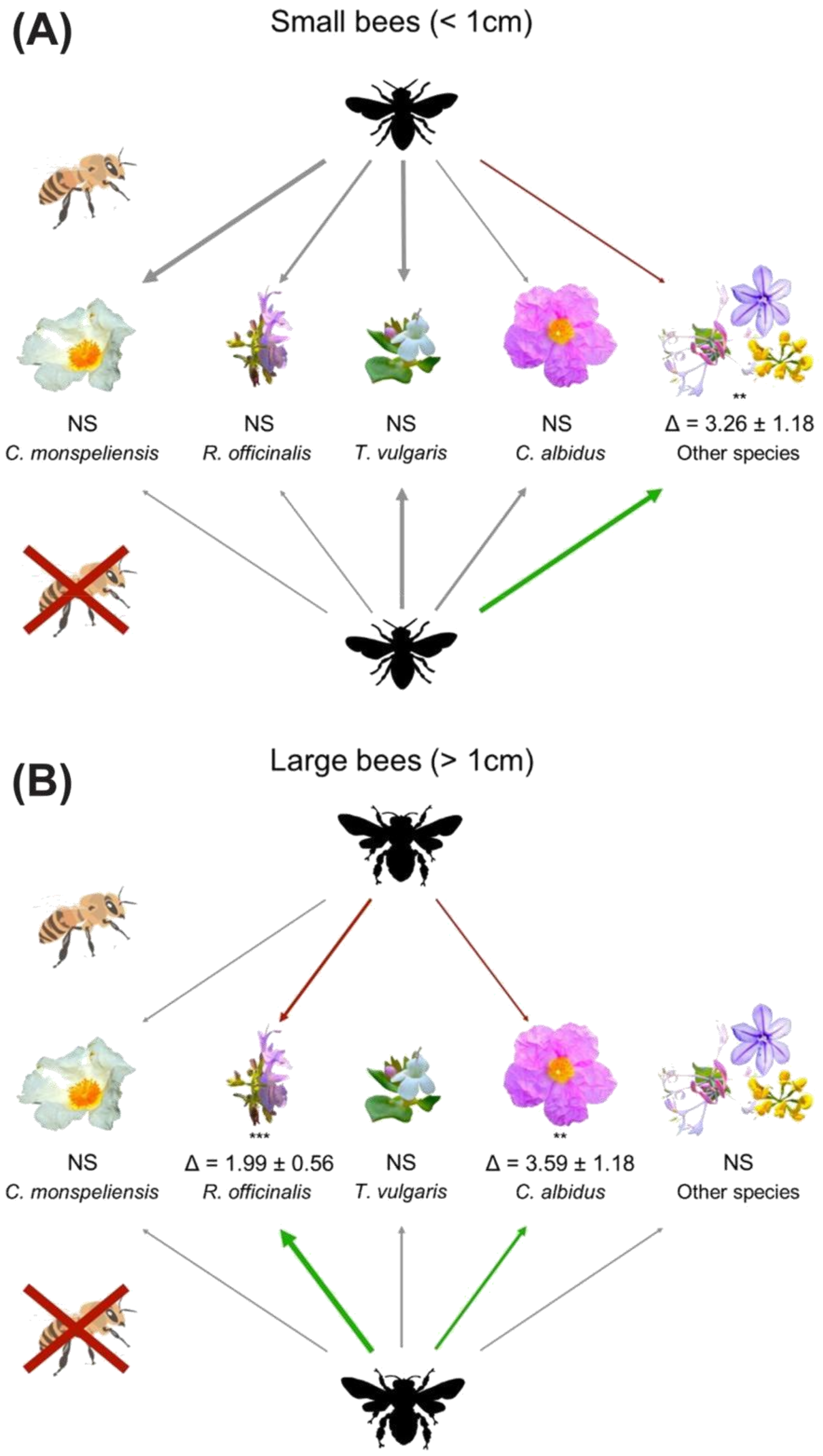
(A)
Small bees (< 1cm)
**
NS
C. monspeliensis
NS
R. officinalis
NS
T. vulgaris
NS
C. albidus
Δ = 3.26 ± 1.18
Other species
(B)
Large bees (> 1cm)
***
**
NS
C. monspeliensis
Δ = 1.99 ± 0.56
R. officinalis
NS
T. vulgaris
Δ = 3.59 ± 1.18
C. albidus
NS
Other species

