



Managed honeybee hives and the diversity of wild bees in a dryland nature reserve

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Abstract – Honeybee hives may influence pollen and nectar availability in natural ecosystems, which may consequently affect wild pollinators. We studied the effects of managed honeybee hives on wild bee diversity in Villavicencio Nature Reserve (Mendoza, Argentina). We placed pan traps at increasing distances from honeybee hives to estimate wild bee abundance, richness, and composition. Wild bee abundance did not change detectably with distance to honeybee hives, although the abundance of the most common species, *Arhysoyage bifasciata*, increased with increasing distance to the hives. Wild bee richness increased weakly with increasing distance to hives. Although wild bee composition did not change significantly with distance to the apiaries for the full data set, it changed significantly when we excluded *A. bifasciata* from the analyses. We found no relationship between body size and distance to the apiaries. Overall, our results indicate that managed honeybee hives had mixed effects on the wild bee assemblage in our study area. Given the relatively low hive density used in our study compared to other studies, we recommend an adaptive management strategy with continuous impact assessment.

honeybee / wild bee community / dryland / bees conservation / natural reserve

1. INTRODUCTION

Native to Africa, west Asia, and Europe, the honeybee (*Apis mellifera* L.) has been introduced to all continents except Antarctica for honey production and crop pollination (Pirk et al. 2017). Viewed historically as a beneficial, sustainable practice, beekeeping may influence natural environments in multiple ways, from species level to the entire community (Dohzono and Yokoyama 2010; Russo 2016; Geslin et al. 2017; Pirk et al. 2017; Agüero et al. 2018; Vanbergen et al. 2018).

Honeybees affect wild bees mainly through resource competition and parasite or pathogen transmission (Russo 2016; Agüero et al. 2018; Henry and Rodet 2018). The high competitive ability of honeybees may result from their generalist habit, which leads to high overlap in resource use with native bees (Paini 2004), and from their complex social organization and efficient foraging, becoming an avid nectar and pollen consumer in many communities (Torné-Noguera et al. 2016; Cane and Tepedino 2017). This high resource overlap and consumption rate may reduce the resource availability for native bees, ultimately decreasing their fitness (Elbgami et al. 2014). Consequently, honeybees are capable to displace other

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pollinators and modify the assemblages of native bees in areas that surround hives (Torné-Noguera et al. 2016).

High density of honeybees may result in decreased abundance of large wild bee species (Torné-Noguera et al. 2016; Henry and Rodet 2018), and a shift towards individuals of smaller body size of some bumblebee (*Bombus*) species (Goulson and Sparrow 2009; Elbgami et al. 2014). A possible explanation of this effect is that larger bees need more pollen and nectar than smaller ones, which becomes difficult when they are close to honeybee hives, and larger bees are drawn away from this area (Goulson and Sparrow 2009; Torné-Noguera et al. 2016; Henry and Rodet 2018). Furthermore, larger bees can fly longer distances and forage far from hives, in sites where the competitive pressure for resources is lower (Greenleaf et al. 2007; Guédot et al. 2009).

Despite the above ecological effects caused by the honeybee, the introduction of hives has been approved in different protected areas around the world (Shavit et al. 2009; Torné-Noguera et al. 2016; Henry and Rodet 2018). In Mendoza, Argentina, the introduction of exotic species in protected areas is forbidden (Law 6045/93). However, managed honeybee introduction for honey production was approved in Villavicencio Nature Reserve, Mendoza, a protected natural area created to preserve the natural, archeological, and historical heritage. While the honeybee has been naturalized for years in Villavicencio (Chacoff et al. 2012), the introduction of managed hives could increase substantially honeybee abundance in the area. Previous studies in other regions found that the introduction of managed honeybees into natural areas caused negative effects in the wild bee community, including lower occurrence, abundance, and flower visitation frequency (Shavit et al. 2009; Torné-Noguera et al. 2016; Henry and Rodet 2018).

