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Land cover composition, local plant community composition and honeybee colony density affect wild bee species assemblages in a Mediterranean biodiversity hot-spot

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A B S T R A C T

Identifying environmental drivers which structure wild bee species assemblages appears essential in a context of worldwide pollinator decline. During a two-year survey, we studied wild bee species assemblages in an 85km^2 protected area dominated by Mediterranean scrubland, the Calanques National Park, located in southern France. Our objectives were (i) to assess the composition of the wild bee species assemblages, and (ii) to explore the effect of a) land cover composition (anthropogenic zone, low scrubland, forest and rocky land cover), b) local plant community composition, and c) honeybee colony density on wild bee species assemblages. On 17 circular 100m^2 plots, we collected 541 specimens belonging to 87 wild bee species. We found that large bee species were significantly influenced by land cover composition within a 1000m radius. More specifically, we observed that the presence of a diversified land cover composition within a 1000m radius maximized large wild bee species richness, whereas large bee abundance and richness were negatively affected by honeybee colony density. Small wild bee species were structured by the local plant community composition within 100m^2 plots and by land cover composition within a 1000m radius. Their occurrence were related to the local composition of plants growing on deep soils in scrublands. The Calanques National Park, which is the only European park located at the interface with a large city and consequently suffers from anthropic pressure, encompasses several types of land cover which are beneficial for a wide diversity of bees. However, we would like to raise awareness among park managers regarding beekeeping activities within this territory which includes diverse types of land cover favorable for wild bee species.

1. Introduction

Over the past decades, several studies have reported major losses of insects mostly due to habitat changes, pollution (fertilizers, pesticides, urban and industrial pollutants), invasive species and climate change (Burkle et al., 2013; Hallmann et al., 2017; Potts et al., 2010; Sánchez-Bayo and Wyckhuys, 2019). Among all insects, pollinators are essential for the maintenance of the pollination function, to support the productivity of agricultural systems and the reproduction of wild plant species (Ollerton et al., 2011; Potts et al., 2016). Their decline has been linked to the decrease in natural habitats and floral resources as a consequence of land cover changes (Potts et al., 2010). For example, in Britain, over the last thirty years, Powney et al. (2019) observed a decline of 33% of hoverflies and wild bee abundance due to habitat loss, climate change, and pesticide use. The European Red List of bees estimated that at least 9.2% of the 1965 wild bees occurring in Europe are threatened (near threatened status - NT) or endangered (vulnerable, endangered and critically endangered status - VU, EN, CR) (Nieto et al., 2014). However, for up to 55.6% of wild bee species, there is still not enough data to determine their protection status. Given this reported loss of insects and pollinators, we still need to survey wild bee species and determine what are the main environmental drivers that structure their species assemblages. In France, 961 wild bee species have been described according to the latest version of the French Taxonomic Referential (Gargominy et al., 2018). The European Red List of bees estimates that species richness ranges from 556 to 730 in southern France, most being endemic to the Mediterranean basin (Gargominy et al., 2018; Nieto et al., 2014). This region is one of the world's biodiversity

hotspots where plant-pollinator communities are the most diverse (Medail and Quezel, 1999; Petanidou and Lamborn, 2005). But to date, few studies have attempted to understand what are the local and landscape drivers that structure wild bee species assemblages in these habitats.

At the local scale, abundance and species richness of wild bees can be influenced by their resource needs such as floral rewards (e.g. pollen and nectar) or nesting sites (clay, sand, gravel, wood, pre-existing cavities, soft-pith stems or snail shells) (Cane et al., 2007; Steffan-Dewenter et al., 2002; Torné-Noguera et al., 2014; Westrich, 1996; Xie et al., 2013). Wild bee richness and abundance can be also linked to land cover composition. For example, the increase in impervious surfaces at the landscape scale due to urbanization could negatively affect wild bee species assemblages (Fortel et al., 2014; Geslin et al., 2013; Hall et al., 2017; but see Hamblin et al., 2018; Theodorou et al., 2020) while the proximity and the amount of natural habitats can increase bee abundance and richness (Le Féon et al., 2010). As a general trend, the response of wild bee species assemblages to environmental conditions strongly depends on their body size (Bennett and Lovell, 2019; Bommarco et al., 2010). Larger bees (i.e., total body length > 11.5 mm) are generally more sensitive to land cover modifications within a radius ranging from 750 to 1250m whereas smaller bees (i.e., total body length ≤ 11.5 mm) are more affected by local environments (Hopfenmüller et al., 2014; Tscheulin et al., 2011).

Finally, wild bee communities can also be influenced by beekeeping activities. For example, a high density of honeybee colonies can lead to indirect competition for floral resources between wild and domesticated pollinators (Cane and Tepedino, 2016; Geldmann and González-Varo, 2018; Geslin et al., 2017; Henry and Rodet, 2018; Mallinger et al., 2017; Ropars et al., 2019; Valido et al., 2019). Recently, at least two studies in Mediterranean ecosystems have highlighted that high honeybee colony density can reduce the availability of pollen and nectar for wild bees (Henry and Rodet, 2018; Torné-Noguera et al., 2016). Torné-Noguera et al. (2016) showed that visitation rates of wild bees decreased as the distance to the nearest apiary decreased in the El Garraf Natural Park in Spain, and Henry and Rodet (2018) showed that the foraging success of wild bees decreased closer to the apiaries in scrubland land cover in southern France.