Figure 3. Changes of small (A) and large (B) bee visitation rates in absence or presence of honey bees. Width of arrows is proportional to the visitation rates per minute realized by wild bees on each plant. Δ corresponds to the difference according to the pairwise Tukey test between the two conditions, with and without the presence of honey bees. Green arrows indicate an increase of visitation rates and red arrows a decrease of visitation rates with the presence of honey bees. Grey arrows and NS correspond to non-significant changes of visitation rates using pairwise Tukey tests, ** corresponds to significant p-values between 0.001 and 0.01 and *** to significant p-values below 0.001. The lack of arrow corresponds to the absence of visit of the bee group on the plant species. Copyrights: *Aphyllantes monspelliensis*, Daniel Villafruela; *Lonicera implexa*, IKAI Wikipedia user; *Coronilla juncea*, Lise Ropars; other pictures are available on <https://pixabay.com>.

Table 1. Effect of honey bee presence on the presence of each wild bee groups. For each wild bee groups, ΔAIC is calculated between the complete models and simplified models with lowest AIC.

| Wild bee groups | ΔAIC | Fixed effects | Estimate ± SE | $\chi^2$ | df |
|---|---|---|---|---|---|
| Small bees | 3.4 | Intercept | −2.357 ± 0.226 | | |
| | df = 325 | Presence of honeybees | −1.05 ± 0.303 | 12.97 | 1 |
| | | Week | 0.424 ± 0.144 | 8.958 | 1 |
| Large bees | 3.3 | Intercept | −1.307 ± 0.221 | | |
| | df = 324 | Presence of honeybees | −2.858 ± 0.346 | 87.967 | 1 |
| | | Week | −0.348 ± 0.157 | 5.037 | 1 |
| | | Year | −0.583 ± 0.301 | 3.767 | 1 |
| Bumblebees | 3.0 | Intercept | −2.966 ± 0.317 | | |
| | df = 325 | Presence of honeybees | −1.619 ± 0.468 | 13.281 | 1 |
| | | Year | −1.914 ± 0.476 | 19.708 | 1 |

## Discussion

In this study, we found that *Apis mellifera* was the most dominant species in the plant–bee network, performing more than 80% of all interactions. While we found a strong potential intraspecific competition among honey bees throughout the pollinating season, the magnitude of this potential competition between wild and domesticated bees varied along the season. In early spring, honey bees shared most of their floral resources with wild bees highlighting a strong potential competition for nectar and pollen. Starting from May, however, we observed a release of interspecific competition either due to an increase in the diversity of flowering plants or to the management of apiaries (transhumance towards other mass-flowering locations). This competition translated into a local exclusion of wild bees which were significantly less detected in flower patches also visited by honey bees. Moreover, the presence of honey bees had implications on the foraging behaviour of small and large bees with a rewiring of their foraging preferences. These results are discussed in the light of potential consequences for wild bee populations and for the pollination of wild plants.

### Temporal variation of exploitative competition

First, we detected a strong potential intraspecific competition among honey bees, which remains very high along the season. The high value of the honey bee's Müller index on itself indicates that wild bee groups have few impact on honey bees. As honey bees are generalists (Giannini et al. 2015), they have the ability to change progressively their floral diet following the phenology of the dominant plant species (Hung et al. 2019). However, even if honey bees are generalist species and can visit many plant species in natural area (Stanley et al. 2020) and even if the diet of honey bees can change from a week to another, this index highlights that, within a single week and for each week, most colonies of the national park focus their visit on the same rewarding plant species triggering potential intraspecific competition. The intraspecific competition is a first signal to observe a limitation of floral resources within a territory and could lead to a decrease of honey yield per colony (Henry and Rodet 2018). As previously stated, mass flowering wild plants are shared resources for wild bees, honey bees and therefore beekeepers. Increasing the density of colonies could thus be counterproductive for honey bees themselves and therefore for those that exploit their honey (Hardin 1968).

Regarding wild bees, we also revealed that the magnitude of the interspecific competition between honey bee and wild bees changed along the season. The competition was more intense from February to April. This corresponds mainly to the flowering peak of *Rosmarinus officinalis* (Flo et al. 2018) which is the first dominant plant species to flourish in our study sites. *Rosmarinus officinalis* is highly attractive to bees for its high production of pollen and even more nectar, which explains why beekeepers installed their numerous honey bee colonies in this period to produce a specific honey. Later in the season starting from May, the competitive pressure exerted by honey bees dropped. This decrease can be due to the removing of honey bee colonies by beekeepers to do transhumance (Henry and Rodet 2018, Herrera 2020), which occurs around the first week of May, leading to a decrease in abundance and visitation rates of honey bees in late spring (Supporting information). According to unpublished data of the Calanques National Parks, about 60% of honey bee colonies leave the territory in early May for transhumance. Another possible explanation lies in the phenology of flowering plants. We observed a higher diversity of flowering plant species later in the season which could offer a wider diversity of floral resources (Flo et al. 2018) (Supporting information) with alternative resources for wild bees in case of competition. With a reasonable density of honey bee colonies (as an example, the national mean density of colonies is 2.5 colonies km¯2 – Chauzat et al. 2013) together with a diverse and abundant co-flowering plant species, the competition between honey bees and wild bees might be reduced, allowing a possible cohabitation between these two groups in a protected area.

