Collateral effects of beekeeping: Impacts on pollen-nectar resources and wild bee communities

Anna Torné-Noguera[a,*], Anselm Rodrigo[a,b], Sergio Osorio[a], Jordi Bosch[a]

[a]CREAF, 08193 Cerdanyola del Vallès, Spain
[b]Universitat Autònoma de Barcelona, 08193 Cerdanyola del Vallès, Spain

Abstract

Due to the contribution of honey bees (*Apis mellifera*) to wild flower and crop pollination, beekeeping has traditionally been considered a sustainable practice. However, high honey bee densities may have an impact on local pollen and nectar availability, which in turn may negatively affect other pollinators. This is exacerbated by the ability of honey bees to recruit foragers to highly rewarding flower patches. We measured floral resource consumption in rosemary (*Rosmarinus officinalis*) and thyme (*Thymus vulgaris*) in 21 plots located at different distances from apiaries in the scrubland of Garraf Natural Park (Barcelona), and related these measures to visitation rates of honey bees, bumblebees (*Bombus terrestris*) and other pollinators. In the same plots, we measured flower density, and used pan traps to characterize the wild bee community. Flower resource consumption was largely explained by honey bee visitation and marginally by bumblebee visitation. After accounting for flower density, plots close to apiaries had lower wild bee biomass. This was due to a lower abundance of large bee species, those more likely to be affected by honey bee competition. We conclude that honey bees are the main contributors to pollen/nectar consumption of the two main flowering plants in the scrubland, and that at the densities currently occurring in the park (3.5 hives/km^2) the wild bee community is being affected. Our study supports the hypothesis that high honey bee densities may have an impact on other pollinators via competition for flower resources.

Zusammenfassung

Wegen des Beitrages der Honigbiene (*Apis mellifera*) bei der Bestäubung von Wildblumen und Nutzpflanzen wurde die Bienenhaltung traditionell als eine nachhaltige Aktivität angesehen. Indessen können hohe Honigbienendichten Auswirkungen auf die lokale Verfügbarkeit von Nektar und Pollen haben, was wiederum andere Bestäuber negativ beeinflussen könnte. Dies wird verstärkt durch die Fähigkeit der Honigbiene, Sammlerinnen zu lohnenden Sammelstellen zu dirigieren. Im Buschland des Garraf-Naturparks bei Barcelona maßen wir den Verbrauch von Blütenressourcen an Rosmarin (*Rosmarinus officinalis*) und Thymian (*Thymus vulgaris*) an 21 Standorten, die unterschiedlich weit von Bienenständen entfernt lagen, und setzten diese Werte in Bezug zu den Besuchsraten von Honigbienen, Hummeln (*Bombus terrestris*) und sonstigen Bestäubern. An den gleichen Standorten bestimmten wir die Blütendichte und setzten Farbschalen ein, um die Wildbienengemeinschaft zu erfassen. Die Nutzung der Blütenressou wurde weitgehend durch die Besuchsraten der Honigbiene erklärt und in geringfügigem Maße durch Hummelbesuch. Nach Berücksichtigung der Blütendichte wiesen Standorte in der Nähe von Bienenständen eine geringere Wildbienen-Biomasse auf. Dies war auf eine geringere Abundanz der großen Wildbienenarten zurückzuführen, also der Arten, die wahrscheinlich durch die Konkurrenz der Honigbiene beeinträchtigt werden. Wir schließen, dass Honigbienen

*Corresponding author. Tel.: +34 93 5814851; fax: +34 93 5814151.
E-mail address: a.torne@creaf.uab.cat (A. Torné-Noguera).

den größten Beitrag zum Pollen- bzw. Nektarverbrauch bei den beiden wichtigsten Blütenpflanzen des Gebietes leisten und dass die Wildbienengemeinschaft bei den gegenwärtigen Honigbienendichten im Park (3.5 Völker/km^2) beeinflusst wird. Unsere Untersuchung unterstützt die Hypothese, dass hohe Honigbienendichten durch Konkurrenz um Blütenressourcen einen Einfluss auf andere Bestäuber haben könnten.

Introduction

The introduction of large populations of highly competitive species into a new area may affect resident populations, ultimately resulting in changes in the structure of native communities (Ehrenfeld, 2010; Levine et al., 2003). This may occur when exotic species, introduced either accidentally or intentionally, turn invasive and compete for limited resources with local species occupying a similar niche (Byers, 2000; Petren & Case, 1996). In addition to exotic species, domesticated species may also affect resident species. A clear example is the presence of cattle or sheep in natural or semi-natural areas, potentially competing with large herbivores for pasture (Young, Palmer, & Gadd, 2005; Stewart, Bowyer, Kie, Cimon, & Johnson, 2002). Domesticated animals benefit from human assistance, including protection against predators and veterinary care, and therefore may have a competitive advantage over wild species.

