

WILD BEES ACROSS THE FOREST-AGRICULTURAL INTERFACE IN NORTHWESTERN MOROCCO

AMINE SAMIH ^{1,2}, DANIEL PETIT³, NOUREDDIN MAATOUF², HASSAN FOUGRACH¹, MOHAMMED HSAINE¹, TAHTAH MERYEM^{1,4}, LATIFA ROHI¹

¹Faculty of Sciences Ben M'sik, Hassan II University in Casablanca, Laboratory of Ecology and Environment, Av. Cdt Driss El Harti, BP 7955, Sidi Othman, 20000 Casablanca, Morocco; e-mail: aminesamih96@gmail.com

²Center for Innovation, Research and Training, National Agency for Water and Forests, Av. Omar Ibn Khattab, BP 763, Agdal-Rabat, Morocco

³Faculty of Science and Technology, University of Limoges, LABCiS UR 22722, Limoges, 87000, France

⁴Department of Basic Sciences, National School of Agriculture, In Vitro Culture Laboratory, BP S/40, Meknes 50001, Morocco

 Corresponding author

Received: 5 December 2025 / **Accepted:** 23 February 2026

Abstract

Samih A., Petit D., Maatouf N., Fougrach H., Hsaine M., Meryem T., Rohi L.: Wild bees across the forest-agricultural interface in northwestern Morocco. *Ekológia (Bratislava)*, Vol. 45, No. 1, p. 39–49, 2026.

In northwestern Morocco, the Larache cork oak forest and the neighboring Gharb plain are facing increasing pressure from urban expansion and intensive agriculture. These land-use changes pose a serious threat to local biodiversity, particularly to wild bee populations. In order to assess the relationship between the wild bee fauna in forest and crop environments, we conducted a comprehensive survey using a combination of trapping methods and direct field observations in sampled stations over the course of 2022 and 2023. A total of 571 specimens were identified, representing 80 species, 21 genera, and 6 families. The results reveal a significant contrast between both landscapes: the higher richness and abundance of almost all families of wild bees in the cork oak forest demonstrate that these seminatural Mediterranean habitats are essential to sustain the functional diversity of wild bees. Approximately 18.75% of species were shared, especially between the forest edge and agricultural lands, which reflects not only the wild bees' adaptability but also the functional interdependence between the two ecosystems. Maintaining forest-agriculture connectivity is, therefore, crucial for sustaining pollinator diversity at the landscape scale.

Key words: ecosystem connection, diversity, pollinator, cork oak, Gharb plain.

Introduction

Wild bees (Apoidea) form one of the most diverse and ecologically important pollinator groups, thanks to their wide range of ecological traits and morphological diversity (Ricketts et al., 2008; Kennedy et al., 2013; Noël et al., 2018). Recognized as highly effective pollen vectors (Michener, 2007), they are essential for successful pollination (Ollerton, 2017; Ouvrard et al., 2018). Their sedentary nature also makes them valuable indicators of local land-use change (Fiordaliso et al., 2024), and their ecological specialization renders them particularly sensitive to environmental disturbances (Schindler et al., 2013). This vulnerability is especially relevant in Mediterranean regions, where wild bee communities are increasingly exposed to intensive farming modern agricultural practices (Petanidou, Lamborn, 2005). In this context, assessing wild bee diversity, abundance, and population trends offers an effective means of gauging the broader state of biodiversity (Duelli et al., 1999; Zayed, Packer, 2005).

Mediterranean cork oak forests, characterized by habitat heterogeneity including woodlands, open meadows, and ripar-

ian zones, provide diverse ecological niches that sustain rich bee communities (Kudrnovsky et al., 2020). In North Africa, and particularly in Morocco, most pollinator studies have focused on agroecosystems (El Abdouni et al., 2022; Bencharki et al., 2022; Sentil et al., 2022a,b,c, 2024). Yet, the role of natural habitats in sustaining pollinator communities is often underestimated, despite growing evidence of the ecological importance of forests as reservoirs of resources and refuges for these insects (Ulyshen et al., 2023). The forest's soil structure and low disturbance regime appear to create favorable nesting conditions, contrasting with the more disturbed agricultural areas nearby, thus reinforcing the role of oak forests as refuges for wild bees within Mediterranean agro-forest mosaics (Tsiakiris et al., 2024).

The Larache cork oak forest (*Quercus suber* L.) and the Gharb plain represent a strategic region for studying cork oak ecosystems along Morocco's Atlantic coast. This landscape is a mosaic of natural forests and modern agricultural fields (including eucalyptus, sugarcane, and sunflower plantations) undergoing rapid urbanization and agricultural intensification (Samih et al., 2024a). Such transformations threaten pollinator communities and the ecological services they provide (Samih et al., 2024b).