## Competitive exclusion of wild bees

Exploitative competition for floral resources was translated into a competitive exclusion of wild bees by honey bees foraging on the same flowered patch. When honey bees were present on flowering patches, the probability to observe a wild bee foraging on the same flowering patches dropped sharply. Close ecological requirements for floral resources between wild bees and honey bees can increase the importance of the concurrence between these groups (Müller et al. 2006, Henry and Rodet 2018). For example, as large bees and bumblebees can easily fly larger distances than smaller bees, large bees and bumblebees could fly away from flower patches already occupied by honey bees (Torné-Noguera et al. 2016, Henry and Rodet 2018, Wignall et al. 2020a). Moreover, most of large bee species also harbor a long tongue making them more prone to visit a large diversity of plant species (Cariveau et al. 2016, Kendall et al. 2019). This result is consistent with a previous work, conducted in the same study area, which showed that richness and abundance of large bee species decreased with honey bee colony density (Ropars et al. 2020b). Henry and Rodet (2018), in a rosemary scrubland, also observed that wild bees were less abundant near apiaries, and that nectar foraging success of all wild bees decreased with the proximity of an apiary.

## Rewiring of small and large bee visitation rates

Our study also revealed a rewiring of visits realized by wild bees on plant species concomitantly visited by honey bees. This result is independent from the amount of floral resources available to bees highlighting a strong effect of the presence of honey bees on the foraging behaviour of wild bees. Our study clearly outlines that honey bees, only through their presence on flowering patches, could modify the visitation rate of small and large bees. It is known that bee species foraging simultaneously within a pollination network can modulate their foraging activity relatively to each individual’s behaviour (Valido et al. 2019). In Spain, solitary bees, hoverflies and bumblebees decreased their visitation rates due to the presence of honey bees on the most abundant or rewarding plant species (Magrach et al. 2017). The most significant trend in our work is, however, the change in the behaviour of large bees. With the presence of honey bees, they visit significantly less *Rosmarinus* flowers and we did not observe any visits of large bees on *Thymus* flowers, two of the most nectar-rewarding species of our study sites which are frequently visited by honey bees. As stated below, this could have major implications both for wild bees that rely on *Thymus* or *Rosmarinus* for their brood and for the reproductive success both plant species.

Contrary to large bees, small wild bees did not significantly change their visitation rates on the early most abundant plant species frequently visited by honey bees when honey bees were present (i.e. *Rosmarinus* and *Thymus*). Small bees require lesser floral rewards than large bees, they consequently could forage on few rewarding plant species, which might have been previously visited (Müller et al. 2006, Hudewenz and Klein 2015). Moreover, small bees are in little abundance in the beginning of the spring (i.e. during the flowering period of *Rosmarinus officinalis*), the competition for floral resources between these two groups could be lower at the beginning of the pollinating season and stronger at the end of the pollinating season, on the last rewarding plant species.

Finally, we did not find a change of visitation rates considering bumblebees probably due to their low abundance in our surveys. Indeed, bumblebees are not common and numerous in Mediterranean habitats (Herrera 1988, Schurr et al. 2019). Furthermore, bumblebees often forage rapidly and methodically all flowers on a single plant individual (Zhao et al. 2016) and can also prevent honey bees to forage on the same plant species (Wignall et al. 2020b).

However, as these fine mechanisms about avoidance seems to depend on the considered plant species and bee groups, it remains difficult to explain and would require additional studies, especially at lower taxonomic resolution such as species level to fully understand the underlined dynamics (see Lázaro et al. 2021 as an example at family level).