Here we evaluate whether the intentional introduction of managed honeybee hives influences the local wild bee community in Villavicencio Nature Reserve. Our hypothesis is that the high honeybee densities resulting from hive introduction allow honeybees to displace wild

bees competitively, leading to decreased wild bee abundance and richness and modified composition in areas surrounding honeybee hives. We also hypothesized that because larger wild bees consume more energy in foraging than smaller bees, honeybee hive introduction will be more detrimental for larger bees than for smaller bees, leading to increased wild bee abundance with increasing distance to hives, especially for larger wild bees.

2. MATERIALS AND METHODS

2.1. Study area

The study was conducted in Villavicencio Nature Reserve, a 62,000-ha private protected area located ca. 30 km north of Mendoza City, Argentina. The sampling sites were located in the lower areas of the reserve (1000–1400 m above sea level) and belong to the Central Monte desert biome (Figure 1) (Dalmaso et al. 1999). The climate is semi-arid and the precipitation ranges between 80 and 250 mm per year (Cabrera 1971). The vegetation is a xerophilous shrub steppe, 1.5–3 m high, dominated by *Larrea divaricata* (Zygophyllaceae), *Condalia microphylla* (Rhamnaceae), *Senna aphylla* (Fabaceae), *Menodora decemfida* (Oleaceae), and *Prosopis flexuosa* (Fabaceae) (Dalmaso et al. 1999).

In October 2018 we placed five clusters of twenty-five honeybee hives (apiaries) in the reserve, located at a distance not less than 3 km between them. The hive density was 4.63 hive/km² (125 hives/27 km²). At each hive cluster we established a fixed 1500 m transect, where we conducted the bee sampling (Table I; Figure 1). Transect direction was dictated by topography and road access.

2.2. Bee sampling

Sampling was conducted three times between October 24 and November 24, 2018. The sampling period overlapped with the peak flowering of dominant plant species in our sites and with

