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ORIGINAL RESEARCH

Relation between honey bee abundance and wild bee communities in Moroccan agro-ecosystems

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Abstract

The expansion of entomophilous crops over the last decades has been accompanied by a growing demand for managed honey bee colonies to provide pollination service. The massive introduction of honey bee in agro-ecosystems has raised concerns about a negative effect on wild bee communities. Here we assess following a standardised sampling the relation between honey bee abundance and wild bee abundance/species richness in six pollinator dependent crops across 201 sites in four different regions in Morocco and during two consecutive years. We also evaluate how multi-croping can modulate the impact of honey bee on wild bees. Our results show that wild bee abundance and richness were not influenced by honey bee abundance regardless of the crop. The response of wild bees to honey bee did not vary between monoculture fields and fields with additional marketable plants. These findings suggest that the current Moroccan agro-ecosystems are not experiencing a strong competition between wild and honey bees and they might co-exist even in the absence of additional habitat plants. However, the effect of honey bee on wild bees remains context-dependent, and we therefore urge caution when generalizing the results.

Keywords Competition · Conservation · Pollinator · Niche-partitioning · Marketable habitat plants

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Introduction

Pollination is one of the key ecosystem services affording a range of direct and indirect benefits to humans. Animal pollinators, particularly insects are a requirement for 75% of the leading food crops (Klein et al. 2007). The economic value of insect pollination from crop yields intended for human consumption ranges from US$ 195 billion to US$ 387 billion (Porto et al. 2020). The proportion of flowering plants, including wild plants, relying on animal pollination is up to 87% (Ollerton et al. 2011). Thus, the sexual reproduction of these plants, the conservation of the species that rely upon them and the ecosystem services they provide depend on animal pollinators (Klein et al. 2018).

The decline of insect pollinators reported in several parts of the world is rising concerns about the service they provide (Sánchez-Bayo and Wyckhuys 2019). One of the main threats of pollinators is agricultural intensification (e.g. increase of pesticides use) and extension (i.e. increase of cultivated areas) (Castree 2018). Paradoxically, this agricultural expansion has been accompanied by a growing demand for crop pollination (Potts et al. 2016). Management of crop pollination is mainly organised by movement of honey bee hives (Gemill-Herren et al. 2020), even if additional bee species were recently domesticated (Bosch et al. 2021). The estimated number of honey bee colonies worldwide is up to 101.6 million (FAO 2021), representing a 47% augmentation compared to 1990. However, the demand for honey bee pollination rose 2.3 times higher than the existing number of honey bee colonies (Mashilingi et al. 2022). This suggests that honey bee alone is insufficient to deliver pollination, and wild pollinator communities need to be conserved. Furthermore, high levels of diversity are required to sustain ecosystem functioning (Isbell et al. 2011). Diverse pollinator communities include a broad range of species with different morphological, behavioral and phenological traits, ensuring functional complementarity (Blüthgen et al. 2007). Nevertheless, in the last few decades, the coexistence of wild and honey bees has been broadly questioned (Steffan-Dewenter and Tscharntke 2000; Paini 2004; Lindstrom et al. 2016; Cappellari et al. 2022; Weaver et al. 2022). The tremendous changes induced in agricultural lands resulted in simplified landscapes with scarce flowering resources and large honey bee populations, which may lead to a decrease in wild pollinator communities (Lindstrom et al. 2016; Weekers et al. 2022).

Honey bees may affect wild bee communities in different ways. First, by competing for floral resources (i.e. pollen and nectar). Honey bee is a strong competitor (Cane and Tepedino 2017) that consumes huge amounts of pollen and nectar to meet the nutritional requirements of its large colony, which forces other flower visitors to forage on less rewarding plants or far from their nesting sites (Ropars et al. 2020). Competition for resources is positively correlated with niche overlap, and thus the extent of the competitive effect is more pronounced on wild bees, than on other insect groups (Cappellari et al. 2022). Second, honey bees may also contribute to the reduction of wild bee populations through the transmission of pathogens (Dolezal et al. 2016). Recent studies, showed a positive association between pathogen prevalence and honey bee dominance (e.g., Mallinger et al. 2017). The occurrence of honey bees in high numbers and their transportation across regions for pollination delivery, make them more likely to host and spread diverse parasites (Nanetti et al. 2021). Third, honey bee is a generalist species that monopolises a wide range of flowering plant species. Thus, its introduction in high density may disrupt the plant pollinator networks by eliminating native interactions and/or reinforcing invasive ones (Weaver et al. 2022). Though, an important part of wild bee species are polylectic (e.g. *Bombus* and *Xylocopa*) and can modify their foraging options, some species have a restricted floral preferences and are less resistant to disruption (e.g. *Dasypoda*) (Scheper et al. 2014).