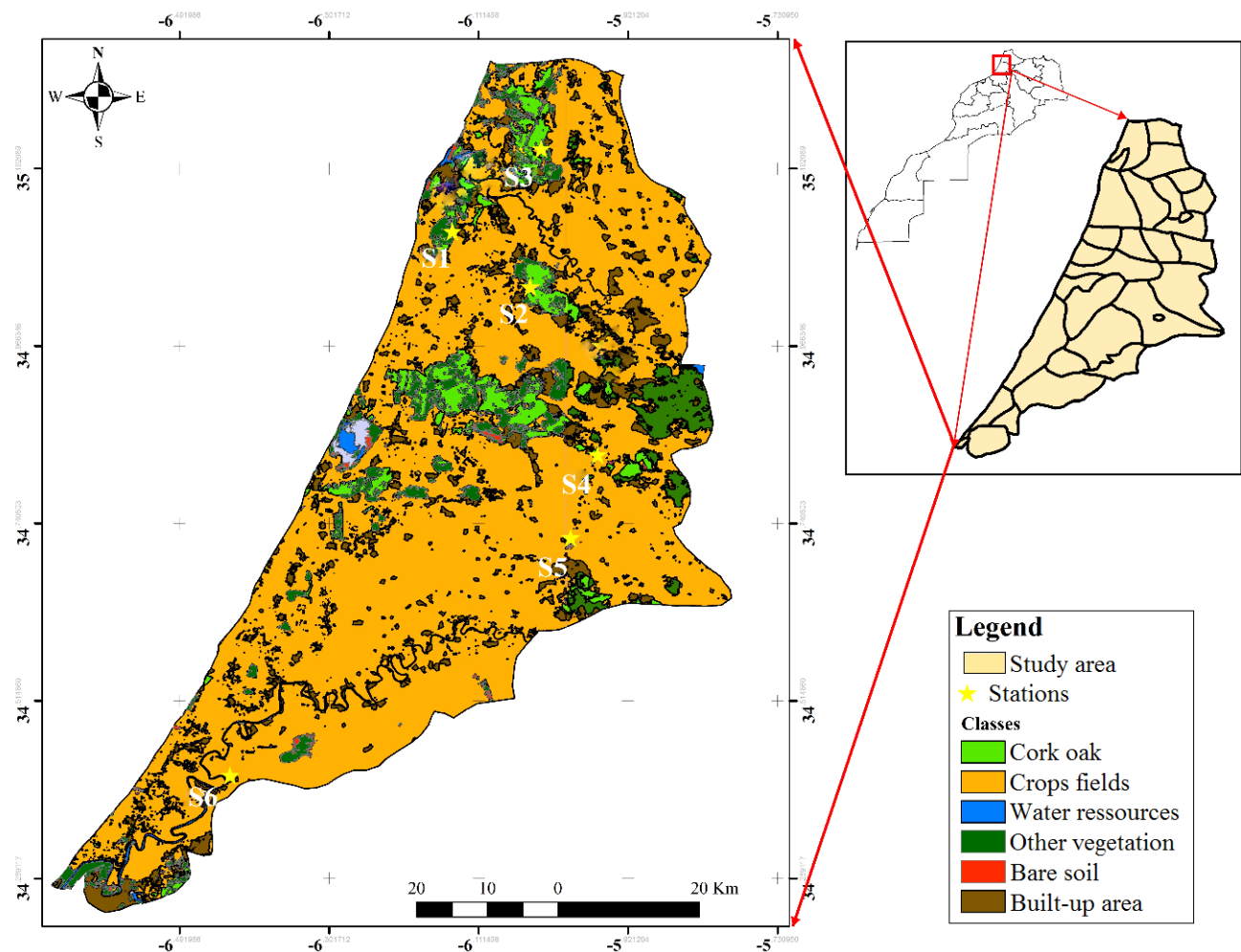


Fig. 1. Presentation of the study area and sampled stations.

This study aims to address the lack of data on wild bees in north-western Morocco, focusing on the Larache cork oak forest and adjacent agricultural lands in the Gharb plain. Over three years (2021–2023), we used a range of standardized trapping and direct observation techniques to document wild bee diversity across forests, floral strips, and crop fields. Our objectives were to (1) conduct a comprehensive inventory of wild bee species across different habitat types and evaluate the effectiveness of various sampling methods using rigorous statistical analyses. This will help determine which methods provide the most accurate and representative data on wild bee diversity, and (2) compare the species richness and abundance of wild bees between forest and agricultural environments, aiming to understand the potential exchanges of species that occur between both ecosystems.

Material and methods

Study area

The study area is located in the northwestern region of Morocco (Fig. 1), and six stations were selected in the Northwest of Morocco: three stations in the forest sector (S1, S2, S3) located

in the cork oak of Larache and three stations in the agricultural sector (S4, S5, S6) situated in the Gharb Plain.

The Larache cork oak forest lies in northwestern Morocco around the Loukkos River plain, bordered by the Sahel and R'Mel plateaus (Ballouche, 2024). The climate is Mediterranean, classified bioclimatically as subhumid thermomediterranean, with mild to temperate winters. The vegetation is dominated by cork oak, described as “subhumid cork oak forests on sand” (Sauvage, 1961). The Gharb plain is among Morocco’s most important agricultural zones, sustained by the Oued Sebou and its irrigation network (Zamrane, 2016). Its Mediterranean climate, with mild winters and hot summers, supports intensive cultivation of crops such as tomatoes, onions, zucchinis, carrots, peppers, citrus fruits, and oilseeds (Chbika, Aouane, 2021). The various sampled stations (Table 1) were established in contrasting sectors: edge habitats, vegetation strips along forest tracks, forests, and flowered vegetation strips in agricultural areas.

The selection of stations was based on the presence of plant species providing pollen and nectar resources, which suggests an interesting diversity of the local pollinating entomofauna essential for the functional integrity of ecosystems. Within the

Table 1. Satellite coordinates of the different sampled stations.

Sector	Station	Biotope	Latitude	Longitude
Forest	S1	Dense forest	35.111667	-6.147250
	S2	Flowering forest track	35.037361	-6.007083
	S3	Edge forest	35.211972	-6.032722
Agricultural	S4	Vegetation field	34.828096	-5.961945
	S5	Flowering strip of vegetation field	34.729699	-5.990363
	S6	Flowering habitat strip	34.418241	-6.428204

forest, a dense forest (S1) was located in a dense cork oak stand (*Quercus suber* L.). Here, the closed canopy filtered much of the sunlight, creating a shaded understorey dominated by Cistaceae shrubs, together with a patchwork of herbaceous plants. Deadwood, present in varying amounts, added further structural diversity (Samih et al., 2025a). The flowering forest track (S2) was a linear opening shaped by both human activity and natural disturbance. Its open, sunlit conditions favored heliophilous species, mainly herbaceous plants such as Asteraceae, Fabaceae, and Apiaceae, occasionally interspersed with shrubs. This track functioned as a corridor of flowers and a key foraging site for many wild bees. The edge forest (S3) corresponded to a flowering forest edge, a transition zone where light was more abundant and plant diversity increased. This site benefited from permanent water resources, including a daya (temporary pond) and natural springs connected to the aquifer (Samih et al., 2025a), which sustained a rich and continuous floral cover. In the agricultural landscape, three complementary stations were surveyed. The vegetation field (S4) was a sunflower field (*Helianthus annuus* L.), cultivated as a monoculture. During the blooming period, it offered an abundance of nectar and pollen, although floral resources were otherwise scarce and mostly confined to field margins. The flowering strip of vegetation field (S5) was a flowering strip within the sunflower field, usually 3–4 m wide, though sometimes no more than a narrow border of a few 40–50 cm. These strips consisted of melliferous and entomophilous herbs, either sown or naturally established, providing food for wild bees before and after the sunflower's peak bloom. The flowering habitat strip (S6) was the flowering habitat strip running along the outer margins of fields and paths. These strips were broader (3–10 m), made up of spontaneous annual and perennial herbs with occasional shrubs. While not directly managed, they were still affected by irrigation and pesticide drift from neighboring crops.

Methodology for wild bees inventory

During this study, various passive and active trapping systems were designed. The trapping method using pan traps was used to passively sample bees (Gonçalves, Oliveira, 2013; Pierre et al., 2017), particularly the Andrenidae and Halictidae families and especially species of small to medium size (Pauly, 2019), with four pan traps (blue, white, yellow, and orange) per station. The colors are the most commonly chosen because they cover a diverse range of wavelengths in the visual spectrum and partly correspond to the colors of flowers and the different color preferences varying among bee species (Leong, Thorp, 1999; Thomson, Wilson, 2008). An important complement to passive

trapping is the use of a Malaise trap per station for capturing certain bee species. The Malaise traps (one per station) were constructed of black and white material and handmade. We deployed multiple trap types, each measuring approximately 1.5 m in height, 1.2 m in width, and 1.5 m in length. Malaise traps, noted for their efficiency in capturing large bees such as bumblebees and megachilids (Pauly, 2019), were complemented by pan traps, sweep nets, and bottle traps.

Note that the pan traps were installed on tree branches 1 meter above the ground and placed along a transect parallel to each Malaise trap. The pan traps and the collecting bottle of the Malaise traps were filled halfway with a mixture of soapy saltwater. Surveys of trap contents were conducted once every 20 days for 5 months (March–July), over two consecutive years (2022 and 2023). These collections were supplemented by observations and captures, during which active trapping was practiced for the direct capture of individuals encountered on flowers, using a sweep net and a bottle along straight transects in the various sampled sites. This is a highly effective technique for inventorying Megachilidae and Melittidae, as they rarely fall into traps (Pauly, 2019).