Among domesticated animals, the European honey bee (*Apis mellifera*) is undoubtedly one of the globally most spread. Native to Eurasia and Africa, honey bees are now kept in all continents except Antarctica, initially for honey production (Crane, 1990), but mostly for crop pollination (Free, 1993), being, by far, the main managed pollinator worldwide (Garibaldi et al., 2013; Breeze et al., 2014; Aizen & Harder, 2009). Consequently, beekeeping has traditionally been considered a beneficial practice, and its sustainability has been taken for granted. This is reflected in the current lack of specific legislation in most countries worldwide, whereby beekeeping is considered to be beneficial and is usually allowed in nature reserves and other types of protected areas, including some National Parks. In many cases, beekeeping in these areas is not only allowed but even promoted as a traditional, sustainable activity (information obtained from natural park and wildlife managers from 8 European countries, see acknowledgements). It is therefore not surprising that *A. mellifera* is routinely reported as a dominant species in plant-pollinator networks worldwide, even in studies conducted in natural habitats (Valido, Rodriguez-Rodriguez, & Jordano 2014; Bosch, Martín González, Rodrigo, & Navarro 2009; Kaiser-Bunbury, Memmott, & Müller 2009; Forup, Henson, Craze, & Memmott 2008; see Davila & Wardle 2008 for a rare exception). However, as in other kinds of animal husbandry, large apiaries resulting in high densities of foragers may have an impact on local food resources (pollen and nectar in this case), which ultimtly

may negatively affect other flower-visiting insects. Because they live in large colonies comprising tens of thousands of individuals and because they maintain elevated hive temperatures even during the winter (Seeley, 1985), honey bees have high energetic requirements, and their foraging ranges span several kilometres (Visscher & Seeley, 1982). In addition, honey bees have the ability (unique to them and some stingless bees) to communicate the location of flower resources to nest mates, thus concentrating large numbers of foragers in highly rewarding patches (Von Frisch, 1967). Thus, honey bees are highly efficient pollen-nectar foragers and, when present in large densities, may potentially create a competition scenario with other pollinators.

Competition may take place through interference or through resource exploitation (Tilman, 1982). Interference competition occurs directly between individuals through aggressive encounters (e.g., honey bees chasing other pollinators out of a flower or flower patch). Such aggressive interactions have sometimes been observed (e.g. Pinkus-Rendon, Parra-Tabla, & Meléndez-Ramírez 2005), but the fact that most studies do not report aggressive encounters indicates that they are not common (e.g. Hudewenz & Klein 2013; Roubik 1978). After several years of field work, we can assert that such interactions are very rare in our study area. Exploitative competition occurs indirectly between individuals through a limiting resource, such as food or nesting sites. Competition for nesting resources can be ruled out in this case because wild bees in temperate zones do not nest in the kind of large cavities used by honey bees, and because feral colonies are very rare in our study area, as in most of Europe (Jaffé et al., 2009). Competition for flower resources is much more likely to occur because honey bees are highly generalistic in pollen and nectar use, and their diet widely overlaps with that of other flower-visiting species.

Various studies have explored potential adverse effects of honey bees on local pollinator communities. However, demonstrating a competition scenario is extremely difficult owing to the large foraging ranges of honey bees (several km) (Goulson, 2003; Seeley, 1985), combined with their ability to communicate the location of rich flower patches, thus allowing colonies to adjust their foraging areas and flower choices as pollen-nectar standing crops vary through time and space (Visscher & Seeley, 1982). For this reason, most studies have so far focused on indirect evidences of competition between honey bees and wild bees, such as resource overlap (Steffan-Dewenter & Tscharntke, 2000), changes

in flower choice (Valido et al., 2014; Forup & Memmott, 2005), foraging activity (Thomson, 2004), and visitation rates (Hudewenz & Klein, 2013; Roubik, 1978) of wild pollinators confronted with different honey bee scenarios. Other studies have measured changes in population abundance and richness of wild bees under different honey bee densities (Forup & Memmott, 2005; Roubik & Wolda, 2001; Steffan-Dewenter & Tscharntke, 2000; Roubik, 1978). Fewer studies have looked for more direct evidence of competition, such as changes in reproductive success (Elbgami, Kunin, Hughes, & Biesmeijer, 2014; Goulson & Sparrow, 2009; Thomson, 2004; Steffan-Dewenter & Tscharntke, 2000), and the outcomes of these studies are not consistent. Some have found negative effects of honey bees (Goulson & Sparrow, 2009; Thomson, 2004) while others have not (Roubik & Wolda, 2001; Steffan-Dewenter & Tscharntke, 2000).

For exploitative competition to occur, floral resources should be limiting. However, to our knowledge, no study has hitherto measured the effects of honey bee abundance on pollen and nectar availability. This is important because we currently do not know the magnitude of the impact of honey bees on flower resources compared to resident pollinators. In this study we address the potential effects of beekeeping on wild bee communities in an environmentally protected natural area. Our objective is to study the impact of honey bee flower visitation on pollen and nectar consumption and the effect of beekeeping on the abundance, richness and composition of the local wild bee community. Because honey bees are very abundant and given their ability to recruit large numbers of foragers to the most rewarding flower patches, we have three hypotheses: (1) Honey bees will be the main contributors to flower resource consumption. We therefore expect pollen and nectar levels to be lower in areas close to apiaries; (2) Structure of the wild bee community will be modified by high honey bee densities. We expect wild bee richness and abundance to be lower close to apiaries; (3) Among wild bees, we expect large species (with higher feeding requirements; Müller et al., 2006), to be most affected.

Materials and methods

Study area

This study was conducted in the Natural Park of el Garraf (Barcelona, Catalonia, NE Spain), a Mediterranean scrubland dominated by *Quercus coccifera*, *Pistacia lentiscus*, *Rosmarinus officinalis* and *Thymus vulgaris*. Over the last years, we identified 64 entomophilous plant species and 288 insect pollinator species in the park.