Here we aim to study the impact of honey bee abundance on wild bee communities in four Moroccan regions, during two consecutive years and using six pollinator dependent crops. We also assess whether the association to diverse marketable habitat plants (i.e. multi-cropping) through the Farming with Alternative Pollinators (FAP) approach can influence the effect of honey bee abundance on wild bees visiting the main crops. FAP is a pollinator conservation approach that supports pollinators through the provision of marketable habitat plants instead of paid wildflower strips (Christmann and Aw-Hassan 2012).

Several publications have evaluated the influence of honey bee on wild bee communities (e.g., Steffan-dewenter and Tscharntke 2000; Cane and Tepedino 2017; Angelella et al. 2021; Prendergast et al. 2021; Weekers et al. 2022; Macinnis et al. 2023; Mackell et al. 2023). However, these studies show contrasting responses depending on the study context (e.g., the availability of floral resources, the heterogeneity of the landscape and the honey bee density). To date, no study assessing the impact of honey bee on wild bees has been conducted in Morocco or in North Africa, and to our knowledge, this is the first time worldwide that the impact of honey bee on wild bees is assessed on faba bean, zucchini, pumpkin, tomato and eggplant. In this study, we aim specifically, to: (1) evaluate the impact of honey bee on the abundance and the species richness of the wild bees visiting six main crops, (2) test if the effect of honey bee on wild bee communities varies between the main crops and (3) assess whether the effect of honey bee on wild bees varies between monoculture fields and fields surrounded with diverse marketable habitat plants. Considering the rich Moroccan flora (Valdès et al. 2002), the dominance of small farms and the heterogeneity of the Moroccan agricultural landscapes (Bouzekraoui et al. 2016; Berred et al. 2020), we presume that: (1) Honey bee abundance will not affect bees visiting the main crops, (2) and this effect is expected to be consistent across monoculture fields and fields with marketable habitat plants, (3) we expect that the response of wild bees to honey bees will not differ between the main crops.

Materials and methods

We based our study on the database downloaded from the research data repository Zenodo (Sentil et al. 2023). The data were collected in four Moroccan agro-ecosystems within the framework of the IKI-FAP project. This database was explored in Sentil et al. (2024). Detailed descriptions of the study area, the experimental designs and the insect sampling are provided in Sentil et al. (2024), but we mention here the main information related to this study.

Study area

The experiments were carried out in 2018 and 2019 in four Moroccan regions: Settat, Errachidia, Sefrou and Kenitra. These regions are characterised by various climate types, landscape profiles and agricultural activities. Settat is a semi-arid region dominated by cereals (e.g. wheat and barley) and legumes (i.g. faba bean, alfalfa, lens). Kenitra is characterised by a Mediterranean climate. The region hosts one of the largest forest trees of cork oak in the world. Cereals and oilseed crops cover more than 85% of the agricultural lands in Kenitra. Sefrou is a mountainous region, experiencing a continental climate. The vegetation in this region is dominated by olive-trees and fodder plants. The forest surface covers more than 49% of Sefrou's area. Errachidia has a desertic climate and the region includes oasis, date palm forests, Sahara and Atlas Mountains.

Experimental design

We investigated the impact of honey bee abundance on wild bees visiting six main crops; faba bean (*Vicia faba*, Fabaceae), pumpkin (*Cucurbita maxima*, Cucurbitaceae), zucchini (*Cucurbita pepo*, Cucurbitaceae), eggplant (*Solanum melongena*, Cucurbitaceae), tomato (*Solanum lycopersicum*, Solanaceae) and apple (*Malus domestica*, Rosaceae). Zucchini, pumpkin and faba bean were planted in the four regions, eggplant in Settat and Kenitra, apple in Sefrou and tomato in Kenitra. All crops were planted in 2018 and replicated in 2019, except zucchini, pumpkin and faba bean in some regions, which resulted in 27 crop trials (6 faba bean trials, 7 zucchini trials, 6 pumpkin trials, 2 tomato trials, 4 eggplant trials and 2 apple trials) (Table 1). The replicated crops were replanted in the same regions, but not necessarily in the fields of the previous year. For each crop trial, 4 to 8 marketable habitat plant species were chosen among 23 crop species (Online Resource 1).