Here, we studied the effects of local and landscape drivers including honey bee colony density on wild bee species assemblages in a protected national park (Calanques National Park) in the vicinity of Marseille (France). Our goals were to identify the main drivers of bee species assemblages in order to provide tools to land managers to achieve more efficient managing practices. On the basis of a two-year census, we explored the following questions: (i) What is the wild bee richness in the Calanques National Park, located in a Mediterranean biodiversity hotspot? (ii) Are large and small wild bee species assemblages structured by a) land cover composition, b) local plant community composition and c) honeybee colony density? We expected large wild bee species assemblages to respond to environmental drivers at a larger scale (i.e. land cover) than small bee species assemblages which should rather be structured by local drivers (i.e. local plant community composition). We also expected honeybee colony density to negatively affect the richness and the abundance of large wild bee species due to their similar qualitative and quantitative feeding requirements.

2. Methods

2.1. Study site

The study was conducted in 2017 and 2018 in the Calanques National Park (43°13′27.55″ N, 5°28′2.92″E, near Marseille, France) (Fig. 1). This National Park is part of the Mediterranean basin and covers 85km^2. The climate is Mediterranean, characterized by hot and dry summers. Precipitation mostly occurs in autumn with an annual mean of 515.4mm (see Supplementary material Table 1). The year 2017 was very dry with a total precipitation of 282.6mm, while 2018 was wetter with 816.6mm. The geological substrate is dominated by dolomitic or Urgonian limestone and puddingstone (Pires and Pavon, 2018). The studied area, dominated by Mediterranean scrubland, presents 1936 plant species, subspecies and varieties, with 83 plant species protected at regional or national level (SILENE Database available on http://flore.silene.eu; com. pers. Calanques National Park). Within the western part of this National Park, we selected 17 circular 100m^2 plots within a homogeneous Mediterranean low scrubland cover dominated by *Rosmarinus officinalis, Thymus vulgaris, Cistus albidus* and *Cistus monspeliensis* as main floral resources. Each plot included at least 3 individuals of *Rosmarinus officinalis* and 3 individuals of *Cistus albidus*. Only one plot, in the eastern part of the park, did not present any *Cistus albidus* individuals but individuals of a closely related species, *Cistus monspeliensis*. The nearest distance between two plots ranged from 460m to 3536m. Plot ranged in altitude from 19m to 274m and their distance to the coast from 309m to 7647m (Fig. 1). The number of honeybee colonies around each plot was taken into account to characterize plots near to and far from apiaries.

2.2. Bee sampling

Sampling sessions were conducted in 2017 (N = 10) and 2018 (N = 5), from February to June, which is the main flowering period of the plant community. Very few flowers were observed in July and August due to severe droughts. When weather conditions were favorable (no rainy or windy days), we sampled wild bees on the 17 plots, through sweep netting, according to two sampling protocols. Following the definition of Nielsen et al. (2011), the first method, 'observation quadrats', consisted in sampling each bee visiting a flower on three well-bloomed one-square meter quadrats for 5 min in 2017 and 10 min in 2018, which equates a total of 50 min per plot for each year. The second method, 'variable transect walks', consisted in sampling all wild bees (foraging on flowers or not) on the entire 100m^2 plot for 20 min in order to actively capture a maximum of bee individuals. Bees were then kept in jars filled with cork fragments soaked with ethyl acetate. To account for temperature variations within a day, we alternatively visited each plot in the morning or in the afternoon.

All captured specimens were pinned and dried prior to identification by professional taxonomists (E. Dufrêne for cuckoo bee species, D. Genoud for Andrenidae, Anthophorinii, *Colletes sp.* and Halictidae and M. Aubert for Megachilidae, Ceratinii and *Hylaeus sp.*). For statistical analyses, we classified bee species according to their total body length following the identification keys of Amiet (Amiet, 2010, 1996; Amiet et al., 2014, 2007, 2001, 1999), with larger body bees > 12 mm which corresponds to the mean body length of *A. mellifera* worker size and smaller body bees ≤ 12 mm (Albrecht et al., 2007; Bosch et al., 1997; Henry and Rodet, 2018).

We estimated the total bee species richness with Chao1, Jackknife1 and Jackknife2 indexes excluding honeybee species (Gotelli and Colwell, 2011). We used the function ChaoSpecies() within the Spade-R package on the R version 3.6 software (Chao et al., 2016; R Foundation for Statistical Computing, Vienna, n.d.). The species accumulation curve was obtained with the specaccum() function from the vegan package and is provided in Supplementary Materials (Oksanen et al., 2015).

2.3. Environmental drivers

2.3.1. Land cover composition

We computed land cover composition within a 500m and 1000m radius around each of our plots using Quantum-GIS (QGIS Development Team, 2019). Radius sizes were chosen based on the literature regarding wild bee mean flight distances (Zurbuchen et al., 2010) to encompass foraging or dispersal ranges of small and large wild bees