Specimen identification

Specimens of wild bees were classified at the family and genus levels, then carefully grouped into collection boxes, and sent to the Zoology Laboratory at the University of Mons in Belgium for identification. Species-level identifications were carried out by a team of taxonomists: Ahlam Sentil and William Fiordaliso for general identification across families, Pierre Rasmont for genera *Bombus* and *Anthophora*, and Simone Flaminio for *Lasioglossum*. Moreover, Thomas James Wood (Naturalis Biodiversity Center, Leiden) was responsible for identifying *Andrena*, *Osmia*, *Megachile*, and other genera, including *Nomiapis* and *Sphecodes*. Achik Dorchin (Steinhardt Museum of Natural History, Tel Aviv) worked on *Eucera*, Guillaume Ghisbain on *Dasypoda*, and Romain Le Divelec focused on *Hylaeus*. Additional genera were identified by Michael Terzo, Max Kasperek (Heidelberg), and Andreas Müller (ETH Zurich).

Data analysis

Sampling effort

Sampling effort and species richness were evaluated using rarefaction curves generated with PAST version 4.17 (Hammer, Harper, 2001, 2024). Rarefaction curves allow the comparison of species richness (Taxa S) (Gotelli, Colwell, 2001) among dif-

ferent samples while accounting for differences in sampling effort (number of specimens collected). This method provides an estimation of species accumulation relative to the number of individuals sampled, enabling a standardized comparison of biodiversity across sampling sites.

Abundance and diversity analysis of the wild bees

We calculated the percentage relative abundance (ni) of species in order to reflect the proportion of individuals belonging to the total number of individuals collected across all individuals (N), according to the forest and agricultural sectors, using the formula:

RA % = (ni/N)*100. (1)

Dunn’s post hoc test (OriginPro 2025) was used to compare the abundance and species richness of the six families of the wild bees (Andrenidae, Apidae, Colletidae, Halictidae, Megachilidae, and Melittidae) in the forest and agricultural sectors. This choice was based on preliminary analyses that confirmed the data did not meet the assumptions for parametric testing. Specifically, the abundance data were not normally distributed (Shapiro–Wilk test: W = 0.63, p < 0.0001) and did not meet the assumption of homogeneity of variance (Levene’s test: F = 4.42, p < 0.05). The data of species richness had similar results with not normally distributed (Shapiro–Wilk test: W = 0.79, p < 0.0001) and did not meet the assumption of homogeneity of variance (Levene’s test: F = 28.25, p < 0.0001). The Venn diagram was generated using PAST version 4.17 (Hammer, Harper, 2001, 2024)-to visualize the distribution of bee species across the different habitat types and to identify both exclusive and shared species.

Results

The inventory of wild bees conducted over two consecutive years, 2022 and 2023, at the sampled stations in the northwestern region of Morocco, resulted in the enumeration of a total of 571 individuals corresponding to 80 species and 21 genera belonging to 6 families (Table 2).

Sampling effort

The rarefaction curves (Fig. 2) illustrate the species richness of wild bees in relation to the number of specimens collected at six studied stations.

At station S3, where 400 specimens were sampled resulting in 50 species recorded, the curve continues to rise steeply, indicating that the sampling effort was insufficient to capture the full diversity of bees at this site and further sampling is needed. Conversely, station S1, with 350 specimens and 45 species recorded, shows a curve that levels off, suggesting that the sampling was thorough and most species have been detected. The remaining stations (S2, S4, S5, and S6) had between 340 and 370 specimens collected and recorded 40–43 species each. Their rarefaction curves increase gradually but do not clearly plateau, indicating an incomplete sampling effort and that some species might still be missing.

Abundance and species richness of wild bees in forest and agricultural sectors

The survey recorded 71 wild bee species in the forest sector, in contrast to only 24 species in the agricultural sector. This difference in species richness was statistically highly significant (Dunn’s test: p < 0.05). These species were distributed across

Table 2. Wild bee species collected from six sites in the northwest region of Morocco.

Families/Species	Forest sector						Agricultural sector					
	S1		S2		S3		S4		S5		S6	
	ni	RA %	ni	RA %	Ni	RA %	ni	RA %	ni	RA %	ni	RA %
Andrenidae												
Andrena aerinifrons (Dours, 1873)											2	2.53
Andrena antigana (Pérez, 1895)					1	0.20						
Andrena avara (Warncke, 1967)					4	0.81						
Andrena bellidis (Pérez, 1895)					3	0.61	1	1.27				
Andrena discors (Erichson, 1841)					1	0.20						
Andrena djelfensis (Pérez, 1895)					2	0.41						
Andrena flavipes (Panzer, 1799)					30	6.10	3	3.80				
Andrena fulvicornis (Schenck, 1853)					1	0.20	2	2.53	1	1.27	2	2.53
Andrena insignis (Warncke, 1974)					2	0.41						
Andrena labialis (Kirby, 1802)					1	0.20						
Andrena lagopus (Latreille, 1809)					2	0.41						
Andrena miegiella (Dours, 1873)							1	1.27	3	3.80	2	2.53
Andrena morio (Brullé, 1832)			7	1.4228	7	1.42						
Andrena oraniensis (Lepelletier, 1841)					1	0.20						
Andrena orbitalis (Morawitz, 1871)					1	0.20						
Andrena poupillieri (Dours, 1872)					2	0.41						
Andrena propinqua (Schenck, 1853)					1	0.20						
Andrena ranunculi (Schmiedeknecht, 1883)					6	1.22						
Andrena rhyssonota (Pérez, 1895)					1	0.20						
Andrena simontornyella (Noskiewicz, 1939)					1	0.20						
Andrena spreta (Pérez, 1895)					4	0.81						
Andrena vulcana (Dours, 1873)					1	0.20						

Table 2. Wild bee species collected from six sites in the northwest region of Morocco - continuation.