For each crop trial, except apple trials, five FAP fields (i.e. multi-crop fields) and three control fields (i.e. single crop field) were selected. The fields in both treatments (i.e. FAP and control) were 300 m^2. The main crop in FAP and control fields was planted in 75% of the field. The remaining area (i.e. the 25% surrounding zone), was occupied by marketable habitat plants in FAP fields and the main crop in control fields (Fig. 1). The apple trials were conducted in four orchards each (i.e. 2 FAP orchards and 2 control orchards). FAP and control fields within each crop trial were separated by distances ranging from 500 m to 20.3 km. Overall, the experiment was developed in 208 sites (26 crop trials*8 fields + 2 apple trials*4 orchards = 208 sites) (Table 1). Seven fields were excluded from the analyses due to insufficient water and nutrients, as well as damage caused by plant pests and diseases.

Bee survey

Four insect samplings were conducted in each FAP and control field: two during, one before and one after the blooming of the main crop. The sampling in the main crop in both FAP and control fields consisted of walking alongside two transects (width: 4 m, length: 28 m) during 5 min for each transect. All insects foraging on the main crop flowers were collected, when possible, using a sweep net and a vacuum. Bees were first identified to the genus level in the laboratory (Michez et al. 2019), then sent to expert taxonomists for species-level identification. 99% of the specimens were successfully identified to the species level.

Statistical analyses

To address the questions of this study, we explored the visitation data recorded in the main crops in FAP and control fields (i.e. the addition of the occurrence records of the two tran-

Table 1 The crop trials conducted in 2018 and 2019 across the four study regions (i.e., Settat, Kenitra, Sefrou and Errachidia). Each crop trial represents a single crop, year, and region. The numbers indicate the number of FAP (75% main crop and 25% marketable habitat plants) and control fields (monoculture of the main crop) used for each crop trial. The total number of fields per year and crop is indicated in the row “Total” and the number of fields that were considered in the analyses after filtering out the fields with low sampling coverage (SC<0.60) are indicated in the row “Total (SC>0.6)”. The initial number of selected fields per crop trial is eight fields. Yet, some fields were excluded from the analyses, due to the low maintenance. Hyphens show the crop trials that were not carried out

	Zucchini		Pumpkin		Faba bean		Apple		Eggplant		Tomato	
	2018	2019	2018	2019	2018	2019	2018	2019	2018	2019	2018	2019
Settat	8	8	7	8	7	-	-	-	8	8	-	-
Kenitra	8	8	-	8	8	8	-	-	8	8	8	8
Sefrou	7	8	8	8	7	8	4	4	-	-	-	-
Errachidia	5	-	-	8	-	8	-	-	-	-	-	-
Total	52		47		46		8		32		16	
Total (SC>0,60)	48		44		37		7		24		13	

sects conducted in the 75% zone). The visitation data of the two insect samplings were grouped by field.

Two response variables were used: wild bee abundance and wild bee species richness. The abundance represents the total number of wild bee individuals collected in each field across the four insect samplings (i.e. FAP or control field) and the species richness indicates the number of distinct species per field across the four insect samplings. For each response variable, we ran separate Generalised Linear Mixed Models (GLMMs). The crop (i.e. pumpkin, zucchini, faba bean, eggplant, tomato and apple), field treatment (i.e. FAP and control) and honey bee abundance were included as interaction effects. The region (i.e. Settat, Errachidia, Kenitra and Sefrou) was used as a random factor. The year (i.e. 2018 and 2019) was included in the model as a fixed factor, due to the low factor levels (Bates et al. 2015) and to account for the inter-annual variations.

The models were fitted with a negative binomial distribution using the function "glmmTMB" from the glmmTMB package (Bates et al. 2015). Model fit and overdispersion were assessed through diagnostic tests of model residuals in the DHARMa package (Hartig 2019). To ensure representative samples, we checked the sample coverage with the function "iNEXT" from the package iNEXT (Hsieh et al. 2016). Fields with a sampling coverage (i.e., the proportion of the bee community that is effectively covered by the sampling effort) lower than 60% were excluded from the analysis (Chao et al. 2020) (Online Resource 2). This threshold was established to minimise the presence of outliers while ensuring that we do not lose significant amounts of data.