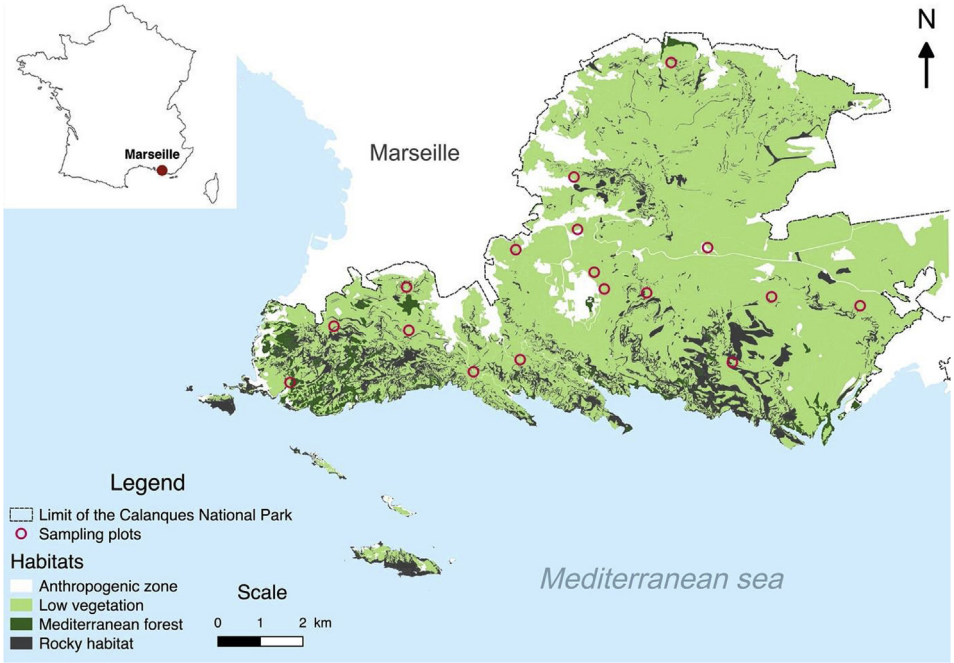

Fig. 1. Boundaries and limits of the western part of Calanques National Park. Red circles correspond to each sampling plot. Geographical data were obtained from the Calanques National Park.

(Greenleaf et al., 2007; Steffan-Dewenter et al., 2002). We used the French CORINE Land Cover 2012 data provided by the Calanques National Park to classify land cover. For each scale (500m and 1000m radius), we computed the area of four different land covers from the polygon layer of CORINE Land Cover 2012: anthropogenic zone (agricultural and artificial land cover), low vegetation (heathland, scrublands, lawns and meadows), forest and rocky land cover (rocks, screes and sand, rocky coasts and sea cliffs). The land cover composition was expressed in our statistical analyses as their proportions within each radius. However, as we did not find any response linking land cover composition within a 500m radius and the assemblages of both small and large bee species, we only present hereafter analyses relative to land cover composition within the 1000m radius; this absence of results is nevertheless discussed in the Discussion section.

2.3.2. Local plant community composition

We performed an exhaustive floristic survey on each circular 100m^2 plot to characterize the plant community. Each plant individual growing in the plot was noted and carefully identified to the species level. For each plant species, we specified a slightly modified Braun-Blanquet index which showed the relative area covered by the species within each 100m^2 circular plot (0: absence of the species; +: scarce individuals; 1: 1–10% of the area covered by species; 2: 10–25% of the area covered by species; 3: 25–50% of the area covered by species; 4: 50–75% of the area covered by species; 5: 75–100% of the area covered by species) (Maabel, 1979; Van Der Maarel, 1975).

2.3.3. Apis mellifera density

Twice a year, we listed apiaries in the park and counted the number of colonies. These surveys were supplemented by information provided by the landowners of the Calanques National Park, the French government's veterinary service, the beekeepers and beekeeping associations. Then, we quantified honeybee density using a spatially explicit density score (SEDs hereafter) inspired by the work of Henry et al. (2012). Several authors report that the average foraging distance achieved by a honeybee is about 1000m and up to 10000m (Couvillon et al., 2015; Steffan-dewenter, 2003). To take this information into account, the number of colonies located outside the 1000m radius around each plot was weighted by 1/D^2 where D is the distance expressed in kilometers between the apiary considered and a plot. This spatially explicit density score is a distance weighted sum of colony numbers in all apiaries located in the Calanques National Park and this score was calculated for each plot. The complete formula is:

$$SEDs_X = \sum_{i=1}^{N} \frac{Colony\ number_i}{{D_{Xi}}^2}$$

With X, a considered plot; i, a considered apiary and N the number of apiaries.

An increase in the number of colonies near the plot will lead to an increase in the SED score. This score allowed us to include both the distance to apiaries and the number of colonies in each apiary.

2.4. Data analysis

2.4.1. Covariation with land cover composition and local vegetation

We conducted multivariate analyses to assess the impact of the land cover composition on small and large bee species assemblages. First, we conducted correspondence analyses (CA) on the bee species assemblages per plot (16 plots for small bees – one plot had no small bee individuals – and 17 plots for large bees). To accurately build the CA analysis, each bee species present in a single plot only was removed from the analysis. Secondly, we built principal component analyses (PCA) relative to land cover composition at 500m and 1000m. Finally, with these two previous analyses, we performed co-inertia analyses between bee data and environmental data. Co-inertia analysis is used to study species-environment relationships and highlights species community composition (Dolédec and Chessel, 1994; Le Féon et al., 2010). Co-inertia significance was obtained using Monte Carlo random permutation tests with 999 repetitions. All these analyses and tests were performed with the ade4 package of the R Cran software (Dray and Dufour, 2007; R Foundation for Statistical Computing, Vienna, n.d.). Following the same method, multivariate analyses with the local plant community composition within the 100m^2 plots were performed. As previously stated, a CA was performed on small and large bee species assemblages. Then, we built PCAs relative to the local plant community composition for each plot. In order to prevent distortion, each plant

species present in only one plot was removed from the PCA (Sydenham et al., 2015). Finally, we performed co-inertia analyses between bee and plant data, and significance was also obtained by Monte Carlo random permutation tests with 999 repetitions.

2.4.2. Effect of land cover composition and local vegetation on wild bee richness and abundance

We analyzed richness and abundance of small and large wild bee species (data were pooled on a yearly basis in each plot). To assess the impact of each land cover on small and large wild bee species, we conducted generalized linear models following a Poisson distribution to deal with count data. No random effect was included in these models because the land cover did not vary between the two years. Then, to explore the effect of local plant community composition, we recorded plant richness per plot and used the same generalized linear models following a Poisson distribution. Finally, to assess the effect of honeybee colony density on wild bee species assemblages, we used generalized linear mixed models. We added the year as a random effect since honeybee colony density varied between 2017 and 2018. We used lme4 package to build these models (Green and Ben, 2019). For all models built, the best models were selected with the lowest AIC criterion, with a $\Delta AIC \geq 2$ against the null model.