The Natural Park of el Garraf is classified as category V of the International Union for Conservation of Nature (IUCN) (Dudley, 2008), which includes the majority (62%) of the environmentally protected land in the Mediterranean region (López Ornat, Pons Reynés, & Noguera, 2007). Category V

parks are defined as protected areas with an important biological, ecological, cultural and picturesque value based on the interaction between human populations and the environment via traditional management practices. In Catalonia, current policies regulating environmental impacts of human activities do not mention beekeeping (Law 20/2009, DOGC 5524). Rather, beekeeping is considered an innocuous activity and *A. mellifera* is declared a "species of special interest" (Decree 110/2003, DOGC 3870).

Our study area is entirely located in the park, encompassing a surface of 32 km². We selected 21 plots of 40 m × 40 m distributed more or less regularly across the study area. Distances between nearest plots ranged from 585 to 1354 m. Based on the information provided by the Department of Agriculture and subsequently verified *in situ*, we located 21 apiaries close to the study area for a total of 475 hives (see Appendix A). Minimum distance of our plots to the nearest apiary ranged from 262 m to 5122 m.

Flower resource surveys

To study flower resource consumption, we worked on rosemary (*R. officinalis*) and thyme (*T. vulgaris*). These two species are, by far, the most abundant entomophilous species in the study area, producing 70–90% of the flowers in the scrubland (Flo, 2014; Bosch et al., 2009). In addition, the two species are very attractive to honey bees and are considered highly desirable for honey production (Cambra, 2008; Bonet, Rita, & Sebastià, 1985). In addition to honey bees, rosemary and thyme attract a variety of other pollinators. We have recorded 46 and 47 species visiting rosemary and thyme, respectively (Bosch et al. 2009). Of these, 13 and 17 species are wild bees, including some early-flying *Andrena* (*A. angustior*, *A. nigroaenea*) and *Anthophora* (*A. acervorum*, *A. dispar*) that concentrate most of their foraging on these two plant species. All surveys were conducted in 2011 under fair weather.

Pollen

Rosemary pollen surveys were conducted in March, when the species was in full bloom. In each plot, we selected between 20 and 30 plants on which we marked 8 recently-opened flowers (with fresh, fully pollen-loaded stamens). Before the onset of pollinator activity (9:00), we collected 4 of the marked flowers per plant, and stored them together in a vial filled with ethanol 70%. After 18:00, when foraging activity had ceased, the remaining 4 flowers per plant were collected and preserved following the same procedure.

Thyme pollen surveys were conducted in April, during peak bloom of this species. We selected between 20 and 30 thyme plants per plot and marked 4 recently-opened flowers in each of them, following the same criteria as for rosemary. Before 9:00 we collected the two stamens of one side (left

or right) of each flower, and stored them together in a vial filled with ethanol 70%. After 18:00 we collected the two remaining stamens of each flower.

In the laboratory, vials with stamens were sonicated for 10 min in an ultrasonic bath to dislodge pollen grains from the anthers. Afterwards, each anther was inspected under the stereomicroscope and pollen grains still adhering to the anthers were manually detached with the aid of an insect pin. Later, we took 8 drops of 2.5 μl of the resulting pollen suspension and counted the number of pollen grains under the stereomicroscope. Previous trials showed that the number of drops necessary to stabilize pollen counts was 6. We then measured the remaining ethanol volume in the vial, and estimated the total number of pollen grains in each sample. From these data, we estimated the number of pollen grains per flower in the morning and in the evening, which we used to calculate pollen consumption. Overall, we sampled 4005 rosemary flowers and 2366 thyme flowers.

Nectar

Nectar consumption is difficult to measure because nectar secretion is a more or less continuous process (Pacini, Nepi, & Vesprini, 2003), so that consumption may be compensated by subsequent secretion. In some cases, secretion may be even stimulated by consumption (Ordano & Ornelas, 2004; Castellanos, Wilson, & Thomson, 2002). In addition, nectar secretion can be strongly conditioned by weather conditions (Petanidou & Smets, 1996; Jakobsen & Kristjánsson, 1994). We therefore decided to measure nectar standing crops at the end of the day as a surrogate for nectar consumption.

Thyme flowers produce very small amounts of nectar (Arnan, Escolà, Rodrigo, & Bosch, 2014), which may become difficult to extract, especially in warm dry days. For this reason, nectar surveys were only conducted on rosemary. At the end of each sampling day, we used 1-μl capillary tubes to measure the volume of nectar remaining in the flowers. This was done on most of the flowers used in the evening pollen surveys. We measured nectar standing crops in 1628 rosemary flowers (mean number of flowers per plot = 86; range = 33–117).

Pollinator visitation rates

To relate pollen and nectar consumption to pollinator activity, we conducted pollinator surveys between 9:00 and 18:00 in each plot on the same day in which pollen and nectar measures were taken. At each plot, we selected 10 rosemary and 10 thyme plants. These plants were not the same used in pollen/nectar surveys to avoid potential accidental contact with flowers marked for pollen-nectar measures. On each marked plant we conducted a number of pollinator counts (mean = 10, range = 5–15) throughout the day. In each count, the selected plant was observed for 2 min and all pollinators contacting flowers were recorded. Total observation time was

72 h 48 min for rosemary and 76 h 34 min for thyme. At the end of the day, we counted the number of open flowers in each plant. *A. mellifera* and the bumblebee *Bombus terrestris* were, by far, the two most frequent pollinators visiting the two plant species. Therefore, we grouped pollinators into three categories: *A. mellifera*, *B. terrestris*, and other pollinators (mostly other bees, along with some dipterans and a few lepidopterans and coleopterans). Visitation rates of each pollinator group were calculated as the number of contacts per minute and per 1000 flowers.