Families/Species	Forest sector						Agricultural sector					
	S1		S2		S3		S4		S5		S6	
	ni	RA %	ni	RA %	Ni	RA %	ni	RA %	ni	RA %	ni	RA %
Apidae												
<i>Anthophora blanda</i> (Percz, 1812)					1	0.20						
<i>Anthophora senescens</i> (Lepeletier, 1841)			2	0.4065	1	0.20						
<i>Bombus terrestris</i> (Linnaeus, 1758)			2	0.4065	3	0.61						
<i>Tetralonia ruficornis</i> (Fabricius, 1804)					1	0.20						
<i>Ceratina cucurbitina</i> (Rossi 1972)			4	0.813	9	1.83	2	2.53				
<i>Ceratina maghrebensis</i> (Daly, 1983)			1	0.2033	1	0.20						
<i>Eucera collaris</i> (Dours, 1873)			1	0.2033	21	4.27						
<i>Eucera dentata</i> (Germar, 1839)			3	0.6098								
<i>Eucera elongatula</i> (Vachal, 1907)					1	0.20						
<i>Eucera grisea</i> (Fabricius, 1793)					1	0.20						
<i>Eucera nadigi</i> (Fries, 1924)			1	0.2033	2	0.41						
<i>Eucera nigrilabris</i> (Lepeletier, 1841)											1	1.27
<i>Eucera oblitterata</i> (Pérez, 1895)									1	1.27	1	1.27
<i>Eucera strigata</i> (Lepeletier, 1841)					21	4.27						
<i>Nomada accentifera</i> (Pérez, 1895)					1	0.20						
<i>Nomada bifasciata</i> (Olivier, 1811)							1	1.27				
<i>Nomada numida</i> (Lepeletier, 1841)							1	1.27				
<i>Nomada panurginoides</i> (Saunders, 1908)					1	0.20						
<i>Nomada stigma</i> (Fabricius 1804)			1	0.2033								
<i>Xylocopa pubescens</i> (Spinola, 1838)							1	1.27	3	3.80	5	6.33
<i>Xylocopa violacea</i> (Linnaeus, 1758)					3	0.61			2	2.53	5	6.33
Colletidae												
<i>Hylaeus cornutus</i> (Curtis, 1831)					1	0.20	3	3.80				
<i>Hylaeus purpurissatus</i> (Vachal, 1895)			1	0.2033	1	0.20						
Halictidae												
<i>Halictus scabiosae</i> (Rossi, 1790)	1	0.20			1	0.20						
<i>Lasioglossum algericolellum</i> (Strand, 1909)					1	0.20						
<i>Lasioglossum brevicorne</i> (Schenck, 1868)	2	0.41			25	5.08	5	6.33	1	1.27		
<i>Lasioglossum callizonium</i> (Pérez, 1895)					1	0.20						
<i>Lasioglossum cedri</i> (Ebmer, 1976)			1	0.2033	6	1.22						
<i>Lasioglossum fertoni</i> (Vachal, 1895)			1	0.2033	15	3.05						
<i>Lasioglossum glabriusculum</i> (Morawitz, 1872)	1	0.20										
<i>Lasioglossum immunitum</i> (Vachal, 1895)			3	0.6098	3	0.61	2	2.53				
<i>Lasioglossum leucozonium</i> (Schränk, 1781)			1	0.2033	2	0.41						
<i>Lasioglossum malachurum</i> (Kirby, 1802)	2	0.41	1	0.2033	8	1.63						
<i>Lasioglossum mediterraneum</i> (Blüthgen, 1925)					3	0.61						
<i>Lasioglossum pauperatum</i> (Brullé, 1832)							2	2.53			1	1.27
<i>Lasioglossum prasinum</i> (Smith, 1848)			8	1.626	16	3.25						
<i>Lasioglossum punctatissimum</i> (Schenck, 1853)					2	0.41						
<i>Lasioglossum puncticolle</i> (Morawitz, 1872)			2	0.4065	1	0.20						
<i>Lasioglossum virens</i> (Erichson, 1835)					4	0.81						
<i>Nomiapis rufiventris</i> (Lepeletier, 1841)			1	0.2033	4	0.81	1	1.27				
<i>Nomioides minutissimus</i> (Rossi, 1790)			1	0.2033								
<i>Seladonia gemmea</i> (Dours, 1872)	1	0.20										
<i>Sphecodes albilabris</i> (Fabricius, 1793)					1	0.20						
<i>Sphecodes rubripes</i> (Spinola, 1838)					4	0.81						
<i>Sphecodes rubicundus</i> (Hagens, 1875)									2	2.53		
Megachilidae												
<i>Anthidiellum strigatum</i> (Panzer, 1805)					1	0.20						
<i>Anthidium diadema</i> (Latreille, 1809)					1	0.20						
<i>Dioxys pumilus</i> (Gerstäcker, 1869)			1	0.2033	1	0.20						
<i>Megachile ericetorum</i> (Lepeletier, 1841)					3	0.61						
<i>Megachile sicula</i> (Rossi, 1792)			4	0.813	9	1.83						
<i>Osmia crenulata</i> (Nylander, 1856)					1	0.20						
<i>Osmia niveata</i> (Fabricius, 1804)			3	0.6098	2	0.41			1	1.27		
<i>Osmia notata</i> (Fabricius, 1804)					3	0.61			1	1.27	1	1.27
<i>Osmia submicans</i> (Morawitz, 1870)					1	0.20						
Melittidae												
<i>Dasypoda cingulata</i> (Erichson, 1835)	98	19.92			32	6.50	10	12.66				
<i>Dasypoda dusmeti</i> (Quilis, 1928)	5	1.02			1	0.20	1	1.27				
<i>Dasypoda maura</i> (Pérez, 1896)	31	6.30			1	0.20			2	2.53	2	2.53
<i>Dasypoda visnaga</i> (Rossi, 1790)	4	0.81			3	0.61	3	3.80	1	1.27		
N	145	29.47	50	10.16	297	60.37	39	49.37	18	22.78	22	27.85
				492					79			

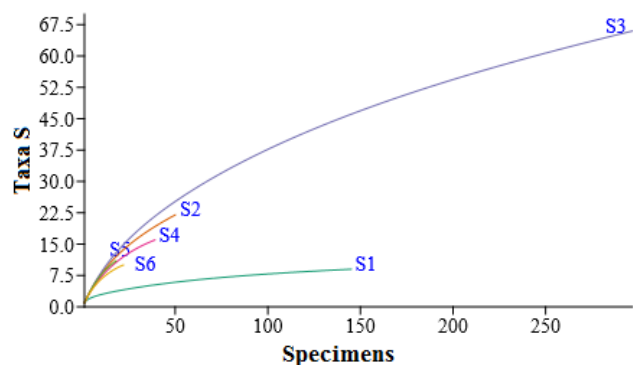


Fig. 2. Rarefaction curves and sampling effort of wild bees in different stations.

Table 3. Descriptive statistics: richness of wild bees in forest and agricultural landscapes.

Landscapes	Families	Mean $\pm$ SD	Significance
Forest	Andrenidae	15 $\pm$ 2.677	A
Agricultural		4 $\pm$ 1.683	Bc
Forest	Apidae	11 $\pm$ 2.345	Ab
Agricultural		4.25 $\pm$ 0.946	Bc
Forest	Colletidae	1.5 $\pm$ 0.5	C
Agricultural		1 $\pm$ 0	C
Forest	Halictidae	14.25 $\pm$ 2.954	A
Agricultural		3.5 $\pm$ 0.86	Bc
Forest	Megachilidae	5 $\pm$ 1.825	Bc
Agricultural		1.25 $\pm$ 0.25	C
Forest	Melittidae	4 $\pm$ 0	Bc
Agricultural		4 $\pm$ 0	Bc

Table 4. Descriptive statistics: abundance of wild bees in forest and agricultural landscapes.

Landscapes	Families	Mean $\pm$ SD	Significance
Forest	Andrenidae	19.75 $\pm$ 5.677	Ab
Agricultural		4.25 $\pm$ 0.478	B
Forest	Apidae	20.5 $\pm$ 8.026	Ab
Agricultural		5.75 $\pm$ 1.436	B
Forest	Colletidae	0.75 $\pm$ 0.25	B
Agricultural		0.75 $\pm$ 0.25	B
Forest	Halictidae	30.25 $\pm$ 5.735	Ab
Agricultural		3.5 $\pm$ 0.5	B
Forest	Megachilidae	7.5 $\pm$ 1.658	B
Agricultural		0.75 $\pm$ 0.25	B
Forest	Melittidae	43.75 $\pm$ 20.450	A
Agricultural		5 $\pm$ 2.041	B

various families (Fig. 3).

Forest habitats showed significantly higher species richness than agricultural areas, particularly for Andrenidae (15 $\pm$ 2.67 species), Halictidae (14.25 $\pm$ 0.94), Apidae (11 $\pm$ 2.34), and Megachilidae (5 $\pm$ 1.82) ($p < 0.05$ for all). In contrast, the Melittidae

and Colletidae families exhibited low species richness and did not show significant differences between habitats (Table 3).