3. Results

3.1. Bee species assemblages

During the two-year survey, we collected 269 and 272 bee specimens in 2017 and 2018 respectively. Net samples over the two years returned 87 wild bee species belonging to five families (Andrenidae – 18 species; Apidae – 21 species; Colletidae – 10 species; Halictidae – 20 species and Megachilidae - 18 species). The three most captured species were *Apis mellifera* (21.4%) followed by *Rhodanthidium sticticum* (7.4%) and *Anthophora dispar* (6.9%) (see Supplementary Materials, Table 2). Three sampled species were considered near threatened and one endangered (respectively *Andrena ovatula*, *Colletes albomaculatus*, *Lasioglossum pygmaeum* and *Lasioglossum soror*) according to the European Red List of bees. Finally, 19 of the captured species (21.8%) were considered as 'data deficient' in the European Red List of bees.

Excluding honeybee species, the total estimated bee species richness reached 113 ± 12 species with Chao1 index, and between 121 ± 8 and 133 ± 14 species with Jackknife1 and 2 indexes respectively. The collected bee species richness thus accounted for 65%–77% of the estimated richness obtained by Jackknife2 and Chao1 indexes respectively (72% for Jackknife1). We plotted a species accumulation curve which is provided in the Supplementary Material Fig. 1.

3.2. Effect of environmental drivers on large bee species assemblage

3.2.1. Land cover composition

The co-inertia analysis linking the land cover composition within a 1000m radius and the large bee species assemblages on the 17 plots (Fig. 2, Supplementary Material Fig. 2) revealed that land cover composition (Principal Component Analysis – the first two axes representing 88% of the total inertia) were significantly associated (RV coefficient = 0.38; Monte Carlo permutation test $p = 0.032$) with the large bee species assemblages (Correspondence Analysis – the first two axes representing 51% of the total inertia). The first axis of the co-inertia plane accounted for 52.89% of the total inertia, whereas the second axis accounted for 38.88%.

For the first co-inertia axis, the anthropogenic land cover was opposed to rocky land cover which represents an increasing distance between the plots and the urban land cover. *Melecta italica, Anthophora mucida, Xylocopa violacea, Melecta albifrons, Nomada succinta, Halictus scabiosae* and *Eucera nigrecens* contributed the most to the construction of the first axis (Fig. 2A). Among those species, *Halictus scabiosae* was related to anthropogenic land cover, conversely *Nomada succinta* and *Osmia tricornis* were related to scrublands (Fig. 2B). For the second co-inertia axis, low vegetation was opposed to Mediterranean forests representing a gradient of vegetation closure. *Eucera caspica* and *Anthophora plumipes* were particularly related to Mediterranean forests (Fig. 2B).

We recorded a significant decrease in large bee species richness with increasing low vegetation proportions within a 1000m radius around each plot (slope = −0.010, $R^2 = 0.126$, $p = 0.045$, see Fig. 2C). Our results did not show any influence of anthropogenic, forest, rocky land cover on the species richness of large bees.

3.2.2. Local plant community composition

The second co-inertia analysis showed that the local plant community composition had no effect on the large bee species assemblages (RV = 0.60, Monte Carlo permutation test $p = 0.245$). Moreover, plant richness within the $100m^2$ plots did not affect the abundance and richness of large bees.

3.2.3. Honeybee density

We found a significant decrease in the richness and in the abundance of large bees with the increase of honeybee colony density (respectively slope = −0.011, $R^2 = 0.158$, $p = 0.006$ and slope = −0.010, $R^2 = 0.199$, $p = 0.002$, Fig. 3), suggesting a negative correlation between the presence of honeybees and the foraging activity of large bee species.

3.3. Effect of environmental drivers on small bee species assemblage

3.3.1. Land cover composition

The co-inertia analysis performed on the 16 plots (Fig. 4A–B, Supplementary material Fig. 3) revealed that the land cover composition within a 1000m radius (Principal Component Analysis – the first two axes representing 88% of the total inertia) had a significant effect (RV coefficient = 0.39; Monte Carlo permutation test $p = 0.046$) on the small bee species assemblages (Correspondence Analysis - the first two axes representing 35% of the total inertia). The first axis of the co-inertia plane accounted for 62.25% of the total inertia, and the second axis accounted for 27.57%.

The first co-inertia axis represented a gradient of vegetation closure with low vegetation cover being opposed to Mediterranean forests. *Nomada flavoguttata, Lasioglossum bluethgeni* were more related to scrubland and *Hylaeus clyperis* and *Andrena lagopus* were more related to Mediterranean forests than other habitats and contributed the most to the construction of the first axis (Fig. 4A–B). For the second co-inertia axis, rocky land cover was opposed to anthropogenic land cover representing an increased in the distance from the urban land cover. *Nomada maculicornis* and *Andrena similis* were related to rocky land cover whereas *Seladonia gr. smaragdula* was related to anthropogenic land cover (Fig. 4A–B).

3.3.2. Local plant community composition

The co-inertia analysis linking the local plant community composition within the $100m^2$ plots and the small bee species assemblages on the 16 plots (Fig. 4C–D, Supplementary Material Fig. 4) revealed that the local plant community composition (Principal Component Analysis - the first two axes representing 39% of the total inertia) was significantly associated (RV coefficient = 0.69; Monte Carlo permutation test $p = 0.041$) with small bee species assemblage (Correspondence Analysis - the first two axes representing 35% of the total inertia). The first axis of the co-inertia plane accounted for 25.25% of the total inertia, whereas the second axis accounted for 14.27%.