Bee community

To assess bee community structure and composition, we placed 6 sampling stations in each plot. Each sampling station consisted of a metal bar holding 3 pan traps painted yellow, white and blue respectively, one metre above the ground (Westphal et al. 2008). We conducted 8 biweekly surveys from mid-March to late June 2010, in which traps were set at 8:00–9:00, before the onset of pollinator activity (around 9:30) and collected after 18:00. All plots were sampled on the same 8 days (see Torné-Noguera et al., 2014 for details). We captured 6580 bee specimens, which were dried and pinned for identification. In addition, we netted and weighed a few individuals of each species/sex to obtain measures of fresh body weight ($n = 1$–52 specimens per species). Species were subsequently classed as small (body weight <55 mg) or large (>70 mg) (see Torné-Noguera et al., 2014 for details).

Flower abundance

To estimate flower abundance in each plot, we considered the main flowering species in the scrubland (*R. officinalis*, *T. vulgaris*, *Dorycnium pentaphyllum*, *Cistus albidus*, *Cistus salvifolius* and *Cistus monspeliensis*), which together accounted for >70% of the flowers in each plot. We measured two perpendicular widths and the height of each flower patch in two 40×1 m perpendicular transects centered in the middle of the plot. Then we estimated the number of flowers of each species based on previously established equations relating patch volume and number of open flowers at peak bloom ($r^2 = 0.36$–0.63, $p = 0.001$–0.015) (see Torné-Noguera et al., 2014). Because the three *Cistus* species were much less abundant than the other species, and their flowering periods largely overlap, we lumped together these three species into a single category (*Cistus* abundance).

Statistical analysis

Visitation rates and pollen/nectar consumption

Preliminary analyses showed no correlation between explanatory variables (visitation rates of the different pollinator groups). In pollen analysis, honey bee visitation rate and other pollinators visitation rate were log-transformed because there was a logarithmic relationship between these variables and pollen consumption. We initially fit a generalized linear

model (GLM) assuming a binomial error distribution (adequate for proportion data such as pollen consumption), with *A. mellifera* visitation rate, *B. terrestris* visitation rate, and other pollinators visitation rate as predictive variables. However, the model showed overdispersion. Therefore, we finally opted for a quasibinomial GLM. We then compared the saturated model with the various non-saturated models and chose the best one using ANOVA (as AIC cannot be calculated for quasi model families). Finally, we checked for normality and homoscedasticity of the residuals. We used pseudo-R^2 as a measure of the goodness-of-fit.

In nectar analyses, we log-transformed the explanatory variable other pollinators visitation rate because it showed a logarithmic relationship with the response variable. We fit a generalized linear model (GLM) with a Gaussian error distribution, with nectar standing crop as the response variable and visitation rate of the various pollinator groups as predictive variables. We selected the best model using the second-order Akaike Information Criterion (AICc), adequate for small samples.

Bee community

We used MiraMon SIG software (Pons, 2014) to establish the linear distance of each plot to the nearest apiary, a measure commonly used in honey bee studies (Elbgami et al., 2014; Hudewenz & Klein, 2013; Thomson, 2004; Steffan-Dewenter & Tscharntke, 2000).

To evaluate the potential relationship between distance to the nearest apiary and wild bee community structure, we run GLM models for wild bee abundance, wild bee richness and wild bee biomass. Because wild bee community structure may also be influenced by flower availability (Torné-Noguera et al., 2014), we included flower abundance of *T. vulgaris*, *R. officinalis*, *D. pentaphyllum* and *Cistus* as predictor variables. Correlations between predictor variables were low (ranging from −0.27 to 0.33) and non-significant. We did not include nesting substrate availability in the analysis because we know from previous studies that this is not a good predictor of bee community structure and composition in the study area (Torné-Noguera et al., 2014).

Bee biomass was analyzed with a GLM with a Gaussian distribution. For bee abundance and bee richness models, we chose a GLM with a Poisson error distribution, adequate for count data. However, both models showed overdispersion, and thus we opted for models with a negative binomial distribution. In all three analyses, we selected the best model with the AICc criterion. Best models were later checked for normality and homoscedasticity. Because large bees might respond differently from small bees due to their higher feeding requirements (Müller et al., 2006), we run additional analyses separately for small (<55 mg) and large (>70 mg) bees. The best model explaining wild bee richness showed heteroscedasticity. Thus, we used White's heteroscedasticity-corrected covariance matrices to make inference.

All analyses were computed with R (R Core Team, 2014).

Results

Pollen and nectar consumption

A. mellifera and *B. terrestris* accounted for the majority of visits to both rosemary (61.2 and 30.1%, respectively) and thyme (39.5 and 34.8%). Visits of other pollinators amounted to 8.7 and 25.7% of the visits to rosemary and thyme, respectively. Honey bee flower visits and bumblebee flower visits were not correlated (rosemary: $\tau = 0.23$, $p = 0.16$; thyme: $\tau = 0.04$, $p = 0.83$). Honey bee visitation rate showed a negative relationship with distance to the nearest apiary ($r^2 = 42.25$, $p = 0.009$).