The survey recorded 492 wild bee individuals in the forest sector, in contrast to only 79 individuals in the agricultural sector. This difference in abundance was statistically highly significant (Dunn's test: $p < 0.05$). These abundances were distributed across various families (Fig. 4, Table 4).

Forests once again outperformed agricultural sites, with Melittidae and Halictidae standing out as particularly dominant, averaging 43.75 $\pm$ 20.45 and 30.25 $\pm$ 5.73 individuals ($p < 0.05$), respectively. The Apidae and Andrenidae families were less abundant, each with fewer than 30 individuals, averaging 20.5 $\pm$ 8.02 and 19.75 $\pm$ 5.67, respectively ($p < 0.05$). In contrast, the Megachilidae and Colletidae families exhibited low abundances and did not show significant differences between habitats.

Species exclusivity and habitat overlap

The Venn diagram (Fig. 5) illustrates the distribution of bee species across four distinct habitat types: the agricultural landscape (S4), the agricultural flower strip (S5–S6), the flower strip along the forest track (S2), and the forest landscape (S1–S3).

We observed that the forest landscape hosts by far the greatest number of exclusive species, with 51 unique species. In comparison, the other habitats show much lower numbers of unique species: two species in the flower strip along the forest track, two species in the agricultural landscape, and four species in the agricultural flower strip. Regarding overlap between habitats, the diagram reveals several notable intersections. For example, six species are shared between the agricultural landscape and the forest landscape. Similarly, the agricultural flower strip and the agricultural landscape share three species, while the agricultural flower strip and the flower strip along the forest track share two species. The center of the diagram, where all four habitats intersect, shows that two species are common to all habitats, representing a group of generalist wild bees, namely *Lasioglossum brevicorne* (Schenck, 1868) and *Dasypoda visnaga* (Rossi, 1790), which are capable of colonizing diverse environments. Our results also reveal a clear ecological linkage between the Larache cork oak forest sectors and the surrounding agricultural zone. The forest edge habitat (S3) shares the highest number of species with the agricultural zone, totaling 15 species, these shared species belong predominantly to the families Andrenidae (e.g., *Andrena bellidis*, *A. flavipes*, *A. fulvicornis*), Colletidae (e.g., *Hylaeus cornutus*), Halictidae (e.g., *Lasioglossum brevicorne*, *L. immunitum*, *Nomiapis rufiventris*), Megachilidae (e.g., *Osmia niveata*, *O. notata*), Apidae (e.g., *Xylocopa violacea*, *Ceratina cucurbitina*), and Melittidae (e.g., *Dasypoda cingulata*, *D. dusmeti*, *D. maura*, *D. visnaga*).

In contrast, nine unique species were recorded in the agricultural zone, including Andrenidae (e.g., *Andrena aerinifrons* and *A. miegiella*), Halictidae (e.g., *Lasioglossum pauperatum* and *Sphecodes rubicundus*), and Apidae (e.g., *Eucera nigrilabris*, *E. oblitterata*, *Nomada bifasciata*, *N. numida*, and *Xylocopa pubescens*).

Discussion

Andrenidae showed significantly higher richness (15 $\pm$ 2.67 species) and abundance (19.75 $\pm$ 5.67 individuals) in forest habitats compared to agricultural areas ($p < 0.05$). This family is predominantly composed of ground-nesting solitary bees, often active

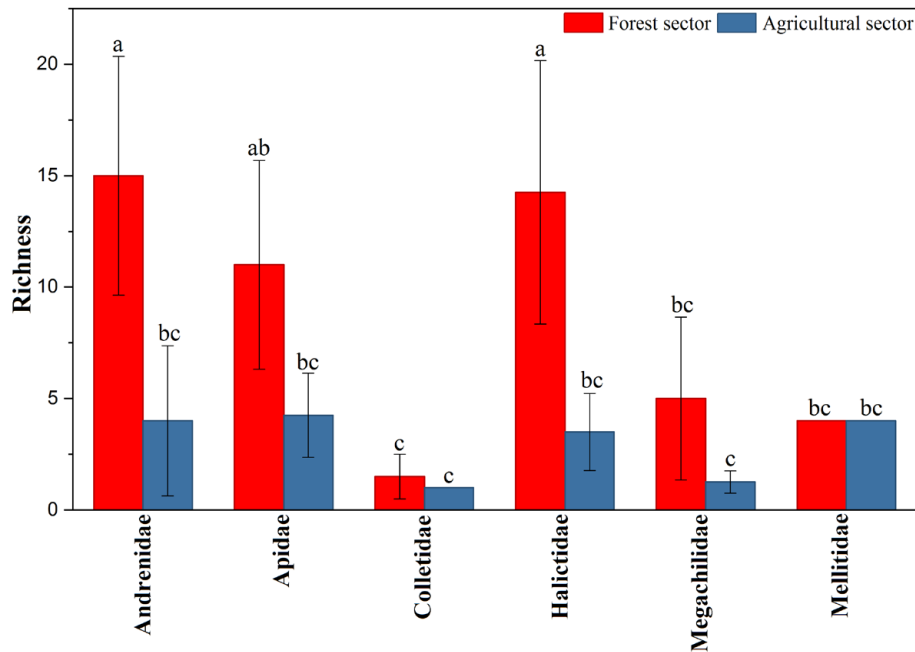


Fig. 3. Richness of wild bee families in forest and agricultural sectors. Different letters correspond to significant differences.

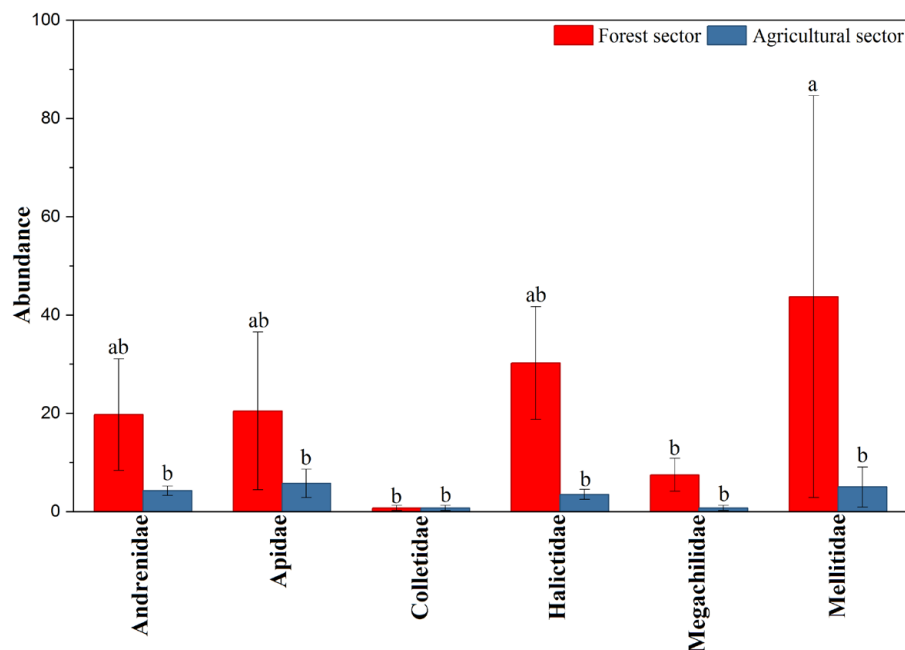


Fig. 4. Abundance of wild bee families in forest and agricultural sectors.