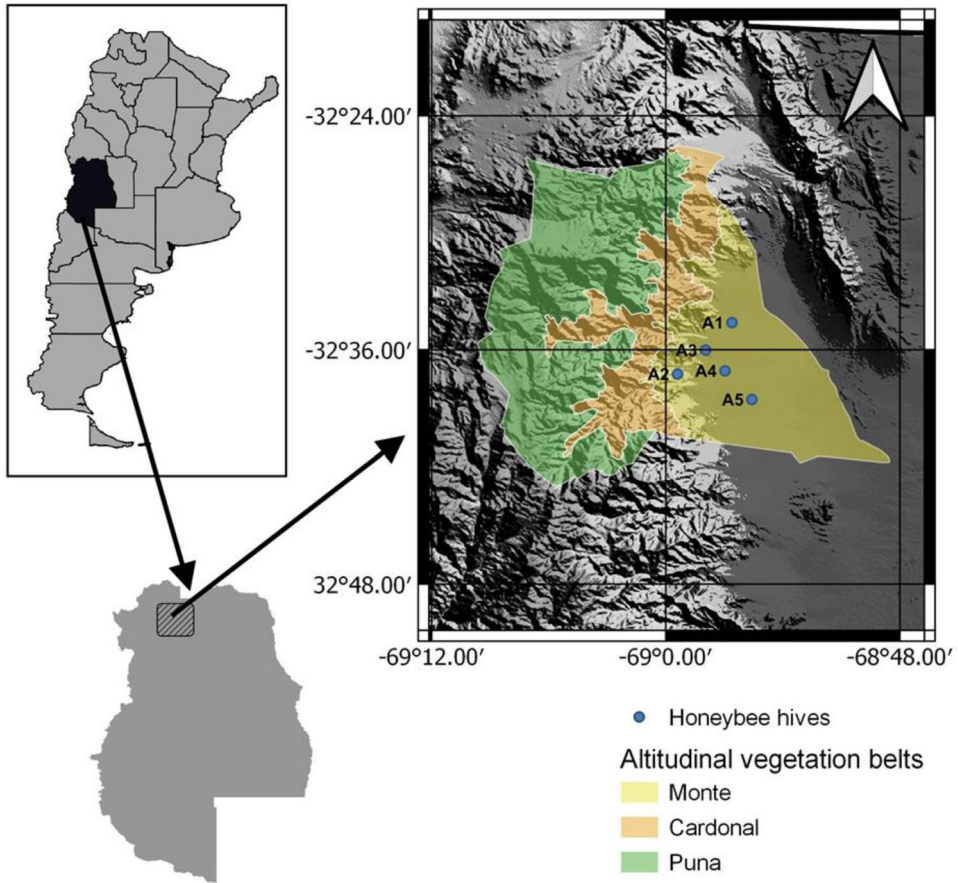


Figure 1. Map of Villavicencio Nature Reserve with the altitudinal vegetation belts (colored polygons) and the locations of the five apiaries (A1 to A5).

the period in which honeybee hives were present in the study area.

Table I

Geographic coordinates and elevation (m above sea level) of the five apiaries

Apiary	Geographic coordinates	Elevation (m above sea level)
1	32°34'36"S, 68°56'36"W	1148
2	32°37'15"S, 68°59'24"W	1367
3	32°36'1"S, 68°57'58"W	1228
4	32°37'16"S, 68°56'47"W	1145
5	32°38'39"S, 68°55'30"W	1015

We sampled bees with pan traps placed on 1500-m transects at increasing distances from the apiaries: 50 m, 100 m, 200 m, 500 m, 1000 m, and 1500 m. At each distance, we placed on the ground two groups of three pan traps painted in yellow, blue, and white, containing water and a few drops of dish detergent. These colors are known to attract bees (Westphal et al. 2008), which sink in the water because the dish detergent breaks the surface tension. We conducted the first two sampling events between 10 am and 4 pm, while the third sampling event was done for 30 h, so as to increase the insect catch in our traps, as in the first two sampling events the catch was low.

We dried the collected specimens, mounted them on entomological pins, and identified them using specific bibliography for each group. The specimens are kept in the Entomological Collection of the Argentine Institute for Dryland Research (IADIZA), CONICET Science and Technology Center, Mendoza.

To estimate bee body size, we measured the intertegular span (IS, in mm) of 5 to 10 individuals of each species and sex using a dissecting microscope with a calibrated lens, and used the Cane's (1987) allometric equation to estimate bee dry weight (DW, in mg):

$$IS = 0.77DW^{0.405}$$

2.3. Statistical analysis

We used general linear models (GLM) to evaluate the effects of managed honeybee hives on wild bee abundance and richness (Bolker et al. 2008), using function `glm` of R statistical software (R Core Team 2015). We used abundance or richness as the response variable and distance to the apiary as the fixed predictor. We used Gaussian and Poisson error distributions, and selected among models with different distributions using AIC. In all cases the best fitting models were those with Gaussian distribution. Furthermore, because the number of bee individuals caught varied among different sampling

points, we used rarefaction to remove sampling effects from our richness estimates, using the `raref` function of the R `vegan` package (Gotelli and Colwell 2001; Oksanen et al. 2019).

We used permutational multivariate analysis of variance (PERMANOVA) and non-metric multidimensional scaling (NMDS) (Legendre & Legendre 1998) to evaluate the effect of managed honeybee hives on wild bee composition. For the PERMANOVA, we used distance and apiary as crossed factors, the Bray–Curtis distance metric to estimate compositional distances, and 999 permutations, using the `adonis` function of the R `vegan` package (Oksanen et al. 2019). We used the function `metaMDS` of the `vegan` package to conduct the NMDS (Oksanen et al. 2019).

We used GLM to evaluate the effects of distance to honeybee hives on wild bee abundance contingent on body size. In this model, abundance was the response variable, and distance and dry weight were the crossed predictors. Dry weight was estimated from intertegular distance as explained above. We used Gaussian and Poisson error distributions, and selected among models with different distributions using AIC. Again, in all cases the best fitting models were those with Gaussian distribution.