For the first co-inertia axis, plant species such as *Teucrium chamaedrys, Ulex parviflorus, Euphorbia serrata* and *Rubia peregrina* were opposed to plots dominated by *Ruta angustifolia, Coronilla juncea* and *Biscutella laevigata.* We found that bee species such as *Nomada*

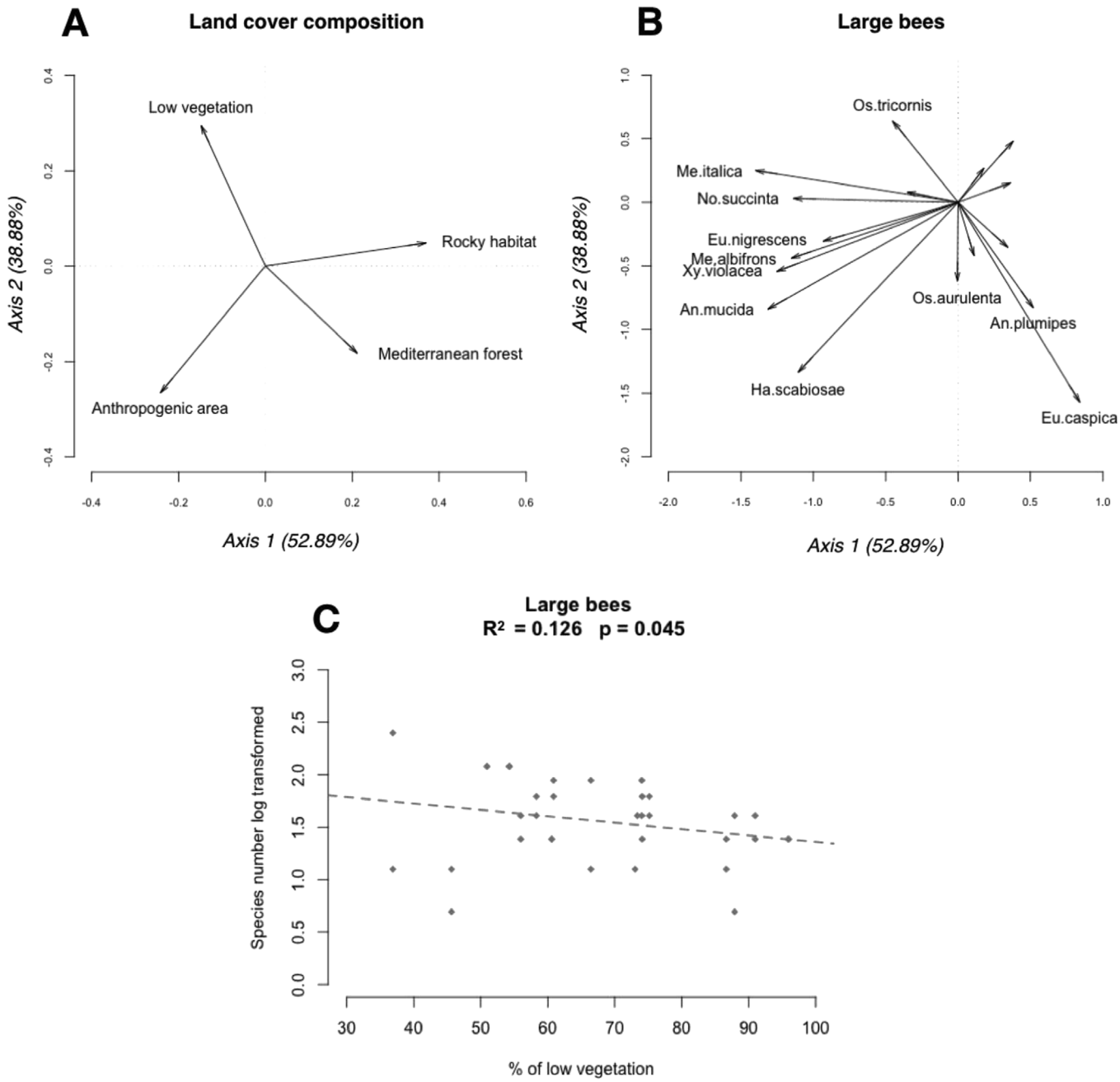

Fig. 2. Land cover composition effect on large bees with **A** Principal Component Analysis projection of land cover and **B** Correspondent Analysis projection of large bee species on the first factorial plane of the land cover composition co-inertia. **C** Relationship between the percentage of low scrubland within the 1000m radius and the large wild bee species richness.

flavoguttata, *Lasioglossum albocinctum, Lasioglossum bluethgeni, Osmia rufohirta* and *Ceratina cucurbitina* were related to *Teucrium chamaedrys, Ulex parviflorus, Euphorbia serrata* and *Rubia peregrina.* We also found that *Seladonia gr. smaragdula, Hylaeus clypearis* and *Andrena lagopus* were related to *Ruta angustifolia, Coronilla juncea* and *Biscutella laevigata*. For the second co-inertia axis, *Centaurea sp.* and *Rhus coriaria* plant species were opposed to *Erica multiflora, Fumana thymifolia* and *Laserpitium gallicum. Osmia versicolor* and *Nomada sheppardana* were related to *Centaurea sp.* and *Rhus coriaria* whereas *Andrena similis* and *Hylaeus cf. imparilis* were related to *Erica multiflora, Fumana thymifolia* and *Laserpitium gallicum* (Fig. 4C–D).

Regression models highlighted that the richness and the abundance of small bees were not significantly affected by land cover composition, plant richness, or honeybee colony density.