in early spring. Seminatural forests such as cork oak woodlands provide open soil patches, stable microclimatic conditions, and a rich spring flora, which are essential for their nesting and foraging (Potts et al., 2005; Kennedy et al., 2013). In Mediterranean contexts, cork oak forest acts as refuges for many *Andrena* species that are highly sensitive to soil compaction, tillage, and the lack of early-blooming plants in croplands (Herrera, C.M.,

1988; Petanidou, Lamborn, 2005). Halictidae were also strongly associated with forests, exhibiting both high richness (14.25 ± 0.94 species) and high abundance (30.25 ± 5.73 individuals; $p < 0.05$). Their success is attributed to their ecological flexibility, as they can nest in the ground and exploit a wide range of floral resources, which are more available in structurally complex habitats (Cane et al., 2000; Rasmont, Iserbyt, 2012; Antoine, Forrest,

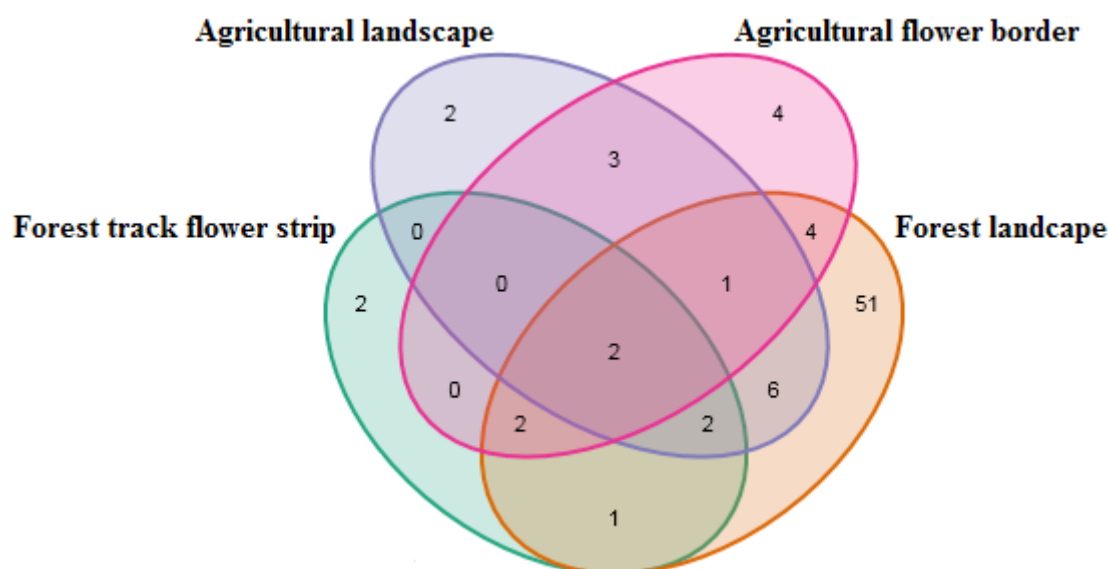


Fig. 5. Venn diagram: the distribution of wild bee species among four habitat types.

2021). The ecological plasticity of Halictidae being able to nest in bare ground, decayed wood, or occasionally stems and to exploit a broad spectrum of flowers gives them an advantage in heterogeneous habitats (Cane et al., 2000; Rasmont, Iserbyt, 2012). In Mediterranean forests, the coexistence of open patches, shrub layers, and understory flowers favors halictid diversity (Potts et al., 2003; Rodríguez et al., 2021).

Apidae were more diverse and abundant in forests (11 ± 2.34 species; 20.5 ± 8.02 individuals) than in agricultural sites ($p < 0.05$). Their dependence on continuous floral resources and nesting substrates such as tree cavities explains their decline in intensively managed agricultural systems (Herrera, C.M., 1988; Michener, 2007; Delaplane, 2021). In cork oak forests, hollow trunks and fallen branches provide nesting opportunities for *Xylocopa* and *Bombus* species, while rich flowering shrubs (e.g., *Cistus*, *Lavandula*, *Erica*) sustain them throughout the season (Herrera, J., 1988). Their decline in agricultural habitats is consistent with the scarcity of nesting substrates and the temporal discontinuity of floral resources due to monoculture practices (Delaplane, 2021).

Megachilidae richness remained relatively low (5 ± 1.82 species), as did their abundance (< 10 individuals), but both were significantly higher in forests. This is explained by their requirement for specific nesting materials (leaves, petals, resins) and preexisting cavities for brood construction (Le Féon, 2010). Agricultural intensification drastically reduces such resources, whereas cork oak forests, with their rich shrub layer and diverse vegetation, maintain suitable conditions. For instance, *Osmia* species are often closely tied to the heterogeneous forest edges where flowers and nesting cavities co-occur (Hudewenz, Klein, 2013).

Melittidae displayed low richness (≈ 3 – 4 species) but surprisingly high abundance in forest habitats (43.75 ± 20.45 individuals; $p < 0.05$). This apparent paradox reflects their ecological specialization: despite being few in species number, certain melittidae bees can reach high local abundances when their spe-

cific host plants are present, which is more often the case in forest habitats than in agricultural lands (Dellicour, Michez, 2010; Delaplane, 2021). Finally, Colletidae showed the lowest richness (≈ 1 – 2 species) and abundance (< 5 individuals) in both habitats, with no significant differences between forest and agricultural sites. Their narrow ecological requirements and restricted floral associations explain their general scarcity under Mediterranean conditions (Michener, 2007; Dellicour, Michez, 2010).

Additionally, the widespread use of insecticides, particularly neonicotinoids, has been shown to reduce pollination services (Park et al., 2015; Stanley et al., 2015) and negatively impact pollinator populations (Rundlöf et al., 2015; Woodcock et al., 2017). In Morocco, the import and continued use of neonicotinoids such as thiamethoxam raises serious concerns (Greenpeace, Public Eye, 2024). These insecticides are widely used in sunflower cultivation worldwide, most often as seed treatments. Once applied, they are systemically translocated into plant tissues, including nectar and pollen, which exposes pollinators to potentially harmful residues (Saleem et al., 2023).

The distribution of exclusive and shared bee species across habitats offers significant insights into the ecological dynamics of pollinator communities in Northwestern of Morocco (Samih et al., 2025b). The cork oak forest of Larache emerges as a biodiversity reservoir, harboring 51 exclusive species. Such high singularity reflects the forest's structural complexity, floristic diversity, and the stability of microhabitats features typical of well-preserved Mediterranean woodlands (Petanidou, Potts, 2006; Blondel, 2010). These habitats sustain specialist and rare taxa, which are often highly sensitive to environmental changes and habitat degradation (Petanidou et al., 2008).