Results

In total 15,398 individuals of wild and honey bees were considered in this study. The wild bees belong to 106 identified species (Table 2, Online Resource 3). Honey bee represented 93% of the total bee abundance, and wild bees 7% (Fig. 2). In 2018, 311 wild bees (from 64 species) and 6,118 honey bees were recorded. In 2019, wild bees accounted for 721 individuals (from 78 species), while honey bees totaled 8,248 individuals. Honey bee was by far the most abundant species in all crops, except tomato (38.5%): 96.3% in pumpkin, 93.6% in zucchini, 94.6% in apple, 82.2% in eggplant and 74.2% in faba bean (Fig. 2). The abundance of wild bees varied widely between the six crops: the highest abundance was recorded in tomato (61.5%), followed by faba bean (25.8%), eggplant (17.8%), zucchini (6.4%), apple (5.4%) and pumpkin (3.7%) (Fig. 2). The six bee families were recorded in this study. Halictidae was the most dominant family, comprising 483 individuals from two genera (*Halictus* and *Lasioglossum*) and 22 species. This was followed by Apidae, with 234 individuals representing eight genera and 29 species, with *Xylocopa* being the most abundant genus. Andrenidae was the third most abundant family, with 132 individuals from two genera (*Andrena* and *Panurgus*) and 25 species. Colletidae, Megachilidae, and Melittidae exhibited lower abundances and species richness (Table 2).

Effect of honey bee on wild bees

Overall, our results did not show any consistent effect of honey bee abundance on wild bee abundance (GLMM, p-value = 0.64; Table 3) and species richness (GLMM, p-value = 0.89;

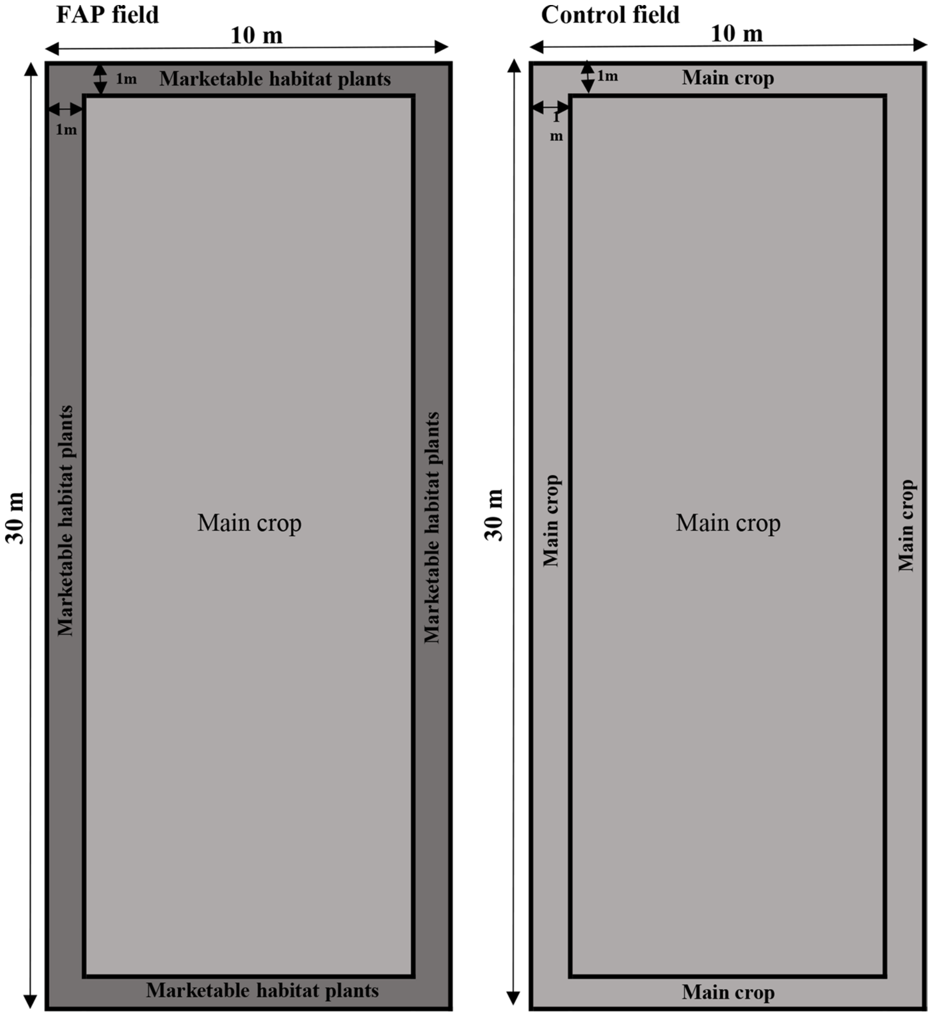

Fig. 1 Experimental designs of FAP and control fields. (a) The main crop in FAP field occupies 75% of the field area and marketable habitat plants cover the surrounding zone (i.e., 25% of the field area). (b) Control field is a monoculture of the main crop

Table 3). Considering the crops separately, neither the wild bee abundance (Fig. 3) nor the wild bee richness (Fig. 4) were influenced by honey bee abundance (Table 3). The effect of honey bee on wild bee abundance and richness did not vary significantly between monoculture fields and fields with marketable habitat plants (Table 3).