Mean ± SE number of pollen grains in newly-opened rosemary flowers was 5185 ± 70, and these numbers decreased to 1831 ± 68 by the end of the day. Pollen consumption in our plots ranged from 25.1% to 90.1% (mean ± SE = 65.6 ± 4.0). The best model for rosemary pollen consumption (pseudo-$R^2 = 0.54$) included *A. mellifera* visitation rate ($p = 0.004$) and, marginally, *B. terrestris* visitation rate ($p = 0.06$) (Fig. 1A and B).

Thyme flowers contained 1220 ± 30 pollen grains in the morning and 577 ± 18 at the end of the day. Thyme pollen consumption in the various plots ranged between 19.2% and 76.5% (mean ± SE = 54.3 ± 3.5). The best model for thyme pollen consumption (pseudo-$R^2 = 0.42$) included *A. mellifera* visitation rate ($p = 0.002$) and *B. terrestris* visitation rate ($p = 0.04$) (Fig. 1C and D).

Rosemary nectar standing crops in the 21 plots ranged from 0 to 6.31 µl/flower (0.26 ± 0.39). The best model explaining rosemary nectar levels (pseudo-$R^2 = 0.42$) included *A. mellifera* visitation rate ($p = 0.04$) and, marginally, *B. terrestris* visitation rate ($p = 0.05$) (Fig. 2).

Bee community

Pan trap surveys yielded 6580 bee specimens corresponding to 98 species. Sixty-three of the non-*Apis* species were small (fresh body weight <55 mg) and 34 were large (>70 mg). Honey bee abundance in the pan traps was negatively related to distance to the nearest apiary (logarithmic relationship, $r^2 = 49.73$, $p = 0.0004$).

No variables entered the model of wild bee richness (Table 1), and similar results were obtained when small and large bees were analyzed separately (Table 1). The best model for bee abundance (pseudo-$R^2 = 0.48$) included *Cistus* flower abundance ($p = 0.002$) and *T. vulgaris* flower abundance ($p = 0.004$). Similar results were obtained when only small bees were taken into account (pseudo-$R^2 = 0.41$; *Cistus* abundance ($p = 0.008$); *T. vulgaris* abundance ($p = 0.03$)). Instead, the best fit model for large bee abundance (pseudo-$R^2 = 0.50$) included distance to the nearest apiary ($p = 0.02$) and, marginally, *Cistus* abundance ($p = 0.06$) (Fig. 3A and B; Table 1). To be conservative, we re-ran the latter analysis without 3 possible leverage points (Cook's $D = 0.5$ to
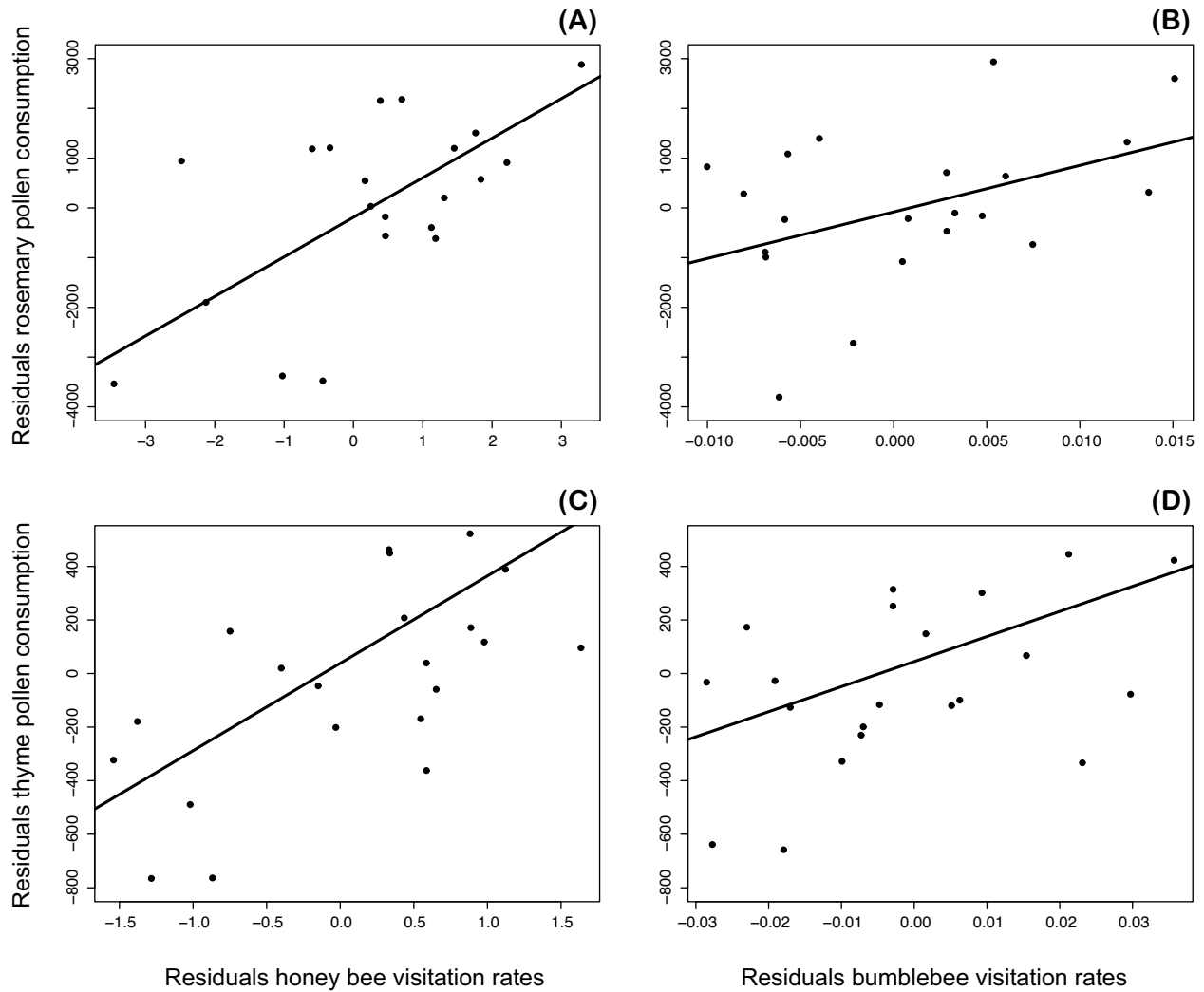
Fig. 1. Partial regression plots showing the contribution of honey bee and bumblebee visitation rates to rosemary and thyme pollen consumption in 21 plots, once the effect of other explanatory variables entering the GLMs has been removed (bumblebee visitation rate in (A) and (C); honey bee visitation rate in (B) and (D)).