In stark contrast, agricultural and seminatural habitats comprising the agricultural matrix, flower strips along forest edges, and agricultural flower strips host only a small number of exclusive species (two in the agricultural matrix, two in the forest-edge flower strip, and four in the agricultural flower strip). This lower exclusivity may stem from reduced habitat heterogeneity

and higher disturbance levels in Mediterranean agricultural systems, which tend to favor generalist species while limiting the persistence of habitat-restricted bees (Potts et al., 2003; Le Féon, 2010). Even though floral enhancements such as flower strips can increase local flower availability, they rarely replicate the ecological complexity of natural Mediterranean habitats (Kleijn et al., 2006; Batáry et al., 2011). The edge forest serves as critical transition zone, offering both rich floral variety and more buffered microclimate than nearby agricultural lands, supporting higher native bee richness associated with stronger canopy structure (Rodríguez et al., 2021). Among the native bees, 15 species were found to be shared with agricultural landscapes. These shared species are mostly polylectic generalists, adept at utilizing different types. Samih et al. (2025a) demonstrated that these shared species forage on a wide variety of plants, particularly those characteristic of open Mediterranean habitats. They were observed visiting ruderal and heliophilous species of the Asteraceae (*Otophysum glabrum*, *Glebionis coronaria*, *Matricaria chamomilla*, *Leontodon saxatilis*, *L. maroccanus*, *Galactites tomentosus*, and *Scolymus hispanicus*), as well as representatives of the Brassicaceae (*Raphanus raphanistrum*, *Biscutella didyma*), the Geraniaceae (*Erodium cicutarium*), and the Ranunculaceae (*Ranunculus graminensis*). These plants are emblematic of cork oak open habitats, as they persist under high levels of disturbance and drought stress, thereby providing continuous floral resources that sustain pollinators with broad trophic niches. From an ecological perspective, the persistence of such disturbance-tolerant plants plays a key role in supporting generalist bees, whose broad trophic niches allow them to exploit diverse resources across space and time. By offering abundant and accessible nectar and pollen over extended flowering periods, these ruderal species act as reliable forage sources, buffering pollinator populations against resource scarcity (Bosch et al., 1997; Petanidou, Potts, 2006). On a broader scale, the mosaic of uncultivated patches, shrublands, and grasslands embedded within Mediterranean farmland provides complementary and sequential floral resources, enabling both the persistence and movement of pollinators across fragmented landscapes (Roth et al., 2023). Such generalist bees, with wide ecological tolerance and flexible foraging strategies, are capable of thriving in both complex natural Mediterranean habitats and simplified anthropogenic environments. Their ubiquity not only reflects resilience but also highlights the limited number of bee species able to persist under such contrasting ecological conditions. This underscores the importance of conserving habitat diversity and heterogeneity to sustain pollinator communities and ensure ecological connectivity in Mediterranean regions (Herrera, C.M., 1988; Blondel, 2010; Potts et al., 2010).

The nine species observed exclusively in agricultural landscapes reflect a particular ecological strategy, closely tied to their strong dependence on ruderal Asteraceae and Brassicaceae occurring along flowering field margins (Samih et al., 2024a). These pioneer plants, typical of open and disturbed habitats, are well known for their ability to thrive in poor soils subjected to trampling or extensive agricultural practices (Grime, 2001; Thompson, 2005). By providing abundant and long-lasting nectar and pollen resources, they play a pivotal role for bees with narrow niches or specialized foraging preferences. In the Mediterranean basin, several *Andrena* species are strongly associated with Asteraceae; for example, *A. mediovittata* collects over 80% of its pollen from this family (Wood, Cross, 2017). Similarly, in North

Africa, the majority of *Andrena* species studied exhibit a high degree of specialization on Asteraceae and Brassicaceae (Benarfa et al., 2021). The occurrence of these “unique” species, therefore, reflects a form of selective ecological tolerance. Their tolerance does not stem from dietary plasticity but rather from their ability to persist in anthropogenic landscapes through the exploitation of marginal habitats rich in Asteraceae. This tolerance is disturbance-dependent: agricultural practices, by maintaining bare soils and early successional plant communities, promote ruderal assemblages that in turn serve as resource anchors for specialist bees (Petanidou, Potts, 2006; Potts et al., 2010).

This dynamic is even more pronounced for cleptoparasitic species such as *Nomada bifasciata*, *N. numida*, and *Sphecodes rubicundus*. Their presence is directly conditioned by the abundance of their hosts (*Andrena*, *Lasioglossum*), which themselves rely on Asteraceae. This underlines the structuring role of floral resources: by sustaining host populations, Asteraceae indirectly support the associated trophic networks (Wcislo, 1987; Michener, 2007).

Conclusion

This study highlights the urgent need to safeguard wild bee biodiversity in Northwestern Morocco, a cornerstone for sustaining ecosystem services and securing food production. Effective conservation and management strategies must be adapted to the distinct requirements of both forest and agricultural landscapes.

In contrast, while polylectic shared species reflect ecological connectivity and adaptive flexibility, the unique agricultural species reveal a tighter dependence on certain plant families and a conditional tolerance to human-induced disturbances. This distinction highlights the critical importance of conserving marginal habitats and flowering field edges, as they represent biodiversity reservoirs that sustain both specialist species and the broader resilience of pollinator communities in Mediterranean agroecosystems.

Acknowledgements

We extend our heartfelt thanks to the Director (Amar Rabhi) of the Center for Innovation, Research and Training in Rabat (National Agency for Water and Forests) for their hospitality and unwavering support in facilitating this work. We are also grateful to El Ayyachi El Mnouar (technician in the field of forest management, National Agency for Water and Forests Rabat, Morocco) for his guidance and assistance. We are grateful to Pierre Rasmont and Denis Michez from the Zoology Laboratory of the University of Mons in Belgium, who agreed to send the specimens for their identification and facilitated the necessary procedures for shipping the scientific material. We would like to thank Ahlam Sentil for her participation in the shipment of specimens and for correcting this study. We also express our gratitude to the team of taxonomists at the Zoology Laboratory of the University of Mons for identifying the specimens, including Simone Flaminio, Thomas James Wood, Achik Dorchin, Guillaume Ghisbain, Romain Le Divelec, Michael Terzo, Max Kasperek, and Andreas Müller.

References

- Antoine, C.M. & Forrest J.R. (2021). Nesting habitat of ground-nesting bees: a review. *Ecol. Entomol.*, 46(2), 143–159. DOI: 10.1111/een.12986.
- Ballouche, A. (2024). Missing Landscapes: A Geohistory of Parkland Landscapes in Northwestern Morocco. *Land*, 13(5), 649. DOI: 10.3390/land13050649.

