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Towards integrated pollination management in Spanish almond orchards

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Abstract – Almond trees are economically important and cultivated across the Mediterranean subtropics. The pollinators of almonds are nearly unknown in Europe. We analysed the species composition of bees visiting flowers of almond trees in twelve almond orchards in three regions near Lleida, Spain. The European honeybee was the most abundant among the 14 bee species found, followed by the European orchard bee; native bees composed 10% of all observed pollinators. In orchards where European orchard bees were kept in nesting blocks, they were the most abundant pollinators, outnumbering European honeybees. When comparing the species visiting almond flowers and other flowers in almond orchards, the managed bumblebees and European orchard bees were present on the almond flowers only and several wild bees (e.g., *Andrena florentina*, *Andrena nigroaenea*), too. The European honey bee can be used to pollinate almonds as it visits the blossoms abundantly, and two alternative managed pollinators (*Osmia cornuta* and *Bombus terrestris*) are also attracted to almond blossoms and could also be used to secure pollination of almonds. Certain native bees can occur abundantly on the almond blossoms and could be managed via habitat creation to secure further pollination, while other wild bees that do not visit the almond blossoms are still benefiting from the flowering vegetation in and around the orchards, as this vegetation supports biodiversity conservation.

Apis mellifera / European honeybee / *Osmia cornuta* / native bees / pollinators / Spain / near-natural patches

1. INTRODUCTION

Many crop species depend on insects or other invertebrates, which transfer pollen among the flowers (Klein et al. 2007, 2012; Garibaldi et al. 2013). These vectors, known as pollinators, are insects of many groups, of which bees, flies, beetles, butterflies and moths are considered the most important (Klein et al. 2007). The European honeybee (*Apis mellifera* L.) stands first among all pollinators because of its polylecty (no specialization on plants visited), greater visitation

and large numbers of individuals living in eusocial populations (Abrol 2011; Breeze et al. 2011; Partap 2011; Reilly et al. 2020; Stanley et al. 2020). Not all crops are pollinated by European honeybees, and quite frequently, other insects also play a critical role in pollinating specific crop species. Currently, the pollination by multiple insect species or groups is known as the integrated pollination concept (ICP), and native bees and other insects are much more used as pollinators and put under conservation practices to stabilise their populations in orchards and surrounding landscapes (Garibaldi et al. 2013; Dainese et al. 2019; Bogusch et al. 2020; Lundin et al. 2021). Studies on apple trees and other fruit trees have shown that native bees, both solitary

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and social, play a key role in pollination and are more effective pollinators than European honeybees (Free 1964; Brittain et al. 2013; Blitzer et al. 2016). The nesting of several solitary bee species can be supported simply by provisioning nesting blocks (Seidelmann et al. 2016; Eeraerts et al. 2022). Thus, four species of mason bees of the genus *Osmia* are frequently kept as pollinators of fruit trees (Bosch 1994; Artz et al. 2013). Several related species (*Megachile rotundata* (F.) the most) are similarly exploited to pollinate alfalfa (Pitts-Singer and Bosch 2010; Pitts-Singer and Cane 2011). However, most recent studies have come to the main conclusion that one pollinator species is insufficient (most of them reviewed by Isaacs et al. 2017). These studies have suggested that the best way to produce good-quality crops of fruit, vegetables and other plants important for humans is to use the primary pollinator, i.e. the European honeybee, in combination with conservation measures that protect the surrounding landscape from increasing the diversity of native pollinators (Saunders et al. 2013; Isaacs et al. 2017; Alomar et al. 2018; Bogusch et al. 2020).

Almond trees (*Prunus dulcis* L.) are usually pollinated by multiple species of bees. Several species of hoverflies and other dipterans have also been observed visiting their flowers (Mandelik and Roll 2009; Klein et al. 2012; Norfolk et al. 2016; Alomar et al. 2018). Although the almond is one of the most important nut trees planted in South Europe, North Africa and the Middle East, there have been only a few published studies on the pollinators of almond orchards. Most authors have focused on European honeybees (Morse and Calderone 2000; Degrandi-Hoffman et al. 2019; Goodrich 2019), but the European orchard bee *Osmia cornuta* Latr. (Torchio et al. 1987; Bosch 1994; Bosch and Blas 1994), its relative *Osmia lignaria* Say (Artz et al. 2013) and the bumblebee *Bombus terrestris* L. (Dag et al. 2006) have also been studied as useful pollinators of almond orchards. Klein et al. (2012) and Alomar et al. (2018) have confirmed the role of native pollinators in the efficient pollination of almond trees. Saunders et al. (2013), Brittain et al. (2013), Norfolk et al. (2016) and several others have discussed the role of native bees and their

habitat demands for almond pollination, while the native pollinators can complement European honeybees in different ways such as filling in spatial and weather-dependent niches and interact with European honeybees to force them switching more often between compatible tree varieties (Brittain et al. 2013). However, most of these studies cannot answer the central questions of every orchard owner, what the primary pollinators are and whether the native bees are essential for pollinating almond trees, similar to European honeybees and other managed bee species.

During our studies of bees in almond orchards in northeastern Spain, we sampled bees and other insects visiting almond flowers only on flowering trees in their main flowering season and compared the species communities of almond pollinators with other native bees occurring in the orchards. The main goal was to find out which species of bees visit the flowers of almonds, if native bees are important in almond pollination and which part of native bee fauna is important in the IPM of almonds. We also checked for the effects of mason bee nesting blocks and native bees, but the study was not designed to differentiate between the orchards with and without nesting blocks in each of the three examined habitats. Last, we studied if bees were more diverse and abundant in orchards in dry regions and orchards in wet regions (both irrigated and not irrigated).