Because one bee species, *Arhysosage bifasciata*, accounted for 57% of the total wild bee individuals caught in our traps, which could mask the patterns for the rest species, we conducted all analyses twice, with and without *A. bifasciata*.

Table II

GLM results for the variables abundance of wild bees, wild bees without *A. bifasciata*, honeybees and *A. bifasciata*, and the variables richness and rarefied richness of wild bees and wild bees without *A. bifasciata*, all as a function of increasing distances from the apiaries

Response variable	Predictors	β	SE	t	P
Abundance	Wild bees	0.01271	0.006356	2	0.0552
	Wild bees without <i>A. bifasciata</i>	-0.001193	0.003407	-0.35	0.729
	Honeybees	-0.00353	0.001443	-2.446	0.0249
	<i>A. bifasciata</i>	0.013064	0.004547	2.873	0.0076
Richness	Wild bees	0.0010126	0.0004665	2.171	0.0386
	Wild bees without <i>A. bifasciata</i>	0.0010126	0.0004665	2.171	0.0386
Rarefied richness	Wild bees	0.00022795	0.0002211	1.031	0.311
	Wild bees without <i>A. bifasciata</i>	4.816×10^{-4}	1.973×10^{-5}	2.441	0.0212

3. RESULTS

We recorded from the traps 1414 individuals of flying Hymenoptera belonging to 66 species, of which 1046 were wild bees (24 species), 88 were *A. mellifera*, and 280 were other hymenopteran species not included in our analyses. We collected 424 individuals (340 bees) in the first sampling date, 332 (252 bees) in the second, and 658 (531 bees) in the third. The most abundant wild bee species were *A. bifasciata* (Andrenidae; 603 individuals) and *Dialictus* sp. (Halictidae; 300 individuals), followed by species of the families Apidae, Colletidae, and Megachilidae (Table S1). The only exotic bee collected was the honeybee,

whose abundance decreased with increasing distance to the apiaries (Table II).

Wild bee abundance tended to increase with increasing distance to the apiaries, although this effect was weak and only marginally significant (Table II; Figure 2). After excluding *A. bifasciata*, wild bee abundance was unrelated to the distance to the apiaries (Table II; Figure 2). In contrast, the abundance of *A. bifasciata* increased with increasing distance to the apiaries (Table II; Figure 3).

Wild bee richness increased with increasing distance to the apiaries, both including and excluding *A. bifasciata* (Table II; Figure 2). After applying rarefaction to eliminate sampling