Table 1. Results of GLMs analyzing wild bee richness, abundance and biomass in 21 plots as a function of distance to the nearest apiary, and abundance of *Cistus* spp., *Thymus vulgaris*, *Rosmarinus officinalis* and *Dorycnium pentaphyllum* flowers. *p*-Values are only given for variables entering the models. Pseudo-R^2 is provided as a measure of goodness-of-fit.

| Response variable		Explanatory variables					Pseudo-R^2
		Distance to apiary	*Cistus*	*T. vulgaris*	*R. officinalis*	*D. pentaphyllum*	
Wild bee richness	Large species[a]	ns	ns	ns	ns	ns	–
	Small species[b]	ns	ns	ns	ns	ns	–
	All species	ns	ns	ns	ns	ns	–
Wild bee abundance	Large species[a]	$p = 0.019$	$p = 0.061$	ns	ns	ns	0.50
	Small species[b]	ns	$p = 0.008$	$p = 0.030$	ns	ns	0.41
	All species	ns	$p = 0.002$	$p = 0.042$	ns	ns	0.48
Wild bee biomass	Large species[a]	$p = 0.007$	$p = 0.059$	ns	ns	ns	0.54
	Small species[b]	ns	$p = 0.016$	ns	ns	ns	0.27
	All species	$p = 0.017$	$p = 0.016$	ns	ns	ns	0.56

[a] Body weight >70 mg:
[b] Body weight <55 mg.
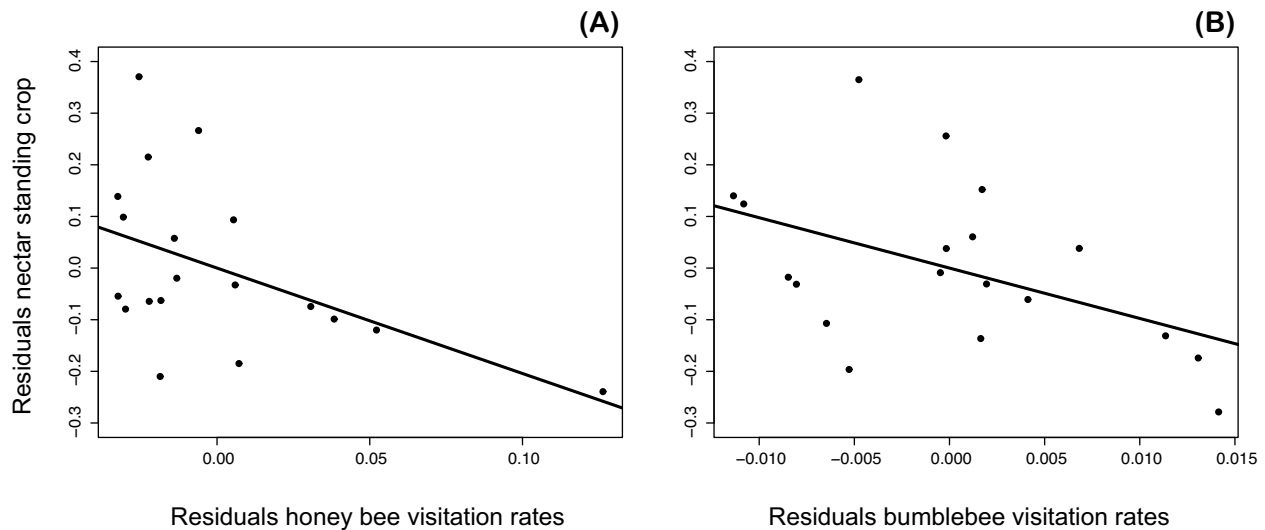
Fig. 2. Partial regression plots showing the contribution of honey bee and bumblebee visitation rates to rosemary nectar standing crops in 21 plots, once the effect of other explanatory variables entering the GLMs has been removed (bumblebee visitation rate in (A); honey bee visitation rate in (B)).

1), and obtained similar results with a lower goodness-of-fit (pseudo-$R^2 = 0.28$, distance to the nearest apiary $p = 0.02$, *Cistus* abundance $p = 0.06$). The best wild bee biomass model (pseudo-$R^2 = 0.56$) included *Cistus* flower abundance ($p = 0.002$) along with distance to the nearest apiary ($p = 0.02$). The best model for small bees (pseudo-$R^2 = 0.27$) included only *Cistus* abundance ($p = 0.02$) (Table 1). Conversely, the best model for large bees (pseudo-$R^2 = 0.54$) included distance to the nearest apiary ($p = 0.007$) and, marginally, *Cistus* abundance ($p = 0.06$) (Fig. 3C and D).