2. MATERIALS AND METHODS

2.1. Study set-up

The study was performed near Lleida in northeastern Spain in 12 almond orchards in 2019 (Table 1; Figure S1), which were categorized into three groups according to location and irrigation. Four orchards were located in the river floodplain and were not irrigated. Four other orchards were located in a semihumid area in the river floodplain and were irrigated. The remaining four orchards were located in a dry hilly region several kilometres from the river floodplain and were not irrigated. Photos in Figure S2 illustrate the character of the landscape around

Table I List of the localities with specified variables

Locality code	GPS (°N, °E)	Area (ha)	Water management	Bee hives	Mason bee no. of blocks	Bumblebee hives	Almond cultivars	Soil bedrock	Altitude (m a.s.l.)	Area NNH (m ²)	Vegetation	Shape
R2	41.527240, 0.830040	4.1	Wet	0	0	2	Vairo, Constantí	Overburden	274	14,324	Ruderal	Linear
R5	41.545249, 0.868950	6.7	Wet	0	0	0	Vairo	Overburden	267	3518	Ruderal	Linear
R8	41.524514, 0.850238	3.6	Wet	0	0	0	Vairo, Constantí, Tarraco, Belona, Soleta	Overburden	276	6937	Ruderal	Linear
R29	41.514432, 0.777764	1.7	Wet	0	3	0	Vairo, Constantí, Tarraco, Belona, Soleta	Limestone	264	2905	Near-natural	Non-linear
RL62	41.612270, 0.717278	4	Irrigated	0	0	0	Vairo	Limestone	195	45,896	Near-natural	Non-linear
RL63	41.602552, 0.779964	11.2	Irrigated	33	0	0	Vairo	Sandstone	234	6800	Ruderal	Linear
RL65	41.612180, 0.929008	2.3	Irrigated	0	0	0	Vairo	Sandstone	274	1427	Ruderal	Linear
RL68	41.609812, 0.850119	4.7	Irrigated	0	0	1	Vairo	Limestone	282	18,908	Near-natural	Non-linear
S35	41.515268, 0.660402	1.8	Dry	0	6	1	Desmayo Ilargueta	Limestone	208	37,948	Near-natural	Non-linear
S28	41.497948, 0.685318	4	Dry	0	0	0	Cristomorto	Limestone	278	6238	Near-natural	Linear
S33	41.485608, 0.756119	5.3	Dry	0	0	0	Cristomorto	Limestone	348	29,415	Near-natural	Non-linear

Table I (continued)

Locality code	GPS (°N, °E)	Area (ha)	Water management	Bee hives	Mason bee no. of blocks	Bumblebee hives	Almond cultivars	Soil bedrock	Altitude (m a.s.l.)	Area NNH (m ²)	Vegetation	Shape
S7	41.519444, 0.942408	2.5	Dry	0	5	2	Cristomorto	Limestone	329	18,869	Near-natural	Non-linear

Vegetation is divided into near-natural (usually steppic and shrubby vegetation) and ruderal (ruderal vegetation). Shape is usually linear on the one side of the orchard, when non-linear, then it forms a kind of a polygon at the orchard NNH near-natural habitat

the orchards. In four orchards (one in a wet area and two in a dry area), nesting blocks for European orchard bees were installed. In one orchard in a wet area, 33 European honeybee hives were present. In four orchards (one in wet, one in irrigated and one in a dry area), bumblebee hives for *B. terrestris* were installed. The nesting blocks for mason bees were 60 cm high, 40 cm wide and 20 cm deep and consisted of a wooden frame filled with paper tubes of 9 mm diameter. There were approximately 2000 tubes per nest. Two hives for bumblebees were placed in each orchard. There were standard Tripol hives from the company Koppert, settled only by the queen and maximally 20 workers at this time. The sites of orchards were of intermediate to large area (1.7 to 11.2 ha, mean 4.3 ± 0.8 ha). In total, eight almond cultivars were present in studied orchards. Different cultivars were in dry orchards compared to those in the wet region. Orchards in the wet region were surrounded by an agricultural landscape, with orchards comprising 80%, followed by near-natural shrubby vegetation and a small proportion of fields. Irrigated orchards in the wet region were usually surrounded by orchards (90%) and near-natural shrubby vegetation and often with small water reservoirs and/or rivers, streams and water canals. In the dry region, the orchards were surrounded by near-natural shrubby vegetation and a dry hilly landscape (60%), less by other orchards.

At the time of tree flowering (the first half of March), we visited the orchards and captured all insects that were present on the flowers of almond trees. We sampled each orchard once and when the weather allowed the insects to be active (sunny, daily temperature at least 20 °C and only mild wind) and only in the warmest part of the day (between 11 a.m. and 3 p.m.). One person captured the insects for 60 min using an entomological net. We counted all insect individuals that were present on flowers and captured all those that we were unable to identify by observation only. Individual European honeybees, bumblebees (only managed *B. terrestris* were recorded) and other easy-to-identify species were counted and not captured. The method of study was performed by walking through the orchard or a part

of it to avoid capturing and observing the same individuals. For comparison, we also kept 60 min collecting other bees in the orchard that were present on flowers of herbs, shrubs and other tree species (if present). We did all captures in 6 days when the weather was very similar to avoid the weather influence on the results.

All captured individuals were put immediately into a container with 75% alcohol and identified to species in the laboratory. Most of the collected individuals were identified by the first author and some groups by other specialists (see the “[Acknowledgements](#)” section). Other insects for which only a sole specimen was collected (butterflies, other hymenopterans and hoverflies) were not identified to species and were not included in the study. The collected material is available in the collections of the University of Hradec Králové, Czech Republic. In several orchards, nesting blocks for European orchard bees, bumblebee hives and European honeybee hives were installed. In this case, we marked the number of nesting utilities and included their presence in the evaluations.