4. Discussion

4.1. Bee species assemblages

In this study, we explored which environmental drivers structured the communities of small and large bee species in the Calanques National Park. During a two-year survey, we inventoried 87 species of wild bees in scrubland land cover dominated by *Rosmarinus officinalis, Thymus vulgaris, Cistus albidus* and *Cistus monspeliensis*. In a similar habitat, in the El Garraf National Park in Spain (32km^2), Torné-Noguera et al. (2014) found a similar bee richness with 98 wild bee species. Two previous studies sampled the bee community within the Calanques National Park (Geslin et al., 2018; Schurr et al., 2019), and the bee richness of this protected habitat now amounts to 131 species. We

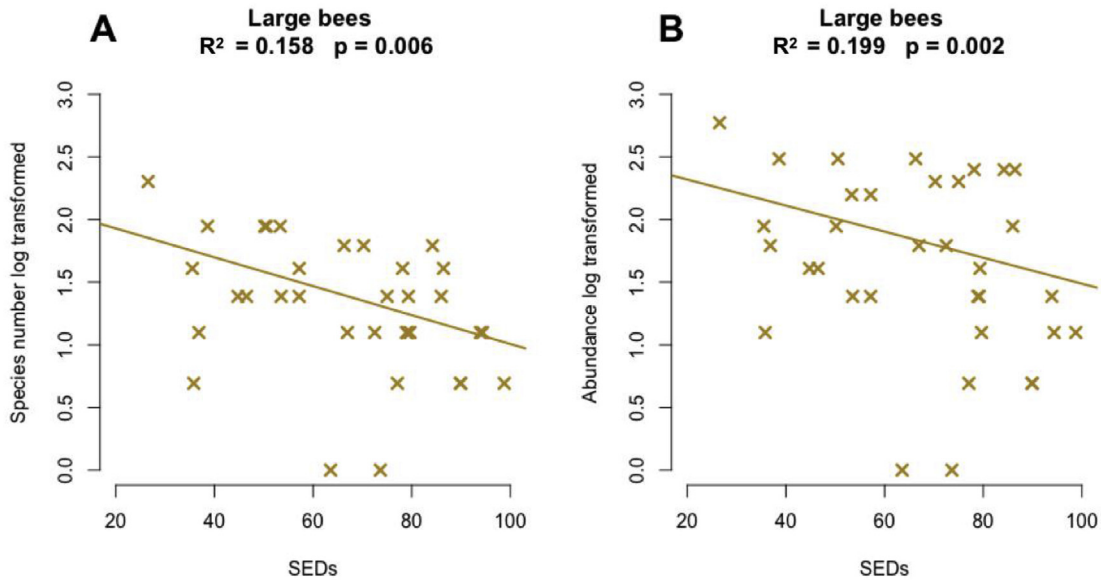

Fig. 3. Linear regressions between the honeybee density score SED and **A** large bee species richness, and **B** large bee abundance.

observed a strong inter-annual variation with 64 species caught in 2017 and 56 in 2018 and with only 34 species in common between the two years. A compilation of all bee surveys within the Calanques National Park from 2008 to 2018 (including the present study) has been provided by Ropars et al. (2020) (Submitted) and the species richness amounts to 192 bee species. As previously stated in the literature, this shows that a single sampling year is insufficient to detect the species richness of a particular location, which should be sampled for several years to precisely account for its richness. For example, Petanidou et al. (2008) showed inter-annual variations in a four-year survey of a pollinator community within Mediterranean scrublands from 183 to 238 insect species collected per year, totaling 661 species. Here, we found almost 10% of the entire French wild bee fauna focusing only on scrubland, the dominant habitat of the terrestrial French Mediterranean. During this survey, we recorded 4 wild bee species which benefit from a protection status: *Andrena ovatula* (NT), *Colletes albomaculatus* (NT), *Lasioglossum pygmaeum* (NT) and *Lasioglossum soror* (EN). Located at 70km in the East of the Calanques National Park, the Port-Cros National Park host a similar percentage (4%) of threatened wild bee species (Gombault et al., 2018).

Our sampling could be completed by other methods as we caught only 65% of the bee species estimated richness and as the species accumulation curve is not stabilized. Net sampling is a well-known method to assess the richness of wild bees visiting a local plant community (Popic et al., 2013; Rhoades et al., 2017), but pan trap methods are a good complement to better reveal small wild bee species richness (Roulston et al., 2007). Moreover, as we inventoried a small fraction of the Calanques National Park, other protected habitats such as sandpits or dry lawns should be investigated to better assess the total wild bee richness.

4.2. Local and landscape drivers of wild bee species assemblages

In protected areas, nesting and floral resources have been highlighted as the most widely studied drivers of wild bee assemblages (Murray et al., 2012; Potts et al., 2005; Torné-Noguera et al., 2014). In Mediterranean habitats, several authors have demonstrated that the effects of land cover and local plant community composition on wild bees depended on the body size of bees (Torné-Noguera et al., 2014; Tscheulin et al., 2011).

4.2.1. Effect of local plant community composition

Small bee species were affected by the local plant community composition within 100m^2 plots, which depends on soil depth (Bernard-Verdier et al., 2012). Small generalist bee species such as *Nomada flavoguttata*, *Lasioglossum albocinctum, Osmia rufohirta* were related to open scrubland plants that grows on deep soil such as *Teucrium chamaedrys, Ulex parviflorus, Euphorbia serrata* plant species. *Hylaeus clypearis* was linked to plant species which are characteristic of rocky scrublands with shallow soils, such as *Ruta angustifolia* and *Biscutella laevigata*. These two plant species provide small and open flowers which correspond to the particular floral needs of *Hylaeus* bee species (Westrich, 1996). As a general trend however, rather than highlighting a direct match between small bee species and the plant species composing their floral diet, we may had highlight here a co-occurrence between small bees species and plant species growing close to their preferential nesting substrates.