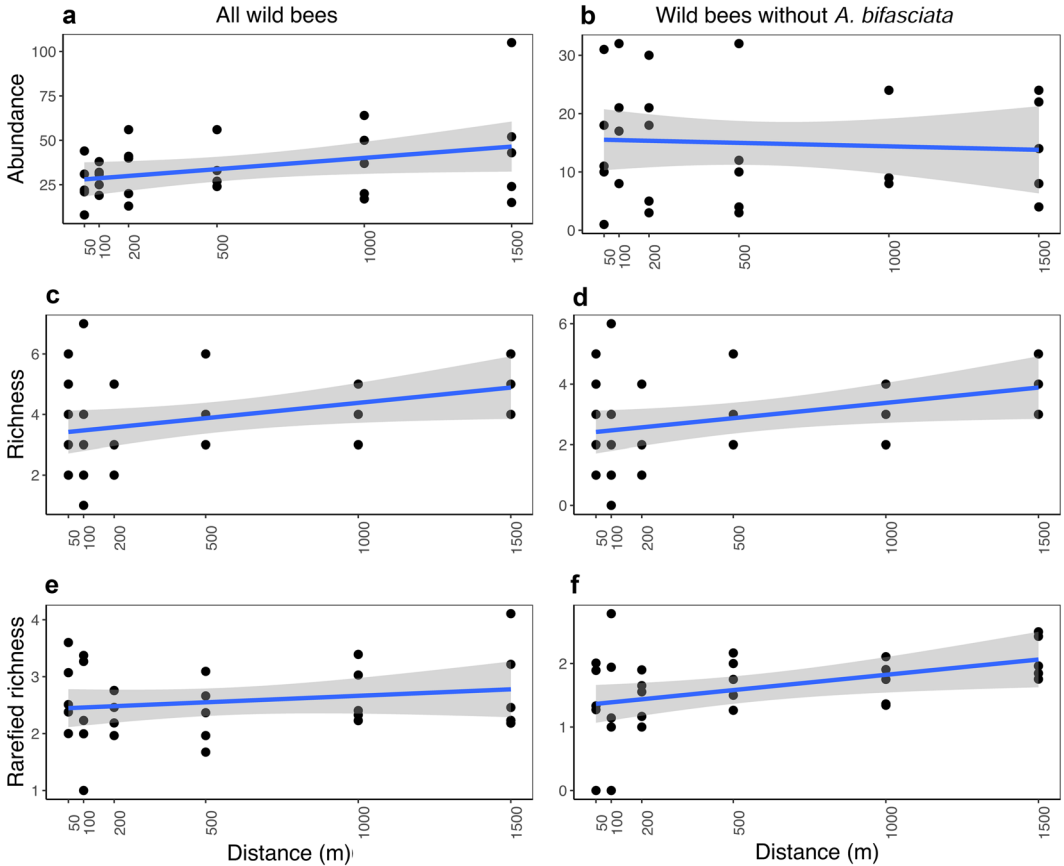


Figure 2. Regression curve shows abundance of (a) wild bees, (b) wild bees without *A. bifasciata*; richness of (c) wild bees and (d) wild bees without *A. bifasciata*; and rarefied richness of (e) wild bees and (f) wild bees without *A. bifasciata*, all as a function of increasing distances from the apiaries. The shaded area is the 95% confidence level interval for predictions.

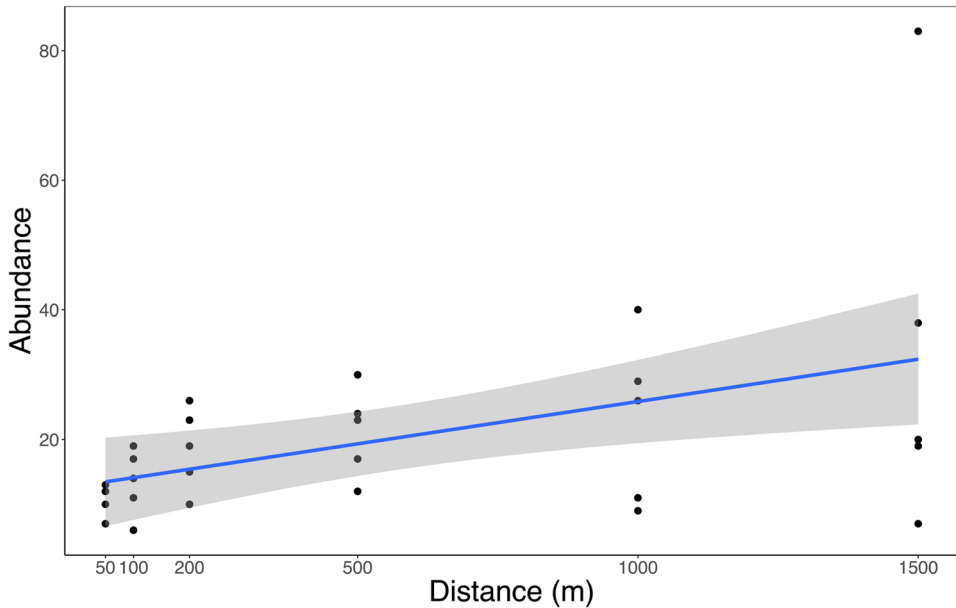


Figure 3. Regression curve shows abundance of *A. bifasciata* as a function of increasing distances from the apiaries. The shaded area is the 95% confidence level interval for predictions.

effects, wild bee richness was unrelated to distance to the apiaries, but after excluding *A. bifasciata* wild bee rarefied richness increased with the distance to the apiaries (Table II; Figure 2).