2.2. Data analysis

We counted the number of individuals and species of all bee species on almond trees and nearby vegetation. Because of the high domination of European honeybees (*A. mellifera*) and European orchard bees (*Osmia cornuta*) in most orchards, we divided the pollinators into four groups: European honeybees, European orchard bees, bumblebees (represented only by managed populations of *B. terrestris*—this species is non-native in this part of the country) and other native pollinators (most of them were solitary bees). For all four above-specified groups, we used the Chao-1 estimator that was corrected for unseen species to estimate their species richness. We also computed the rarefaction curves based on the log gamma function for computing combinatorial terms (Krebs 1989). The rarefaction procedure consists of selecting a specified number of samples equal to or less than the number

of samples in the smallest sample and then randomly discarding reads from larger samples until the number of remaining samples is equal to this threshold (Willis 2019). To compare the assemblage compositions of the analysed datasets (bees on almond flowers vs. bees on flowers under almond trees), we calculated the Sørensen and Chao-Sørensen-estimated abundance-based similarity indices. We used the Shannon diversity indicator and *t* test to check for differences between the two assemblages. We used one-way permutational multivariate analysis of variance (PERMANOVA), followed by pairwise comparisons, to analyse the differences in the abundance and number of species on the flowers of almonds and other orchard plants among the three orchard types. To perform a one-way PERMANOVA of (a) the abundance of honeybees, mason bees and native bee species and the total number of bee species on the flowers of almonds and (b) the abundance of bee species and the total number of bee species on the other orchard plants, we used the Gower distance measure and the number of calculated permutations was 9999, followed by pairwise comparisons. PERMANOVAs were accompanied by plots resulting from non-metric multidimensional scaling (NMDS) analyses using the Gower similarity measure, disclosing also the Shepard plot and testing for stress value and disclosing R^2 values for axis 1 and axis 2. We calculated Spearman correlation coefficients to analyse the associations between the explanatory variables and individual taxa or their groups. We used the Mann-Whitney rank-sum test to analyse the differences in the numbers of mason bee individuals found in the presence and absence of mason bee nesting blocks inside the orchard; these data did not have a normal distribution (Shapiro-Wilk test, $p < 0.05$). We used one-way ANOVA to analyse the differences in the number of species among the three groups of orchards. We performed all calculations in SigmaPlot 12.0 (ANOVA, Mann-Whitney rank-sum test, Shapiro-Wilk test and Spearman correlation coefficients), EstimateS 9.1.0 (Sørensen and Chao-Sørensen-estimated abundance-based similarity indices) and PAST 2.14 and 4.07b

(diversity indices, rarefactions, PERMANOVA and NMDS). Data are shown as the mean \pm SD unless stated otherwise. We used mapy.cz and Google Earth for area measurements and creating maps.

3. RESULTS

3.1. Species compositions on almond flowers vs. other plants

We found 2625 individuals of 14 bee species on the flowers of almonds. European honeybees (*A. mellifera*) were the most abundant, with 1730 individuals comprising 66% of all observed pollinators, which were found at all sites and in seven orchards that had more than 100 individuals. The highest number of European honeybees (450 individuals) was at locality RL63. RL63 is the largest of the study orchards and was in a wet

area; 33 beehives were present in this orchard. The lowest numbers of European honeybees were in orchards that were situated in the dry region (Figure 1).

The European orchard bee had 538 individuals and was the second most abundant species. The number of individuals found in each orchard was higher by over one order of magnitude when mason bee nesting blocks were present inside the orchard (160 ± 56 individuals vs. 6 ± 10 individuals; Mann-Whitney rank-sum test, $T=33.0$, $n_1=3$, $n_2=9$, $p=0.01$). In three orchards where nesting blocks were available, the European orchard bee was the most abundant pollinator (in two orchards, it was more abundant than the European honeybee, and in the third orchard, the numbers of individuals of the European honeybees and European orchard bees were equal (Table S1)). However, the abundance of the European orchard bee found in orchards that lacked nesting blocks was lower by one order