Table 2 The abundance (number of individuals) and species richness (number of species) of wild bees recorded in the main crop of the 27 crop trials per genus

Family	Genus	Abundance	Species richness
Andrenidae	*Andrena*	125	25
	Panurgus	7	3
Apidae	*Xylocopa*	126	1
	Eucera	40	10
	Amegilla	24	4
	Bombus	17	1
	Anthophora	13	8
	Ceratina	12	3
	Ammobates	1	1
	Schmiedeknechtia	1	1
Colletidae	*Hylaeus*	12	7
	Colletes	7	3
Halictidae	*Lasioglossum*	483	22
	Halictus	95	2
	Nomioides	43	2
	Seladonia	8	2
	Ceylalictus	5	1
	Nomiapis	2	1
	Vestitohalictus	2	1
Megachilidae	*Osmia*	3	2
	Heriades	2	2
	Rhodanthidium	2	2
	Lithurgus	1	1
Melittidae	*Dasypoda*	1	1

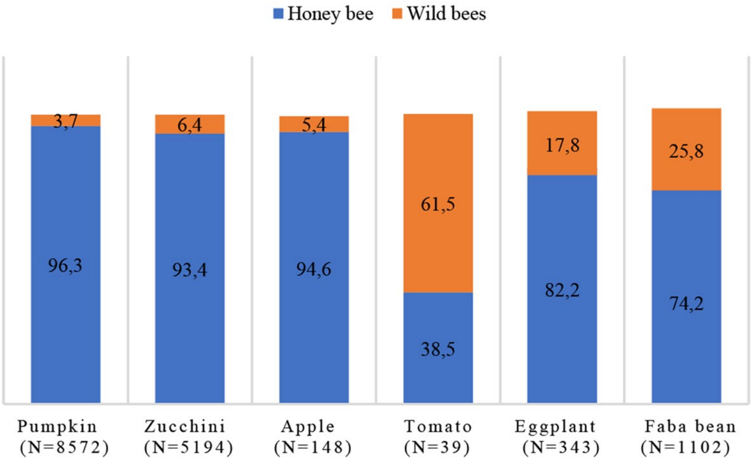

Fig. 2 The proportion of the overall abundance of wild bees and honey bee in each main crop. The numbers between brackets indicate the total abundance of wild and honey bees

Table 3 Generalised linear mixed effect models assessing the impact of honey bee abundance and its interactions with the main crop (i.e., eggplant, faba bean, pumpkin, zucchini, tomato and apple) and the field treatment (i.e., FAP and control) on wild bee abundance and richness. The table shows the explanatory variables, the interaction effects and the models outputs (i.e., estimates, standard errors, z-value and p-values)

GlmmTMB (Wild bee abundance~(Honey bee abundance*Field treatment)+(Honey bee abundance*Main Crop) + Year+(1|Region), family = nbinom2(), data)

Predictor variable/ Interaction factor	Estimate	Standard error	Z-value	*P*-value
Honey bee abundance	-1.50*10−2	3.22*10−2	-0.47	0.64
Honey bee abundance *Field treatment	4.64*10−4	1.28*10−3	0.36	0.72
Year	6.67*10−1	1.82*10−1	3.17	2.05*10−4
Honey bee abundance*Eggplant	5.68*10−2	3.6*10−2	1.60	0.11
Honey bee abundance*Faba bean	5.05*10−3	3.31*10−2	0.15	0.88
Honey bee abundance*Pumpkin	1.34*10−2	3.22*10−2	0.42	0.68
Honey bee abundance*Tomato	-5.37*10−2	0.16	-0.33	0.74
Honey bee abundance*Zucchini	1.70*10−2	3.21*10−2	0.53	0.6

GlmmTMB (Wild bee richness~ (Honey bee abundance*Field treatment)+(Honey bee abundance*Main Crop) + Year+(1|Region), family = nbinom2(), data)

Predictor variable/ Interaction factor	**Estimate**	**Standard error**	**Z-value**	**P-value**
Honey bee abundance	4.17*10−3	2.99*10−2	-0.14	0.89
Honey bee abundance*Field treatment	9.25*10−4	9.84*10−4	-0.94	0.35
Year	2.68*10−1	8.22*10−1	1.48	6.58*10−2
Honey bee abundance*Eggplant	3.30*10−2	3.34*10−2	0.99	0.32
Honey bee abundance*Faba bean	-3.27*10−3	3.04*10−2	-0.11	0.91
Honey bee abundance*Pumpkin	3.71*10−3	2.99*10−2	0.12	0.90
Honey bee abundance*Tomato	-3.11*10−2	0.13	-0.23	0.82
Honey bee abundance*Zucchini	7.11*10−3	2.99*10−2	0.24	0.81