Wild bee composition did not change significantly with distance to the apiaries, site, and their interaction (Table III; Figure 4). After excluding *A. bifasciata*, wild bee composition changed significantly with distance to the apiaries, but not so with site and their interaction (Table III; Figure 4).

Wild bee abundance, dry weight, and their interaction did not change significantly with distance to the apiaries (Table IV). For the data excluding *A. bifasciata*, wild bee abundance and dry weight decreased significantly with distance to apiaries, but not their interaction (Table IV).

4. DISCUSSION

Our results indicate that managed honeybee hives had mixed effects on the wild bee assemblage of Villavicencio Nature Reserve. Wild bee

abundance decreased weakly with decreasing distance to the apiaries, but this effect disappeared after excluding *A. bifasciata*, the most abundant wild bee species in our study, and did not depend on wild bee body size. In turn, wild bee richness tended to decrease with decreasing distance to the apiaries. Although this effect disappeared once rarefaction was applied to richness data to account for sampling effects, after excluding *A. bifasciata* wild bee rarefied richness was again negatively related to distance to the apiaries. In turn, wild bee composition was unaffected by distance to the apiaries when including *A. bifasciata*, but changed significantly with distance to the apiaries when excluding this species from the analyses.

Although our results indicate that managed honeybees had no detectable effects on wild bee abundance, it is remarkable that honeybees seemed to hinder the abundance of *A. bifasciata*, which, as we mentioned above, was the most abundant wild bee species in our study. *Arhysoyage* bees have affinity for flowers of cacti (*Opuntia*, *Gymnocalycium*, etc.), upon which they are oligolectic (Schlindwein and