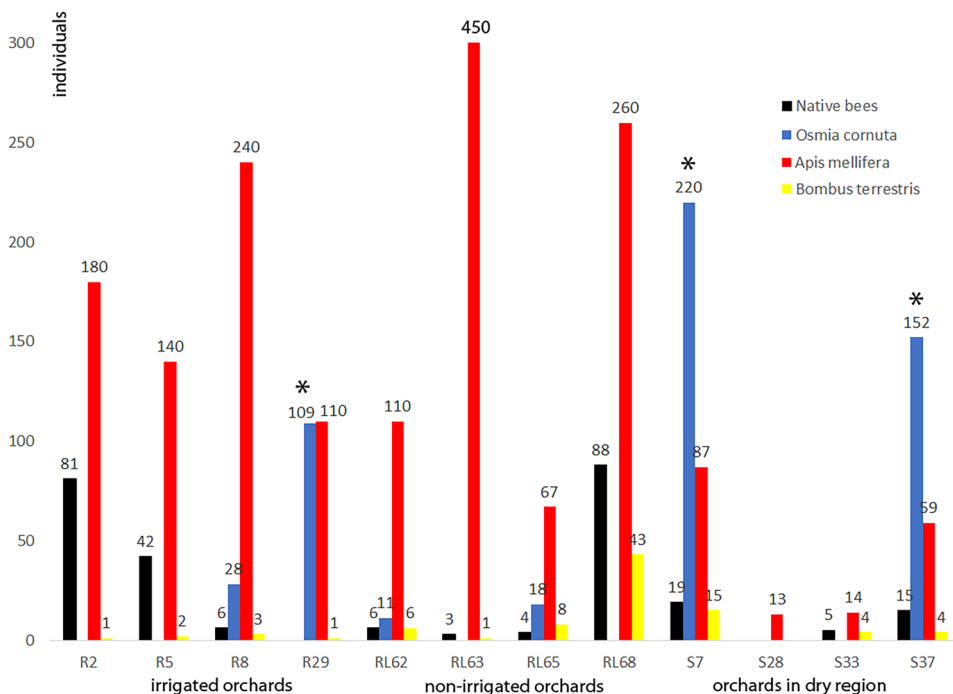


Figure 1. Numbers of individuals of native bees (black column), European orchard bees (blue column), European honeybees (red column) and bumblebees (yellow column) in all studied orchards. Asterisks mark the presence of beehives (RL62) and nesting blocks for European orchard bees (R29, S7 and S37).

of magnitude (0–28 individuals per orchard), or the species was absent altogether (six orchards).

We further found 88 individuals of *B. terrestris*, which belong to the managed populations. Interestingly, bumblebees were found only on almond flowers, not on other plants.

Concerning the native bees (thus excluding *A. mellifera*, *O. cornuta* and *B. terrestris*), we found 269 individuals of 11 species, which thus represented 10% of all pollinators found on almond flowers. The total number of pollinators was highly variable among orchards; therefore, the differences between orchard types were not significant (one-way ANOVA mean squares between groups, 0.58 ($df=2$); residual, 7.97 ($df=9$); $F=0.07$, $p>0.05$). Orchards with only one pollinator species and those with eight to nine species per orchard were present in all three groups of orchard type (Figure 1). One-way PERMANOVA of the abundance of honeybees, mason bees and native bee species and the total number of bee species on the flowers of almonds revealed that there was a trend towards differences among the three analysed orchard types (Gower; permutation $N=9999$, $F=6.17$, $p=0.0004$). The pairwise comparisons revealed significant differences between wet and dry orchards ($F=9.1$; $p=0.03$), between irrigated and dry orchards ($F=5.7$; $p=0.03$) and between wet and irrigated orchards ($F=3.2$; $p=0.03$).

Species collected from non-crop flowers totalled 852 individuals of 41 species, of which 495 individuals of 40 species represented native bees and 357 individuals represented European honeybees. The other two managed species, *B. terrestris* and *O. cornuta*, were lacking in the other flowers within almond orchards. Most native bee species were found in fewer than 10 individuals (23 species), while only a few comprised higher tens of individuals: *Eucera nigrilabris* Lep. with 70 individuals in nine orchards, *Rhodanthidium sticticum* (F.) with 59 individuals in five orchards and *Lasioglossum mediterraneum* (Blüthgen) with 46 individuals across six orchards (Table S2).

The assemblages of bees present at almond flowers and other flowers differed significantly from one another (Shannon diversity t test:

$t=-22.441$, $df=1226.2$, $p<0.001$). When comparing the species visiting almond flowers and other flowers in almond orchards, the managed bumblebees and European orchard bees were present at the almond flowers only. The honeybees visited both, almond flowers ($n=1730$) and other flowers ($n=357$), but were much more abundant at the almond flowers compared to the other flowers. In contrast, the native bees visited mostly the other flowers ($n=495$), but some of the native bee species were also abundantly present at almond flowers ($n=269$). Interestingly, some *Andrena* spp. were found nearly exclusively at almond flowers; these included *Andrena nigroaenea* (58 individuals vs. 5 individuals) and *Andrena trimmerana* (26 individuals vs. 1 individual). The bees of the genus *Eucera* were also abundant at almond flowers, but they did not show a preference for almond flowers over other flowers (*Eucera nigrescens*, 18 individuals at almond flowers vs. 13 individuals at other flowers, and *Eucera nigrilabris*, 34 individuals vs. 70 individuals) (see Tables S1 and S2 for more details). Rarefaction curves (Figure S3) showed that the observed number of pollinator species on almond flowers was nearly complete (15), contrary to species found at other orchard plants, at which the total number of bee species was certainly slightly higher than what was observed. The Chao-1 estimator indicated the presence of an additional four to five bee species at other orchard plants, contrary to the dataset of almond pollinators, which was probably complete (Table II). The Sørensen similarity index value was 0.37, indicating some similarity among the bee assemblages in both datasets, and most of the species found on almond flowers (10 of 13; 77%) were found on other plants in the orchard. There were trends towards a higher abundance of native bees in orchards with higher numbers of European honeybees, while the abundance of native bees and European orchard bees displayed a mutually opposite trend. The European orchard bees showed a trend towards a higher abundance in orchards with fewer European honeybees. However, the study was underpowered to address these differences ($n=12$ orchards); therefore, the above trends were not significant (Pearson

Table II Species composition, species richness and diversity of bees visiting almond flowers and other flowers in the study orchards

Variable	Almond flowers	Other flowers
Number of species	14	41
Number of individuals	2625	852
Chao-1 \pm SD	15 \pm 0.3	48.5 \pm 4.4
Sørensen similarity index	0.36	

The selected species richness and diversity indices are indicated

correlation coefficients: $r = 0.254$, -0.208 and -0.279 , respectively; $p > 0.05$ for each).