Discussion

Effect of honey bee on wild bee abundance and richness

In line with what we predicted, we did not observe any negative correlation between honey bee and wild bee abundance and species richness. These findings support previous studies reporting a neutral effect of honey bee on wild bees in agricultural systems (Steffan-Dewen-

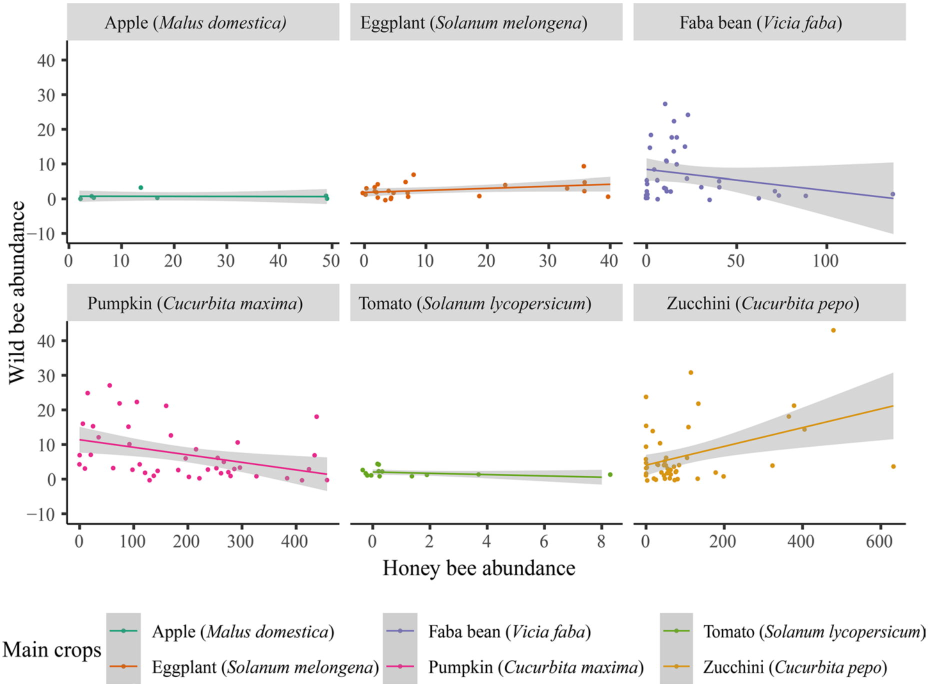

Fig. 3 Linear regressions of wild bee abundance against honey bee abundance in **a**) apple, **b**) eggplant, **c**) faba bean, **d**) pumpkin, **e**) tomato and **f**) zucchini

ter and Tscharntke 2000), natural systems (Goras et al. 2016) and urban areas (McCune 2020). Closely related species with niche overlap tend to compete to ensure coexistence (Woodcock et al. 2019). This is likely the case for bees sharing similar niches and competing for similar resources, mainly nectar and pollen. However, this classical definition predicts a potential competition between two species, but does not necessarily equate competition. Indeed, competition to occur between two species, requires in addition to niche overlap, the incapacity of one or both species to acquire enough resources (Paini 2004). This suggests that the neutral effect of honey bee on wild bees is either associated with the absence of niche overlap between wild and honey bees or the availability of food sources. Here we suggest in the context of our study five potential explanations for the neutral effect of honey bee on wild bee abundance and richness. First, the effect of honey bee might be mediated by the availability of floral resources. On the one hand, Morocco hosts diverse and abundant flowering plants (Goras et al. 2016; Valdès et al. 2002). Hence, the floral resources may have been sufficient to provision both wild and honey bees, and alleviate any possible competition. On the second hand, the Moroccan agricultural landscapes are characterised by a high heterogeneity. This heterogeneity is driven by the high proportion of small farms, the crop diversification, the high diversity of native flowering plants (Vadès et al. 2002; Sentil et al. 2022b) and the limited use of chemicals (Wanner and Tubiello 2022). Second, apiculture is widespread in the Mediterranean region where honey bee has been managed for thousands of years (Crane 1990). The co-evolution of honey bee with wild bees over time has probably resulted in niche partitioning, and thus reduced competition (Tautz 2008). Third, the effect