A tight correspondence between specialist bees and their related plant species was not observed. As few examples, *Lasioglossum bimaculatum* preferentially forages on Cistaceae, *Andrena lagopus* and *Lasioglossum transitorium* on Brassicaceae (D. Genoud, pers. comm.). This mismatch between bees' diet and their floral resources in our results could be due to the few captured individuals or to a lack of knowledge regarding the ecology of small wild bees. The known floral diet of bees is more related to plant species used to make bee-breads than plant species used to collect nectar. Likewise, numerous small bee species recorded in this survey were generalists and no clear pattern appeared with a particular plant species as they could forage on a wide range of plants. Unlike small bees, large bees were not affected by the local plant community composition. Considering their ability to forage and nest over larger distances than small bees, large bees could feed on distant floral resources which may explain their insensitivity to local flora or habitats.

4.2.2. Effect of land cover composition

Surprisingly, both small and large bees did not respond to land cover composition within a 500m radius. This result is unexpected, as a 500m radius around sampling sites is commonly used to evaluate the land cover effect on wild bee assemblages (Dorchin et al., 2018; Geslin et al., 2014; Kovács-Hostyánszki et al., 2011; Wilson and Jamieson, 2019). Other studies such as Tscheulin et al. (2011), found that the abundance of small bees reacted to the land cover composition within a smaller radius of 250m and the lack of response of large and small bees we observed here, could be due to an inappropriate choice of radius.

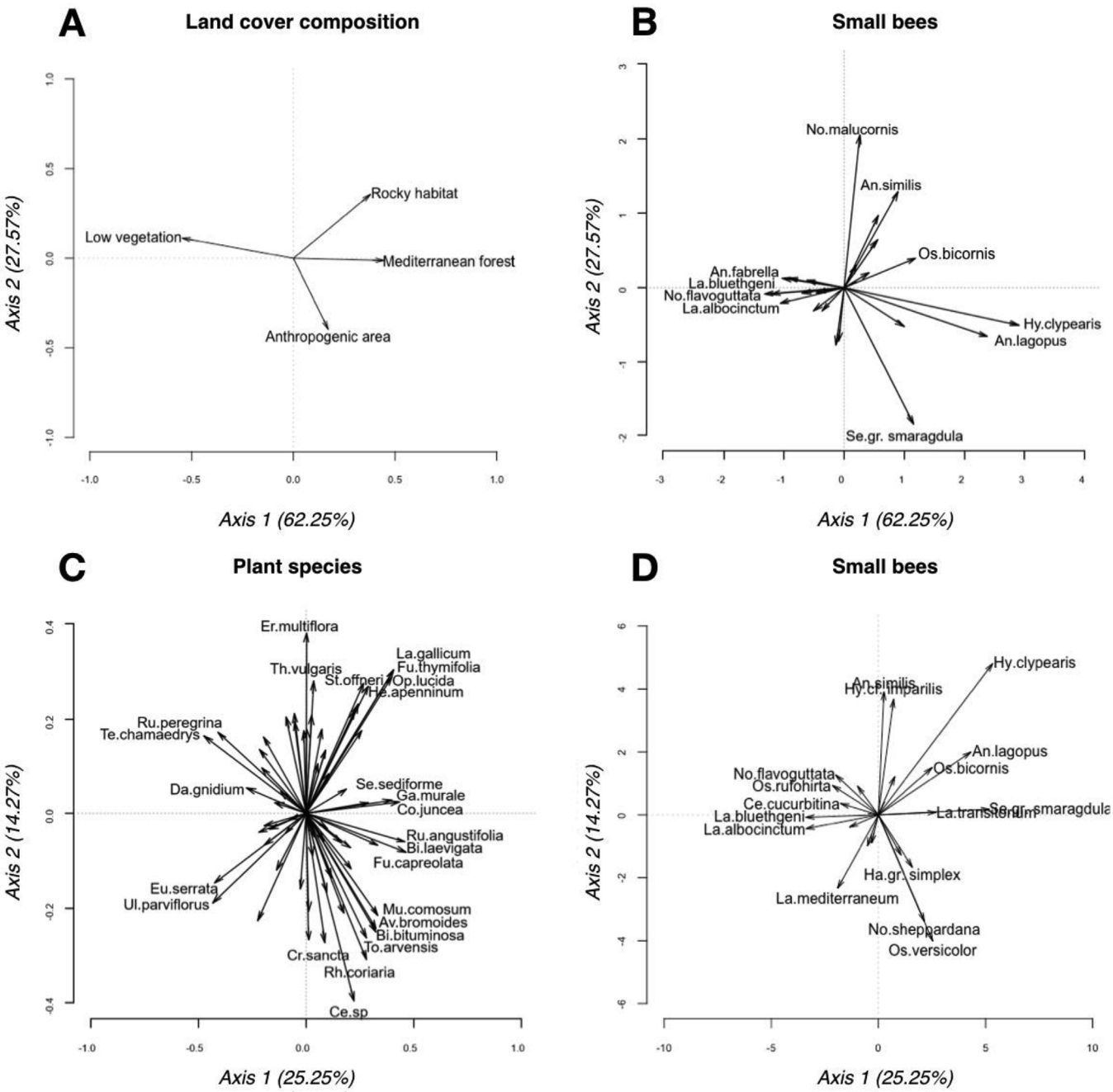

Fig. 4. Land cover composition effects on small bees with **A** Principal Component Analysis projection of land cover and **B** Correspondent Analysis projection of small bee species on the first factorial plane of the land cover composition co-inertia. Local plant community effects on small bees with **C** Principal Component Analysis projection of plant species and **D** Correspondent Analysis projection of small bee species on the first factorial plane of the local plant community composition co-inertia.