The support for non-native pollinators was effective. The abundance of managed pollinators was higher in orchards with managed bee nests/hives. The examined sampling sites included one orchard with bee hives present. At this site, the abundance of bees on almond flowers ($n = 450$) was higher relative to any other orchard (mean 116 ± 79 individuals; range 13–260 individuals). Similarly, in the three orchards with nesting support for European orchard bees, their abundance at almond flowers was higher (160 ± 46 individuals; range 109–220 individuals) compared to that in the other orchards (6 ± 10 individuals; range 0–28). The effects of bumblebee hives were less prominent. There were four orchards with nesting support for bumblebees; two of these orchards were associated with a high abundance of *B. terrestris* at almond flowers ($n = 43$ and $n = 15$), whereas the other two orchards did not have high *B. terrestris* abundance ($n = 4$ and $n = 1$). The abundance of *B. terrestris* at the other orchards was generally low (3.1 ± 2.6 individuals; range 1–8 individuals).

3.2. Differences in the composition of pollinators among orchards in wet and dry areas and irrigated orchards

We found a similar number of species ($n = 11$; Chao-1 estimates 12 ± 1 and 11 ± 1 , respectively) visiting almond flowers in wet and irrigated

orchards compared to orchards in dry regions, where nine species (Chao-1 estimate 9 ± 0.5) were found (Table III). Rarefaction curves (Figure S4) revealed that this difference was negligible when compensating for differences in sample sizes. The Sørensen similarity indices indicated that there was quite a low similarity among the bee assemblages in the three analysed orchards (0.4–0.6), which correlates with the ecologically different environmental conditions in the three types of orchards.

The abundance of European honeybees on other flowers closely correlated with their abundance on almond flowers (Spearman $\rho = 0.764$; $p = 0.003$; Figure 2). The numbers of native bee species per orchard were highly variable when considering those found on almond flowers, and there were no significant differences between the three orchard types (one-way ANOVA: $F = 0.07$; $p > 0.05$). In contrast, the differences in the number of native bee species per orchard found on other flowers were significant (one-way ANOVA: $F = 4.88$, $p = 0.04$), with the pairwise comparisons significant for wet and dry orchards (Student-Newman-Keuls test: $q = 34.1$, $p = 0.04$) and irrigated and dry orchards (Student-Newman-Keuls test: $q = 23.4$, $p = 0.04$). The higher species richness of native bees was thus associated with orchards situated to dry hilly regions, with the presence of native steppic grass and shrub vegetation that was rich in flowering plants; bare soil patches were also common in these orchards. Note that orchard RL68 was also species-rich despite being located in the wet region, but it possessed pieces of near-natural vegetation with many flowering herbs in its neighbourhood. In contrast, we did not find any bees in orchard RL65, where flowering plants were completely lacking around and inside the orchard, and the orchard environment was useless for bees.

Regarding native bee species observed on other orchard plants, we found more native bee species in dry orchards (30 species; Chao-1 estimate 33 ± 9 species) than in orchards in wet regions (16; Chao-1 estimate 16 ± 6 species) and irrigated orchards (22 species; Chao-1 estimate 30 ± 8 species) (Table III). Rarefaction curves (Figure S4) confirmed this difference. The Sørensen similarity indices indicated a low similarity among the bee assemblages in the three analysed orchard types

Table III Species composition, species richness and diversity of bees visiting almond flowers in analysed orchard types (wet, irrigated and dry)

	Wet orchards	Irrigated orchards	Dry orchards
Almond flowers			
Number of species	11	11	9
Number of individuals	943	1075	607
Chao-1 \pm SD	12 \pm 1	11 \pm 1	9 \pm 0.5
Sørensen similarity index WO-IO	0.60		
Sørensen similarity index WO-DO	0.40		
Sørensen similarity index IO-DO	0.53		
Other flowers			
Number of species	17	23	31
Number of individuals	212	338	302
Chao-1 \pm SD	17 \pm 6	31 \pm 8	34 \pm 9
Sørensen similarity index WO-IO	0.20		
Sørensen similarity index WO-DO	0.20		
Sørensen similarity index IO-DO	0.40		

The selected species diversity indices are indicated. Data are analysed separately for pollinators and other bees in orchards

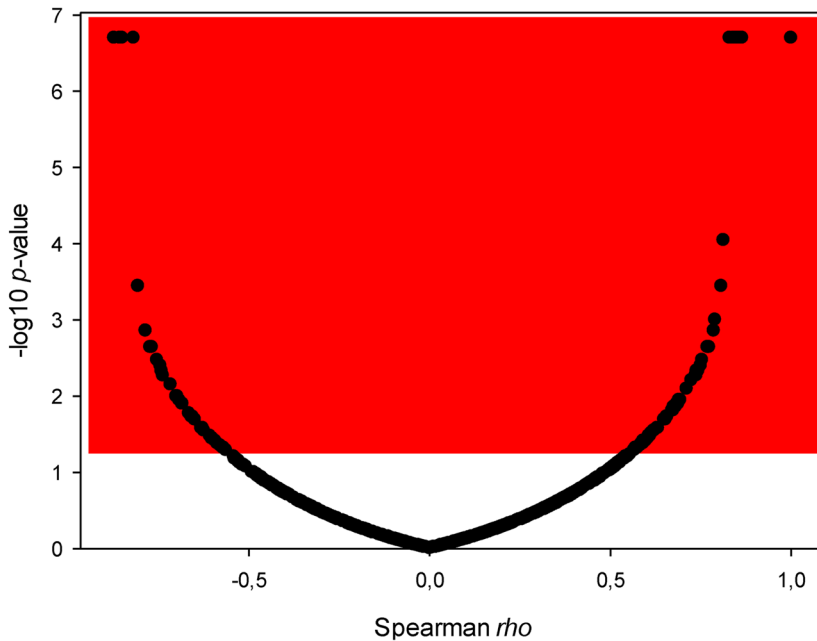
(0.2–0.4) (Table III). The honeybees and mason bees were absent from the other orchard plants. One-way PERMANOVA of the abundance of bee species and the total number of bee species on the other orchard plants revealed that the three analysed orchard types differed from one another (Gower; permutation $N=9999$, $F=2.10$, $p<0.05$). The pairwise comparisons revealed significant differences between wet and dry orchards ($p=0.03$). In contrast, the differences between the irrigated and dry orchards ($p=0.06$) and between the wet and irrigated orchards ($p=0.23$) were not significant. The NMDS plot is provided in Figure 3. The NMDS analysis (using the Gower distance measure) revealed that the wet and dry orchards differed in their characteristics. However, there was some similarity between the irrigated orchards with both dry and wet orchards.