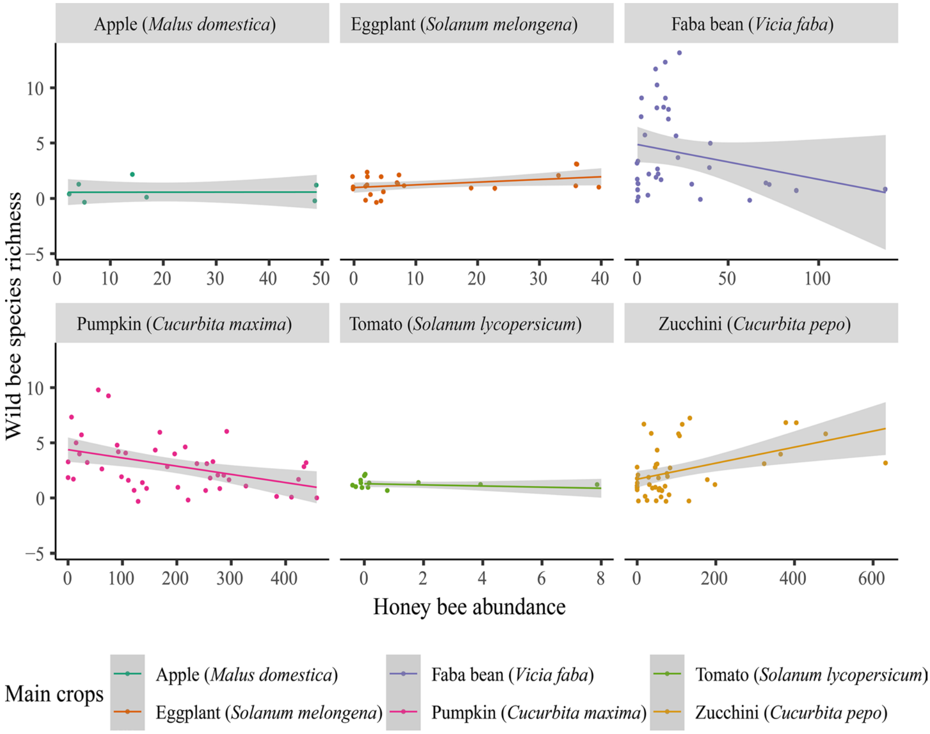

Fig. 4 Linear regressions of wild bee species richness against honey bee abundance in **a**) apple, **b**) eggplant, **c**) faba bean, **d**) pumpkin, **e**) tomato and **f**) zucchini

of honey bee on wild bees might be shaped by the field size. Small fields, usually harbor less bee diversity (Inners and Earns 2012), as they do not encompass all the necessary resources for wild bees. For instance, Macinnis et al. (2023) has demonstrated a pronounced negative effect of honey bee on wild bees in larger fields compared to smaller ones. This, could also explain the contrasting results of our findings compared to Weekers et al. (2022) who used predominantly data from large orchards, whereas our data is derived from smaller fields (i.e. 300 m²). Fourth, the neutral effect of honey bee on wild bees might be associated with the abundance of honey bee that was probably not high enough to induce a negative effect on wild bee abundance and richness. In fact, areas where honey bee density is low can allow coexistence between honey bee and wild bees. For instance, a neutral effect of honey bee on wild bees was observed when using 0.32–1hive/km2 (Mccune et al. 2020), whereas a significant negative effect was demonstrated in areas with higher honey bee density (6.5–9.5 hives/km2) (Alton and Ratnieks 2016; Ropars et al. 2020). This suggests that the effect of honey bee on wild bees did not reach a statistical significance due to the low or intermediate honey bee abundance in our fields or the low sampling effort in each crop trial (20 min). However, given the high relative abundance of honey bee reported in the main crops, with the exception of tomato it is unlikely that the neutral effect of honey bees on wild bees stems from low abundance. Further investigations with increased sampling effort are needed to better understand the impact of honey bee abundance on wild bees.

Due to greater niche overlap, some bee taxa might be more susceptible to competition with honey bee (Ropars et al. 2020; Prendergast et al. 2021), and thus evaluating the impact of honey bee on the entire wild bee community could potentially weaken or mask this effect. This hypothesis is supported by the research of Macinnis et al. (2023), which showed a neutral effect of honey bee on wild bees when considering the entire dataset, while significant effects were identified at the species level. It was not possible to test this hypothesis using our data, due to the low sampling effort (20 min per field per year), which does not support data division. This division reduced the power of the models, and led to inconclusive results (i.e., p-value = “NA”).