We explored if a strong homogeneity or heterogeneity in the land cover composition of our sites at a 500m radius could explain this lack of response compared to the 1000m radius. However, we found no difference in the variance of the land cover composition between the two considered scales. Another possible explanation lies in the important number of sampling sites that did not include the four differents land cover we chose within a 500m radius (11 sites). Within the 1000m radius, only 4 of the 17 sites did not include the four differents land cover.

Small bee species were related to land cover composition within a 1000m radius; however, the pattern between small bee species and the land cover is difficult to explain. Even though several studies documented that small bee species have limited dispersal abilities (Gathmann and Tscharntke, 2002; Greenleaf et al., 2007), other works have reported that flight distances of small solitary bees could be underestimated and may reach between 500 and 1000m (Zurbuchen et al., 2010). Small bee species were distributed across the gradient of vegetation closure with *Nomada flavoguttata, Lasioglossum bluethgeni* being related to scrubland and *Hylaeus clyperis* and *Andrena lagopus* being related to Mediterranean forests. *Nomada*, *Andrena* and *Lasioglossum* genera are often generalist when seeking for nectar and there is no supporting literature regarding their general soil requirements for belowground nesting to confirm or infirm our results.

As expected, large bees respond to land cover composition with the

1000m radius due to their ability to forage within larger area (Greenleaf et al., 2007). For several species, it may be linked with their nesting preferences. For example, *Halictus scabiosae* was related to anthropogenic land cover, and this species generally nests in anthropogenic sites or in disturbed places (Ulrich et al., 2009). *Rhodanthidium sticticum* was related to rocky land cover as it often nests in snail shells easily detectable on bare soils (Moreno-Rueda et al., 2008). For other species, such as *Xylocopa violacea*, *Melecta species*, *Anthophora mucida* and *Eucera nigrecens*, it was more difficult to link their presence to a particular nesting habitat, as they were mostly related to the interface between anthropogenic zone and scrublands. Likewise, the diversity of land covers within a 1000m radius around our plots was linked with a higher species richness of large bees. We found that large bee species richness decreased when the scrubland land cover increased. This might underline that land cover diversity within a 1000m radius around plots increases the number of plant species and nesting substrates which can shelter large bee species (Dafni and O'Toole, 1994). Several studies demonstrated a loss of bee species diversity linked to the homogenization of one land cover in agricultural landscapes (Holzschuh et al., 2007; Tscharntke et al., 2002). The bee species richness we observed here might also be linked to the interface between anthropogenic land cover and scrublands. Fortel et al. (2014) found a maximum in the species richness of bees at an intermediate proportion of anthropogenic land cover, illustrating the Intermediate Disturbance Hypothesis.

4.3. Effect of honeybee colony density

Semi-natural habitats with dominant flowering species, such as scrublands (with *Rosmarinus officinalis, Cistus albidus*), are also particularly attractive to beekeepers to settle their honeybee colonies (Geldmann and González-Varo, 2018). Through the practice of transhumance during spring in the scrublands of southern France, beekeepers can set up apiaries that include large numbers of colonies at the same time for a short period (Henry and Rodet, 2018). In the Calanques National Park, the mean honeybee colony density is more than twice the national mean (respectively 5.3 colonies/km^2 and 2.5 colonies/km^2 Chauzat et al., 2013). Our results showed a decrease in abundance and richness of large bees with the increase of honeybee colony density, which could be linked to an emerging issue relative to the competition for resources between honeybees and wild bees (Geslin et al., 2017; Mallinger et al., 2017). The intensive installation of beehives may lead to the monopolization of available nectar and pollen resources by honeybees. As demonstrated by several studies, *Apis mellifera* is a highly generalist species and can easily use resources that are common to the diet of large wild bee species (Geslin et al., 2017; Henry and Rodet, 2018). Large bee species have greater food requirements for their progeny than smaller bee species (Müller et al., 2006) and they have the capacity to collect larger quantities of pollen than small bee species (Greenleaf et al., 2007). Furthermore, large bees can fly further away to avoid honeybee competition and forage where the competitive pressure is low. This may explain why we found fewer individuals and species of large bees when the local density of honeybee colonies was high. Henry and Rodet (2018) demonstrated a similar trend with large bees being particularly affected by honeybee colony density, especially for nectar resources.

5. Conclusion

In this study, we observed that responses of bee species assemblages to land cover composition in the Calanques National Park depend on their body size. The assemblage of small bee species was particularly sensitive to local plant community composition and land cover composition within a 1000m radius. Large bee species assemblages were also sensitive to land cover composition within a 1000m radius with an observed peak of species richness at the interface of different land covers. In this context, the Calanques National Park, by its localization in the vicinity of Marseille, maintains and protects a diversity of land covers which seems essential to preserve and sustain a wide range of bee species. However, the density of honeybee colonies appeared to be a non-negligible determinant acting negatively upon wild bee species assemblages. Our study suggested a negative effect of honeybee colony density on large bee species richness and abundance. As semi-natural protected areas may cover endangered habitats and consequently protected species, we would like to raise awareness among land managers to encourage the limitation of honeybee colonies in protected areas. To better assess the exploitative competition between wild bees and domesticated honeybees, future studies should take into account the quantity of floral resources available for flower-visitors.

Authors contributions

L. Ropars wrote the draft of the manuscript. L. Ropars, C. Mutillod and F. Flacher performed the field work. L. Ropars and B. Geslin conducted the data analyses. L. Affre, F. Flacher, D. Genoud, B. Geslin, C. Mutillod, L. Schurr revise the manuscript.

Declaration of competing interest

The authors state that they have no conflict of interest.

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