4. DISCUSSION

4.1. Managed bee pollinators of almond trees

Almond trees are visited mainly by European honeybees, which was also the result of

previous studies (Klein et al. 2012; Alomar et al. 2018; Pardo and Borges 2020). Interestingly, European orchard bees can be considered good pollinators, too. Our results showed that the European orchard bees were the most numerous visitors of almond flowers in orchards, where they were kept in nesting blocks with paper tubes, while the abundance of European orchard bees found on almond flowers in the other orchards was lower by 1 order of magnitude. However, these results are hardly comparable with those of previous studies, which were performed in North America, where this species was introduced but does not occur in a large area or dense populations, and the use of European orchard bees for pollination in the USA is limited (Pardo and Borges 2020). Alomar et al. (2018) studied pollinators of almond flowers in Mallorca and did not detect *O. cornuta*. Compared to most native pollinators of fruit trees, *O. cornuta* is polylectic but strongly prefers pollen and nectars from Rosaceae, especially from fruit trees (Bosch and Blas 1994; Westrich 2018). Thus, this bee species, with established protocols for management (Maccagnani et al. 2007), can be considered to



Selected most significant correlations:

Driver variable	Dependent variable	rho	p
Orchard area	<i>Osmia cornuta</i>	-0.873	2E-07
<i>Osmia</i> nesting blocks	<i>Osmia tricornis</i>	0.850	2E-07
Dry orchards	<i>Osmia ferruginea</i>	0.857	2E-07
<i>Osmia</i> nesting blocks	<i>Osmia cornuta</i>	0.813	9.01E-05
Dry orchards	<i>Osmia tricornis</i>	0.807	0.0004
Almond cultivar - Vairo = 1	<i>Apis mellifera</i>	0.769	0.0023
Almond cultivar - Vairo = 1	Other flowers - No. of species of other bees	-0.769	0.0023
Soil - overburden = 1	<i>Andrena bicolorata</i>	0.771	0.0023
Soil - overburden = 1	<i>Lasioglossum mediterraneum</i>	0.771	0.0023
Soil - overburden = 1	<i>Andrena longibarbis</i>	0.771	0.0023
Water management - dry = 1	<i>Apis mellifera</i>	-0.769	0.0023
Water management - dry = 1	Other flowers - No. of species of other bees	0.769	0.0023
Water management - dry = 1	<i>Sphecodes ruficrus</i>	0.773	0.0023
Water management - wet = 1	<i>Lasioglossum mediterraneum</i>	-0.745	0.0040
Water management - dry = 1	<i>Rhodanthidium sticticum</i>	0.742	0.0047
Vicinity - ruderal [%]	Other flowers - No. of species of other bees	-0.717	0.0071
Water management - dry = 1	Other flowers - abundance of pollinator species	0.693	0.011
Water management - dry = 1	Abundance - Native bees	0.693	0.011
Vicinity - near-natural vegetation [%]	Other flowers - No. of species of other bees	0.656	0.019
Vicinity - orchards [%]	<i>Osmia cornuta</i>	-0.650	0.020
Altitude	Other flowers - No. of species of other bees	0.595	0.039
Vicinity - ruderal [%]	Abundance - Native bees	-0.588	0.042
Vicinity - near-natural vegetation [%]	<i>Apis mellifera</i>	-0.579	0.045
Water management - wet = 1	<i>Osmia ferruginea</i>	-0.571	0.048
Water management - wet = 1	<i>Rhodanthidium sticticum</i>	-0.571	0.048
Water management - wet = 1	<i>Sphecodes ruficrus</i>	-0.572	0.048

◀**Figure 2.** Volcano plot of Spearman correlation coefficients calculated between the explanatory variables and individual taxa or their groups. Selected most significant correlations are listed on the bottom of the figure.

be an important pollinator of almonds and probably also of other fruit trees for the future, as was suggested by Torchio et al. (1987), Bosch and Blas (1994), Kratschmer et al. (2020) and many other authors.

4.2. Native bee pollinators of almond trees

Regarding native bees, their role in almond pollination is variable (Vicens and Bosch 2000; Eraerts et al. 2020). In most studies, the proportion of native bees was relatively small, comprising barely 15%. Alomar et al. (2018) described that in Mallorca, most of the trees were pollinated by European honeybees, while solitary bees comprised only 4.5% of all visitors to almond flowers. Reilly et al. (2020) recorded only European honeybees as pollinators of almonds. The proportion of native bees on almond flowers was higher in California, comprising approximately 11% (Klein et al. 2012). This number is close to the proportion of native bees found in our study. However, our results support the fact that this low proportion was partially a result of the high numbers of European honeybees in the landscape, which usually prefer the most abundant source of pollen and nectar. Native bees then visit flowers of other plants inside and around the orchard (Klein et al. 2012; Bogusch et al. 2020) but can substitute for European honeybees when the population of European honeybees rapidly decreases.