Effect of honey bee on wild bees between the main crops

Considering each crop separately, the effect of honey bee on wild bee abundance and richness remained non-significant. Pumpkin, zucchini and apple provide high amounts of nectar and pollen, and display accessible flowers (Pardo and Borges 2020; Paola Mazzei et al. 2021). These crops are associated to a wide array of wild bee species (e.g. El Abdouni et al. 2022). Though eggplant and tomato provide showy open flowers, these crops lack nectar and the poricidal opening of their anthers allow access to buzz pollinators and discourage generalist non-buzzing pollinator species (Cooley and Vallejo-Marín 2021). This aligns with our finding, as most of visits to tomato and eggplant were made by *Xylocopa pubescens* and *Amegilla quadrifaciata*, both of which are buzz pollinators (Online resource 3). In contrast, faba bean has deep curved corolla that allows mainly species with long tongue to access the floral resources (Sentil et al. 2021). In light of these, we should expect a pronounced impact of honey bee on wild bees in pumpkin, zucchini and apple, due to a potential niche overlap between the diverse species they attract compared to other crops. Yet, in the previous revisions, the reviewers asked us to align the third hypothesis with the two first hypoheses. We did so, but we forgot to adjust this part of the discussion to align with the new hypothesis (i.e., the impact of honey bee on wild bees will not differe between crops). Honey bee is a supergeneralist species. It forages on more than 100 plant families (Michez et al. 2019), including the six studied crops. Honey bee was by far the most dominant species in all the main crops (i.e. its proportion varied between 96–70%), except tomato (38.5%). Consequently, the consistent high abundance of honey bee in all crops may explain the lack of disparities in the results between the main crops. The absence of variations in wild bee abundance and richness in response to honey bee across crops might be also related to the availability of floral resources in the surrounding landscapes (Sentil et al. 2022b) and/or the moderate abundance of honey bee. However, we cannot confirm the latest hypothesis, due to the unknown bee hive densities in our sites, the inability to convert the honey bee observation data into hive density, and the absence of references regarding the threshold of bee hive density beyond which competition occurs.

Influence of multi-cropping on the effect of honey bee on wild bee abundance and richness

The availability of diverse flowering plants offers a broad range of morphological, phenological and physiological traits, which ensure niche partitioning and allow coexistence between honey bee and wild bees (Blüthgen et al. 2007). However, in the context of our study, the provision of marketable habitat plants surrounding the main crops did not influence the effect of honey bee on wild bees, contrary to what was previously observed in other European countries (Bommarco et al. 2021; Raderschall et al. 2022). This finding could be driven by the heterogeneity of the Moroccan agricultural landscapes. Indeed, the average farm size in Morocco does not exceed 5 ha, while in Europe the average farm size is up to 16 ha (Eurostat 2019). The small farms in Morocco are characterised by subsistence farming, wherein farmers opt for producing diversified crops, including fruits, vegetables, cereals, and other crops, to meet their own nutritional requirements. Furthermore, Moroccan farmers tolerate the presence of wild plants, as they are partially used to feed their livestock. In such heterogeneous agricultural landscapes, honey bee may not necessarily lead to a decrease in wild bee populations in the absence of habitat plants. Even in simplified agricultural landscapes, such as Settat (Morocco), the native wild flowering plants were found to contribute to the pollen diet of 85% of the wild bees visiting the main crops, whereas the pollen of the introduced marketable habitat plants was recorded in less than 35% of the main crop flower visitors (Sentil et al. 2022a). Considering this evidence, it appears that the current Moroccan agricultural context may allow cohabitation between wild and honey bees without the need of additional floral resources (e.g. marketable habitat plants).

Conclusion

Honey bee was not found to affect the overall wild bee abundance and richness. The introduction of marketable habitat plants did not shape the interaction between wild and honey bees. Several factors may potentially modulate the effect of honey bee on wild bees. These factors might include the landscape context, the availability of the floral resources, the abundance of honey bee, the season and the metrics employed. We confirm that the response of wild bees to honey bee is context-dependent and difficult to predict and generalise. Thus, comprehensive evaluations of the factors influencing bee population dynamics and interactions (e.g. the landscape context, the availability of the floral resources, honey bee density) are necessary to gain a better understanding of what shapes the interaction between wild and honey bees.

Supplementary Information The online version contains supplementary material available at https://doi.org/10.1007/s10531-024-02972-0.

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Author contributions A.S. wrote the original draft, prepared figures and conceptualized the manuscript, A.S. and W.F. conducted the statistical analyses. All authors reviewed and edited the manuscript.

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Data availability No datasets were generated or analysed during the current study.

Declarations

Competing interests The authors declare no competing interests.

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