Discussion

Honeybees outnumbered the most frequent wild bee (the bumblebee *B. terrestris*) on rosemary and thyme flowers, the two main flowering plants in the study area. All workers of these two bee species collected nectar, and some of them also collected pollen. Our results demonstrate that honey bees were the main species contributing to pollen and nectar consumption. The contribution of *B. terrestris* was much lower, and other pollinators played a non-detectable role in flower resource consumption. In addition to being the most frequent visitors to rosemary and thyme, *A. mellifera* and *B. terrestris* visit more flowers per individual plant than other pollinators (Arnan et al., 2014). Mean pollen consumption per plot was slightly higher for rosemary (mean = 65.6%, range = 25.1–90.1%) than for thyme (mean = 54.3%, range = 19.2–76.5%), but to a greater or lesser extent, most plots had considerable amounts of pollen and nectar available at the end of the day. This may suggest that flower resources are not a limiting factor for the bee community. However, the energetic gain obtained from flowers with pollen-nectar levels below a certain threshold may be insufficient to compensate foraging costs, especially for large bees, with higher energetic demands (Heinrich, 1975). Bees

have been shown to move away from less rewarding patches (Heinrich, 1979). Our pollen-nectar surveys were conducted during peak bloom of the two main flower species in the study area. By the end of April, flower resources are much scarcer in the Park, and overall visitation rates are much higher (Flo, 2014; Filella et al., 2013; Bosch et al., 2009). Consequently, we expect the potential effects of intensive honey bee foraging to be greater in late-spring. In the summer, when floral resources in the Park are very low, some beekeepers move their hives to mountain areas.

Our study also shows that the wild bee community is affected and modified in areas close to apiaries, with a lower overall wild bee biomass mediated by a lower abundance of large bees. Small bees require less energy to fly and sustain foraging and nesting activities (Heinrich, 1975). In addition, small bees require smaller pollen/nectar amounts to produce an offspring (Müller et al., 2006). Thus, pollen and nectar standing crops in areas close to the apiaries may be sufficient for small bees but not for large bees. If so, large bees may be forced to nest somewhere else or widen their foraging ranges, which are well known to be positively related to body size (Guédot, Bosch, & Kemp, 2009; Greenleaf, Williams, Winfree, & Kremen, 2007; Gathmann & Tscharntke, 2002). As for small bees, even if their abundance did not diminish close to apiaries, their fitness might still be affected by the lower pollen/nectar standing crops. At the intra-specific level, bee adult body size is directly related to the amount of pollen-nectar consumed by the larva (Bosch & Vicens, 2002; Ribeiro, 1994), and some studies have shown reductions in offspring body size in populations flying in areas with low levels of flower resources (Bosch, 2008; Peterson & Roitberg, 2006). Other studies have found that bumblebee colonies produce smaller workers in areas with managed honey bees, probably due to pollen/nectar scarcity (Elbgami et al., 2014; Goulson & Sparrow, 2009). Small offspring are
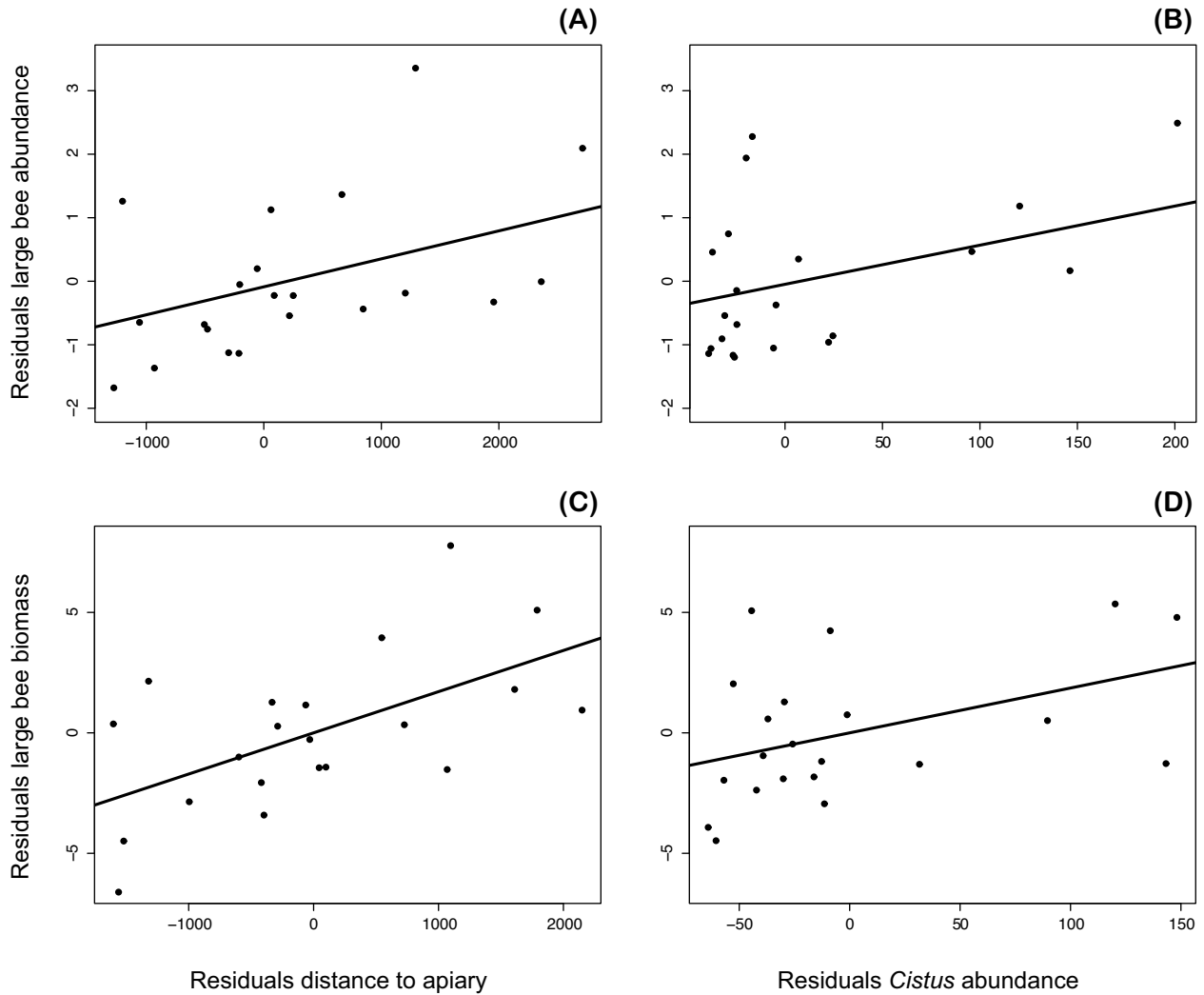
Fig. 3. Partial regression plots showing the relationship between distance to the nearest apiary and large bee (body weight >70 mg) abundance and biomass in 21 plots, once the effect of other explanatory variables entering the GLMs has been removed (*Cistus* flower abundance in (A) and (C); distance to the nearest apiary in (B) and (D)).