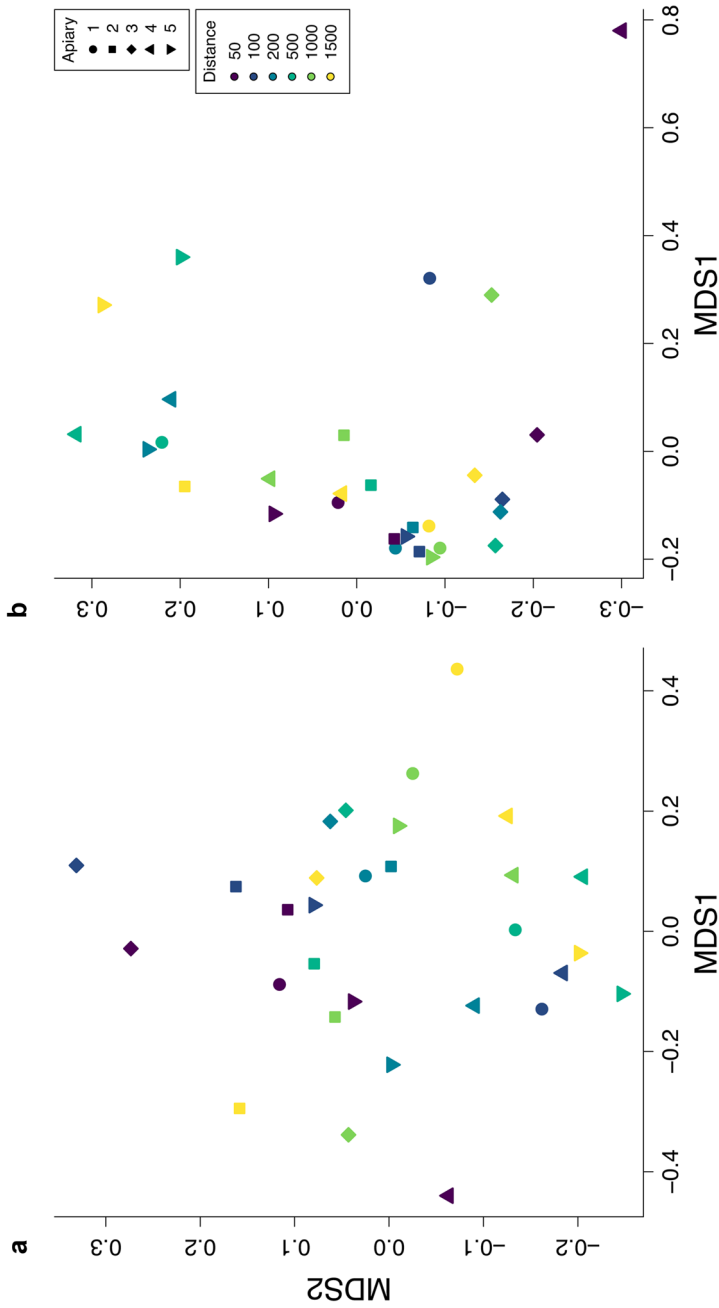


Figure 4. Multidimensional scaling (NMDS) for analysis of the composition of (a) wild bees and (b) wild bees without *A. bifasciata*. The shapes correspond to the different apiaries and the colors to the increasing distances from the apiaries.

Table III

Results for the composition of all wild bees and wild bees without *A. bifasciata*. Analysis PERMANOVA using distance and apiary as crossed factors

Composition	Predictor variables	Df	SS	MS	Pseudo-F	R ²	P
All wild bees	Distance	1	0.1864	0.18638	1.7815	0.05887	0.137
	Apiary	1	0.1563	0.15632	1.4941	0.04937	0.206
	Distance:apiary	1	0.1033	0.10325	0.9869	0.03261	0.424
Wild bees without <i>A. bifasciata</i>	Distance	1	0.5885	0.5885	2.66274	0.09275	0.031
	Apiary	1	0.1111	0.11109	0.50266	0.01751	0.815
	Distance:apiary	1	0.1204	0.12043	0.54493	0.01898	0.768

Wittmann 1995; Engel 2000), and the scarce data on natural history indicate that they are ground-nesting (Rozen and Roig-Alsina 1991). A previous study in our study area (Chacoff et al. 2012) found that the cactus *Opuntia sulphurea* was the species most frequently visited by *A. bifasciata*, while no *A. mellifera* were recorded visiting this species. However, we conducted our bee sampling before the start of *O. sulphurea*'s flowering period and it is likely that *A. bifasciata* visited flowers of the same species as the honeybee, competing for this resource. It would be important to repeat this study in the future during the flowering period of *O. sulphurea* to evaluate if the effect of managed honeybees on the abundance of *A. bifasciata* persists when its main floral resource is present. It would also be ideal to survey this species in the long term, to assess potential consequences of the honeybee on its demography and population dynamics.

Wild bee richness increased with increasing distance to the apiaries. As we discussed above, although rarefied richness did not change significantly with distance to the apiaries, rarefied richness changed significantly with such distance after removing *A. bifasciata* from the data. Arguably, the strong dominance of *A. bifasciata* may have obscured the change in rarefied richness for the rest of the wild bee assemblage. Thus, we conclude that our data suggest that managed honeybees have a detectable negative impact on wild bee richness.

We also found that wild bee composition was unaffected by managed honeybees when the analyses included *A. bifasciata*, the most abundant wild bee species in our study. Yet, when excluding *A. bifasciata*, we found a significant effect of distance to the apiaries on wild bee composition, suggesting that the high abundance of *A. bifasciata* could mask the subtler changes in the rest of the wild bee assemblage. These results

Table IV

GLM results for the abundance of wild bees and wild bees without *A. bifasciata*, in function of the distance to the hives in interaction with the dry weight

Response variable	Predictors	β	SE	t	P
Wild bee abundance	Distance	1.114 × 10 ⁻³	2.855 × 10 ⁻³	0.39	0.6971
	Dry weight	-0.1679	0.2004	-0.838	0.40371
	Distance:dry weight	2.134 × 10 ⁻⁵	1.946 × 10 ⁻⁴	0.11	0.912884
Wild bee abundance without <i>A. bifasciata</i>	Distance	-0.0029485	0.0016499	-1.787	0.0776
	Dry weight	-0.284563	0.1089047	-2.613	0.0107
	Distance:dry weight	0.0001738	0.0001059	1.641	0.1046

suggest that wild bee composition is affected by the presence of honeybee hives, despite the low hive density used in our study. Future studies should attempt to go beyond wild bee abundance, richness, and composition, to assess the impact of the honeybee on plant-pollinator interactions and the pollination service to wild plants.