## Consequences for wild bees and plant communities

Through a quantitative network approach, we highlighted changes on floral preferences of morphological groups of bee species. These changes could have major implications for the fitness and the maintenance of the wild bee fauna and the wild flora. In a previous study in the same area, seven species were listed as near threatened or endangered species by the European Red List of bees (Ropars et al. 2020a). Some of these threatened wild bee species could suffer from the presence of a high density of honey bees (Rasmussen et al. 2021), which may lead to a reduction in their fitness. For example, as a response to competition, a female can lengthen its foraging bouts to feed or to go back to their nest which can generate a lower quantity of floral resources for the larva, an increase of the predation risks, a decrease in the number of offspring or a sex ratio biased in favor of males, leading to a weakening of local populations (Cane and Tepedino 2017). Likewise, a change of floral preferences could lead to poorer nutrient performance and an imbalance in the optimal foraging strategy. As an example, *Cistus albidus* is a highly polliniferous plant species but also contains a low concentration of amino acid and is known to slow down the growth of bumblebee colonies (Baloglu and Gurel 2015, Moerman et al. 2015). Specialist bee species, will also be particularly vulnerable to the presence of honey bees on their host plant species (Biesmeijer et al. 2006). Large wild bee species are also suffering from many anthropogenic pressures, and protected areas should be a haven for these species. Emblematic species such as *Rhodanthidium sticticum* that nests in empty snail shells have a narrow ecological niche and feed preferentially on *Cistus* spp. Such a species could be particularly vulnerable to the presence of a high density of honey bee colonies (Henry and Rodet 2018). We suggest that long-term studies should be necessary to follow the trend of bee populations at the species level, with a focus on the impact of honey bees on their reproductive success (Meeus et al. 2021). One of the limitations of our work lies in the use of networks based on bee groups rather than at the species level. This method allows observing numerous visitation events for each studied bee group, which allows to draw conclusions about changes in the visitations rates of bee groups. At the species level and in a typical plant–pollinator network, most interactions are observed only once or twice (Ropars et al. 2020a) and it is impossible to detect changes in the visitation preferences based on such rare events.

Finally, plant species may also suffer from a high abundance of honey bees through a decrease in their reproductive success (Magrach et al. 2017). Indeed, numerous visitations by honey bees can damage the style due to over visitation, or lead to an over deposition of pollen grains on stigmas, generating the growth of too numerous pollen tubes (Aizen et al. 2014). *Apis mellifera* is not the most efficient pollinator (Willmer et al. 2017) as shown on cultivated plants (Park et al. 2016), and they could reduce the germination ability of pollen due to their inhibitory effects of their glandular secretions. Also, a previous study in invaded sites where *Apis mellifera* is not native, showed that honey bees could favor the reproduction of a few plant species at the expense of others (Morales and Aizen 2002). Therefore, the abundance of honey bees could favor the most rewarding plant species triggering changes in the wild plant community. Future study should explore the reproductive success of dominant flowering plant species in presence or absence of honey bees to understand their contribution to the dynamic of wild plant communities.

## Conclusion

Several recent studies have highlighted competition between honey bees and wild bees in diverse landscapes (urban, agricultural or natural). The increase of honey bee livestock in the past few years has led to the dominance of this species in some plant–pollinator networks (Hung et al. 2019) especially in Mediterranean ecosystems (Herrera 2020). Consequently, the presence of honeybees could negatively affect the visitation rates (Klein and Hudewenz 2013, Ropars et al. 2019), diet preferences (Rasmussen et al. 2021), specific richness and abundance of wild pollinators (Torné-Noguera et al. 2016, Henry and Rodet 2018, Jeavons et al. 2020 – see an example on hoverflies, Ropars et al. 2020b, Lázaro et al. 2021, Leguizamón et al. 2021, Renner et al. 2021) as well as the structure of pollination networks (Valido et al. 2019, Lázaro et al. 2021). Our study brings additional knowledge on the effects of honey bees on the temporal dynamics of plant–bee networks, showing that even if apiaries are installed only for a short period of the year, they could change the presence and the floral preferences of wild bees in a protected natural area. It underlines the need to mitigate the installation of honey bee colonies in protected areas such as National Parks, especially to release the competition pressure between wild bees and honey bees. Land managers should be cautious when allowing apiaries to be installed in protected areas. At this stage, we can suggest to land managers, depending on the level of protection of their territory, to sow local (native) and attractive plant species for bees and more broadly for pollinators, and/or to reduce the competitive pressure by decreasing the number of honey bee colonies or to move them away from each other. In their recently study, Henry and Rodet (2020), developed an interesting framework for managing the cohabitation of honey bees and wild bee communities through an increase in the distance between apiaries. Also, to provide land managers accurate advice regarding the potentiality of an area to host apiaries, we should improve our capacity to precisely estimate the number of resources in terms of nectar and pollen produced by habitats. Future studies should go down that road if we want to conserve a traditional beekeeping activity, on the one hand, and the integrity of wild bee ecological communities, on the other hand.

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