more likely to die during development (Bosch, 2008) and during wintering (Bosch & Kemp, 2004; Tepedino & Torchio, 1982). Smaller females are also less likely to found a nest (Bosch & Vicens, 2006; Tepedino & Torchio, 1982). Low levels of floral resources may also enhance parasitism in solitary bees (Goodell, 2003), as females are forced to make longer foraging trips to gather a pollen/nectar load, thus leaving the nest unguarded and exposed to cleptoparasites (Seidelmann, 2006). In agreement with our results, some studies investigating the potential impact of honey bees on wild bee communities have found wild bee abundance to be lower near apiaries (Thomson, 2006; Forup & Memmott, 2005), but others have not (Roubik & Wolda, 2001; Steffan-Dewenter & Tscharntke, 2000). On the other hand, and in agreement with other studies (Forup & Memmott, 2005; Roubik & Wolda, 2001; Steffan-Dewenter & Tscharntke, 2000), bee richness was not influenced by proximity to apiaries in our study.

In addition to honey bee density, bee abundance and biomass may also be influenced by flower abundance and distribution. Our models show that *Cistus* flowers have an important role in structuring the Garraf bee community. The three *Cistus* species occurring in the park bloom in April, at a time when wild bee abundance and diversity are high, and flower resources show a strong decline after the blooming period of *R. officinalis* and *T. vulgaris* (Flo, 2014; Filella et al., 2013; Bosch et al., 2009). Other plants blooming at this time are either very scarce (*Gladiolus illyricus*, *Orobanche latisquama*), or produce smaller amounts of pollen and nectar (*D. penthaphyllum*) (Flo, 2014). Previous studies in the same area have shown that *C. albidus* and *C. salvifolius* constitute a hub in the Garraf pollination network, attracting higher numbers of pollinator species and receiving higher flower visitation rates than any other plant species (Bosch et al., 2009).

Our study provides evidence to support the hypothesis that high densities of managed honey bees have a negative impact on wild bee communities. Our results point to pollen-nectar depletion as a mechanism explaining this negative impact. To our knowledge, this is the first time flower resource

consumption has been measured in studies exploring the potential effects of managed honey bees on wild pollinators. To confirm or refute this hypothesis, future studies should include long-term monitoring of wild bee populations and direct measures of fitness. From a land management perspective, decisions on the number of hives allowed in an environmentally protected area should be based on the carrying capacity of the flower community at the landscape level. However, to provide a range of appropriate hive densities is extremely difficult for several reasons. First, even in a natural habitat such as the Garraf Natural Park, flower spatial distribution is far from homogeneous (Torné-Noguera et al., 2014). Second, availability of flower resources in our study area changes dramatically throughout the season and from year to year (Flo, 2014). Third, foraging ranges of honey bees span several kilometers and are highly variable in time (Visscher & Seeley, 1982). Fourth, resource depletion may also depend on the abundance of wild pollinator populations. Given all these uncertainties, our study suggests that, in this particular habitat, wild bee communities are likely to be affected at densities over 3.5 hives/km^2 (475 hives/134 km^2).

Epilogue

The Garraf Natural Park is partially located in the municipality of Olivella. In May 2012, the city council discussed a petition to install 357 new honey bee hives in the Park. The council examined a report commissioned by the board of directors of the Park cautioning about the potential effects of intensive beekeeping on other pollinators. The council finally approved the installation of the additional 357 hives based on current legislation considering beekeeping an "innocuous activity".

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Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.baae.2015.11.004.

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