4.3. Differences between pollinators of almond trees and apple trees

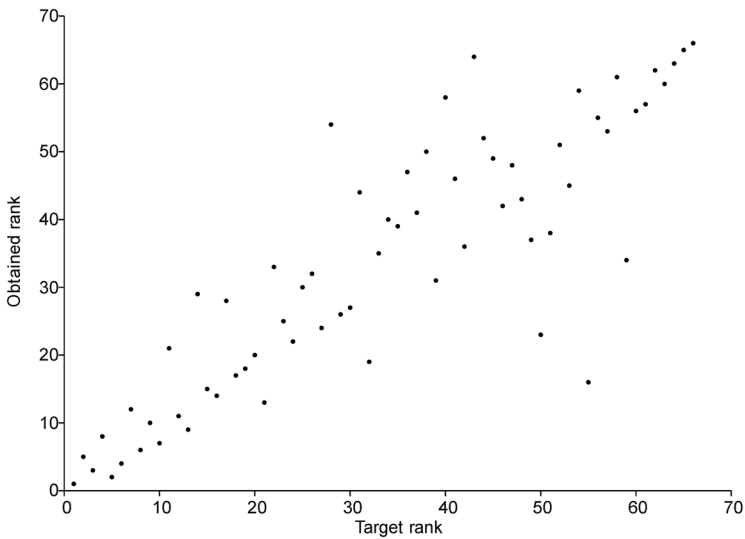
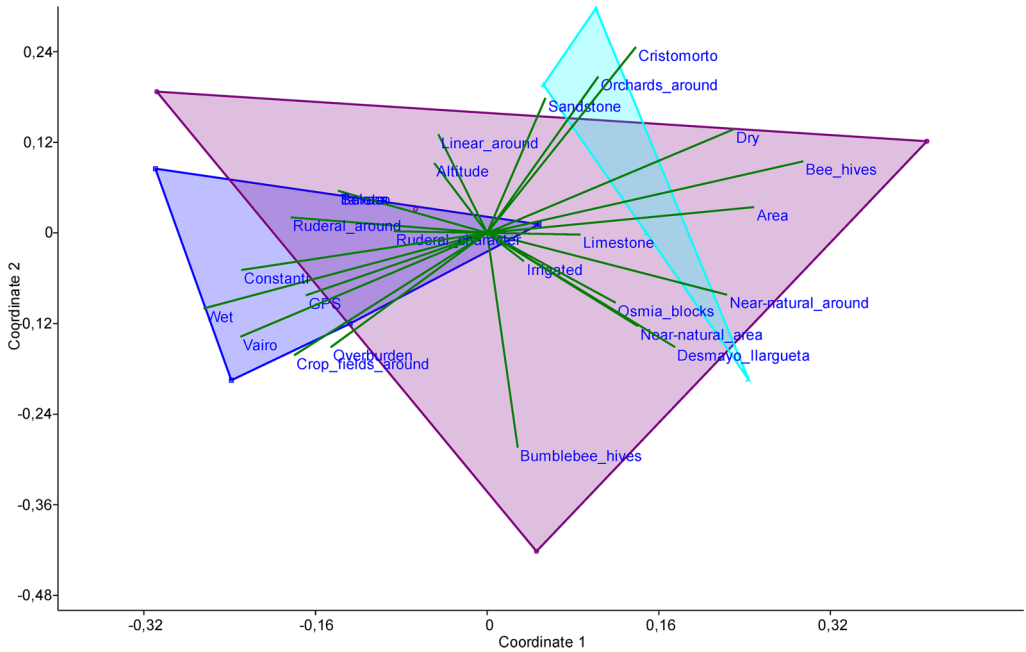
When we compare the species diversity of almond pollinators to those of apple trees in various parts of the world, we can see similar results: European honeybees are dominant pollinators, usually comprising more than 80% of all insects/bees found on flowers, and the proportion of

native bees is usually between 5 and 20% (Botero and Morales 2000; Gardner and Ascher 2006; Garratt et al. 2014, 2023; Földesi et al. 2015; Eraerts et al. 2019; Pardo and Borges 2020; Leclercq et al. 2022). However, the proportions of native pollinators on apple trees differ among orchards, regions and apple varieties, and several authors have reported native bees to be more abundant than European honeybees (Adamson et al. 2012; Campbell et al. 2017a) or found these two groups to be similarly abundant (Blitzer et al. 2016). Campbell et al. (2017b) also reported that bumblebees are the most abundant pollinators of apple trees. However, all these studies were conducted in the USA, where the native bees differ from those of Southern Europe. Recent studies of bees visiting the flowers of apple trees in the Czech Republic reported ratios similar to those of most published studies: European honeybees (67%) were the most abundant species. In comparison, 29 species of native bees represented 29% of all known pollinator species (Leclercq et al. 2022). The genus *Andrena* was the most abundant in both species and individuals, which also corresponds with the results of Gardner and Ascher (2006), Campbell et al. (2017a) and Russo and Danforth (2017). Six of 14 *Andrena* species found in this study pollinated almond flowers. All these species were the most numerous species of the genus and comprised approximately three-fourths of all native pollinators (204 individuals, 76% of all native pollinators).

4.4. Management implications

The combined messages of the present study and previous studies on pollinators in almond orchards are as follows:

1. European honeybee is the main floral visitor and certainly also the pollinator of almond flowers in the continent (as was published by Alomar et al. (2018), Reilly et al. (2020) and many others).
2. European orchard bees should be kept in almond orchards to improve pollination



services. We found that their presence can be managed to sufficiently high quantities, which may even exceed the quantity of honeybees. Furthermore, several authors confirmed that they are more efficient pollina-

tors than European honeybees (Bosch and Blas 1994; Artz et al. 2013).