We expected the abundance of larger-bodied wild bee species to decrease more strongly in the proximity of managed honeybee hives. However, the lack of a significant interaction between distance to the apiaries and bee dry weight allows us to reject our expectation. This result may be explained by the fact that we failed to collect species larger than the honeybee, such as large carpenter bees (*Xylocopa*, Latreille) or bumblebees (*Bombus*); the largest species collected had a body size similar or barely larger than the honeybee.

As we mentioned above, a potential explanation for the mixed effects of managed honeybees concerns the low number of collected specimens. In addition, pan traps may not be an efficient sampling method during the peak flowering of dominant plant species, as flowers may compete with pan traps (Wilson et al. 2008). Nevertheless, previous studies offer mixed evidence on the relative effectiveness of pan traps relative to other collection methods: while some studies indicate high effectiveness of pan traps compared to other collection methods (Westphal et al. 2008; Nielsen et al. 2011), other studies indicate higher effectiveness of net sampling (Roulston et al. 2007; Popic et al. 2013). All sampling methods have inherent biases, and which influence their detection of species composition therefore, whenever possible, studies of wild bees should use multiple sampling methods to improve the characterization of bee composition (Roulston et al. 2007; Wilson et al. 2008).

An alternative explanation of the mixed effects of managed honeybees on wild bee diversity results from the low number of hives per apiary (25 hives) and the high distance between the apiaries (at least 3 km), which represents a low honeybee hive density (4.63 hives/km²). Furthermore, it must be considered that the floral resource was abundant at the sampling time, as it

encompassed the flowering peak of the dominant species in the area, so it is reasonable to think that the floral resource was not limited. However, previous studies with a similar or lower density of honeybee hives found negative effects of managed honeybees on wild bee diversity (Shavit et al. 2009; Torné-Noguera et al. 2016), while other studies with substantially higher densities of honeybee hives found no effects on wild bee abundance and richness (Steffan-Dewenter and Tschardt 2000). These contrasting results suggest that the impact of honeybee hives on wild bees may depend on the intrinsic properties of each ecosystem. Therefore, studies should include robust experimental designs and high replication to assess the impact of any introduction in a natural environment.

In addition to the potential effects of honeybees on wild bee abundance, richness, and composition, there are other potential effects that we did not study here. For example, long-term studies indicate that wild bee foraging behavior may change in the presence of honeybee hives, including switching the floral resource spectrum and the foraging times (Roubik 2009; Roubik and Villanueva-Gutiérrez 2009). In addition, the presence of managed honeybees may influence the fitness of wild bees, especially in colonial species such as bumblebees (*Bombus*; Goulson and Sparrow 2009; Elbgami et al. 2014). These and other dimensions of the potential impact of managed honeybees should also be included in future studies in our study area for a more complete understanding of the impact of beekeeping in this protected area.

SUPPLEMENTARY INFORMATION

The online version contains supplementary material available at <https://doi.org/10.1007/s13592-021-00882-6>.

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AUTHOR CONTRIBUTION

YL and DPV designed the study. YL and GD identified the insect specimens. All authors contributed to statistical analyses. All authors contributed to the final version of the manuscript.

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AVAILABILITY OF DATA AND MATERIAL

Data will be made available in a public repository. Insect specimens will be deposited at the Entomological Collection of the Argentine Institute for Dryland Research (IADIZA).

CODE AVAILABILITY

Not applicable.

DECLARATIONS

Ethics approval The authors declare that all ethical issues have been appropriately dealt with.

Consent to participate All authors have given their consent to be part of this publication.

Consent for publication All authors have given their consent to publish this manuscript.

Conflict of interest The authors declare no competing interests.

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