3. Native bee visitation is variable across orchards and linked to local- and landscape-level factors, and their effects on the pol-

◀**Figure 3.** NMDS plots (Gower similarity measure) of the abundance of honeybees, mason bees and native bee species, and the total number of bee species on the flowers of almond flowers and other flowers compared to the 26 environmental variables. Shepard plot is shown at the bottom of the figure. Stress=0.18, R^2 axis 1=0.37, R^2 axis 2=0.28. Blue, wet orchards; purple, irrigated orchards; turquoise, dry orchards. Points show individual sampling sites; convex hulls indicate sampling sites of the same type. Acronyms of the environmental variables: GPS, longitude ($^{\circ}$ E); Area, orchard area (m^3); Wet, wet orchards=1; Irrigated, irrigated orchards=1; Dry, dry, non-irrigated orchards=1; Bee_hives, the number of bee hives present in the orchard; Osmia_blocks, the number of *Osmia* nesting blocks present in the orchard; Bumblebee_hives, the number of bumblebee hives present in the orchard; Orchards_around, area coverage by orchards in the vicinity of examined orchard (%); Ruderal_around, area coverage by ruderal vegetation in the vicinity of examined orchard (%); Crop_fields_around, area coverage by crop fields in the vicinity of examined orchard (%); Near-natural_around, area coverage by near-natural vegetation in the vicinity of examined orchard (%); Linear_around, vicinity shape (linear=1, non-linear=0); Ruderal_character, overall character of surrounding vegetation type (ruderal=1, near-natural=0); Near-natural_area, area of nearby near-natural habitats (m^2); Altitude, altitude (m a.s.l.); Overburden, soil overburden (=1); Limestone, soil limestone (=1); Sandstone, soil sandstone (=1); Vairo, almond cultivar Vairo (=1); Constanti, almond cultivar Constanti (=1); Tarraco, almond cultivar Tarraco (=1); Belona, almond cultivar Belona (=1); Soleta, almond cultivar Soleta (=1); Desmayo Ilargueta, almond cultivar Desmayo Ilargueta (=1); Cristomorto, almond cultivar Cristomorto (=1).

ination of fruit trees are underestimated; several authors discussed they can be even higher than those of European honeybees (Mallinger and Gratton 2015; Russo and Danforth 2017). Although they are effective, their abundance is usually limited by the high abundance of European honeybees (the comprehensive study of the negative effect of the European honeybee on native species of bees was recently published by Rasmussen et al. 2021). Here, we found that native bee pollinators comprised only 10% of the total bee pollinators found at almond flowers. However, this means that native bees have the potential to secure the pollina-

tion of almond flowers when the support for non-native pollinators is lacking.

4. The near-natural characteristic of the orchard understory and the environment go hand-in-hand with the diversity and efficiency of native pollinators and significantly improve the pollination rate of fruit trees (García and Miñarro 2014; Campbell et al. 2017a, b; Bogusch et al. 2020). Here, we found that the abundance and diversity of native bees are highly variable, reflecting the available nesting and feeding habitats within and around the orchards.

4.5. Limitations

The present study has several limitations. The whole study was limited to a single geographic region, and the results might differ when the almond orchards are present in different landscape contexts. Additionally, some of the research questions were addressed using an unbalanced set of sampling sites; this applies particularly to the examination of the effects of the presence of mason bee nesting blocks inside the orchards because the study was primarily designed to reflect the three types of orchards according to their location and irrigation. There also could be an intercorrelation between the management type (presence/absence of irrigation) and the surrounding landscape complexity, as the proportion of orchards surrounding the sampling sites differed between the wet and dry regions. As the study had to reflect real environmental settings, we were unable to fully compensate for this possible intercorrelation.

5. CONCLUSIONS

The results of our survey provide data on floral visitors and possible pollinators of almond trees in Europe (Spain). We found, in addition to the most numerous European honeybees, the European orchard bee *Osmia cornuta* serves as one of the most important pollinators of

almond flowers. In orchards where this species was kept in nesting blocks, this species was the most abundant that was found on almond flowers and was not found on flowers of other plants in the orchard. This observation supports the strong preference of this species for the family Rosaceae and especially fruit trees (Torchio et al. 1987; Westrich 2018). In addition to the generalistic European honeybee, the European orchard bees is an interesting and essential pollinator for almonds and probably other fruit trees with the help of native bees, especially the genera *Andrena*, *Eucera* and *Lasioglossum* Curtis. Similar to Czech apple orchards, we found that many native pollinators in Spanish almond orchards consisted of polylectic species of *Andrena*. Therefore, the presence of polylectic bees of the genus *Andrena* and native bees, in general, is essential for sufficient pollination of fruit trees. Keeping beehives, blocks for mason bees and near-natural patches with bare soil and flowering plants is the best way to pollinate all almond trees (and other fruit trees) and help native bees thrive.

SUPPLEMENTARY INFORMATION

The online version contains supplementary material available at <https://doi.org/10.1007/s13592-023-01033-9>.

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AUTHOR CONTRIBUTION

PB designed the research, identified the bees and wrote the manuscript, PB and LH did the field research, PH did the analyses and partly wrote the manuscript.

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DATA AVAILABILITY

The data are available in supplementary files and on a request from the first author.

CODE AVAILABILITY

Not applicable.

DECLARATIONS

Ethics approval and consent to participate Not applicable.

Consent for publication Not applicable.

Competing interests The authors declare no competing interests.

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