- Batáry, P., Báldi, A., Kleijn, D. & Tscharntke T. (2011). Landscape-moderated biodiversity effects of agri-environmental management: a meta-analysis. *Proc. R. Soc. B Biol. Sci.*, 278(1713), 1894–1902. DOI: 10.1098/rspb.2010.1923.
- Benarfa, N., Michez, D., Rasmont, P. & Patiny S. (2021). Pollen host-plant use by *Andrena* bees in North Africa: specialization patterns and ecological implications. *Journal of Hymenoptera Research*, 84, 1–15. DOI: 10.3897/jhr.84.64323.
- Bencharki, Y., Christmann, S., Lhomme, P., Ihsane, O., Sentil, A., El Abdouni, I., Hamroud, L., Rasmont, P. & Michez D. (2022). 'Farming with alternative pollinators' approach supports diverse and abundant pollinator community in melon fields in a semi-arid landscape. *Renewable Agriculture and Food Systems*, 38. DOI: 10.1017/s1742170522000394.
- Blondel, J. (2010). *The Mediterranean region: biological diversity in space and time*. Oxford: Oxford University Press.
- Bosch, J., Retana, J. & Cerdá X. (1997). Flowering phenology, floral traits and pollinator composition in a herbaceous Mediterranean plant community. *Oecologia*, 109(4), 583–591. DOI: 10.1007/s004420050120.
- Cane, J.H., Minckley, R.L. & Kervin L.J. (2000). Sampling bees (Hymenoptera: Apiformes) for pollinator community studies: pitfalls of pan-trapping. *J. Kans. Entomol. Soc.*, 73, 225–231.
- Chbika, S. & Aouane E.M. (2021). The adoption of sustainable development indicators in agricultural practices in the Gharb region (Morocco). *E3S Web of Conferences*, 234, 00098.
- Delaplane, K.S. (2021). Wild bees. *Crop Pollination by Bees. Evolution, Ecology, Conservation, and Management*, 1, 128–133. DOI: 10.1079/9781786393494.0010.
- Dellicour, S. & Michez D. (2010). Biologie, observations et collectes de trois espèces sœurs du genre *Melitta* Kirby, 1802 (Hymenoptera, Melittidae). *Osmia*, 4, 29–34. DOI: 10.47446/osmia4.7.
- Duelli, P., Obrist, M.K. & Schmatz D.R. (1999). Biodiversity evaluation in agricultural landscapes: above-ground insects. *Agric., Ecosyst. Environ.*, 74(1–3), 33–64. DOI: 10.1016/s0167-8809(99)00029-8.
- El Abdouni, I., Lhomme, P., Christmann, S., Dorchin, A., Sentil, A., Pauly, A., Hamroud, L., Ihsane, O., Reverté, S., Patiny, S., Wood, T. J., Bencharki, Y., Rasmont, P. & Michez D. (2022). Diversity and Relative Abundance of Insect Pollinators in Moroccan Agroecosystems. *Frontiers in Ecology and Evolution*, 10. DOI: 10.3389/fevo.2022.866581.
- Fiordaliso, W., Saiz, S.R., Ghisbain, G., Wood, T., Ruelle, E., Lefebvre, A., Reese, A., Looockx, M., Tougeron, K. & Michez D. (2024). Reconciling community-level responses of wild bees to highly anthropized landscapes. *Authorea*. DOI: 10.22541/au.172251690.07903371/v1.
- Gonçalves, R.B. & Oliveira P.S. (2013). Preliminary results of bowl trapping bees (Hymenoptera, Apoidea) in a southern Brazil forest fragment. *Journal of Insect Biodiversity*, 1(2), 1. DOI: 10.12976/jib/2013.1.2.
- Gotelli, N. J. & Colwell R.K. (2001). Quantifying biodiversity: procedures and pitfalls in the measurement and comparison of species richness. *Ecol. Lett.*, 4(4), 379–391. DOI: 10.1046/j.1461-0248.2001.00230.x.
- Greenpeace & Public Eye. (2024). *Syngenta exports banned pesticides to Morocco, raising public health and environmental concerns*. <https://en.hespress.com/98436-syngenta-exports-banned-pesticides-to-morocco-raising-public-health-and-environmental-concerns.html>
- Grime, J.P. (2001). *Plant Strategies, Vegetation Processes, and Ecosystem Properties*. Chichester: John Wiley & Sons.
- Hammer, Ø. & Harper D.A. (2001). Past: paleontological statistics software package for education and data analysis. *Palaeontologia Electronica*, 4(1), 1.
- Hammer, Ø. & Harper D.A. (2024). *Paleontological data analysis*. Wiley.
- Herrera, C.M. (1988). Variation in mutualisms: the spatiotemporal mosaic of a pollinator assemblage. *Biol. J. Linn. Soc.*, 35(2), 95–125. DOI: 10.1111/j.1095-8312.1988.tb00461.x.
- Herrera, J. (1988). Pollination relationships in southern Spanish Mediterranean shrublands. *J. Ecol.*, 76(1), 274–287. DOI: 10.2307/2260469.
- Hudewenz, A. & Klein A.M. (2013). Competition between honey bees and wild bees and the role of nesting resources in a nature reserve. *J. Insect Conserv.*, 17(6), 1275–1283. DOI: 10.1007/s10841-013-9609-1.
- Kennedy, C.M., Lonsdorf, E., Neel, M.C., Williams, N.M., Ricketts, T.H., Winfree, R., Bommarco, R., Brittain, C., Burley, A.L., Cariveau, D., Carvalheiro, L.G., Chacoff, N.P., Cunningham, S. A., Danforth, B.N., Dudenhöffer, J., Elle, E., Gaines, H.R., Garibaldi, L. A., Gratton, C. & Kremen C. (2013). A global quantitative synthesis of local and landscape effects on wild bee pollinators in agroecosystems. *Ecol. Lett.*, 16(5), 584–599. DOI: 10.1111/ele.12082.
- Kleijn, D., Baquero, R.A., Clough, Y., Díaz, M., De Esteban, J., Fernández, F., Gabriel, D., Herzog, F., Holzschuh, A., Jöhl, R., Knop, E., Kruess, A., Marshall, E.J.P., Steffan-Dewenter, I., Tscharntke, T., Verhulst, J., West, T.M. & Yela J.L. (2006). Mixed biodiversity benefits of agri-environment schemes in five European countries. *Ecol. Lett.*, 9(3), 243–254. DOI: 10.1111/j.1461-0248.2005.00869.x.
- Kudrnovsky, H., Ellmauer, T., Götzl, M., Paternoster, D., Sonderegger, G. & Schwaiger E. (2020). *Report for a list of Annex I habitat types important for Pollinators*. ETC/B D Report to the EEA, Paris, France.
- Le Féon, V. (2010). *Insectes pollinisateurs dans les paysages agricoles: approche pluri-échelle du rôle des habitats semi-naturels, des pratiques agricoles et des cultures entomophiles*. DXoral dissertation, Université Rennes 1, Rennes 1.
- Leong, J.M. & Thorp R.W. (1999). Colour-coded sampling: the pan colour preferences of oligolectic and nonoligolectic bees associated with a vernal pool plant. *Ecol. Entomol.*, 24, 329–335. DOI: 10.1046/j.1365-2311.1999.00196.x.
- Michener, C.D. (2007). *The Bees of the World*. Baltimore: The Johns Hopkins University Press.
- Noël, G., Bebermans, J., Gengler, N. & Francis F. (2018). Rôle de la transmission des maladies dans le déclin des pollinisateurs–Synthèse bibliographique. *Entomologie Faunistique*, 71.
- Ollerton, J. (2017). Pollinator Diversity: Distribution, Ecological Function, and Conservation. *Annual Review of Ecology, Evolution, and Systematics*, 48(1), 353–376. DOI: 10.1146/annurev-ecolsys-110316-022919.
- Ouvrard, P., Transon, J. & Jacquemart A.L. (2018). Flower-strip agri-environment schemes provide diverse and valuable summer flower resources for pollinating insects. *Biodivers. Conserv.*, 27(9), 2193–2216. DOI: 10.1007/s10531-018-1531-0.
- Park, M.G., Blitzer, E.J., Gibbs, J., Losey, J.E. & Danforth B.N. (2015). Negative effects of pesticides on wild bee communities can be buffered by landscape context. *Proc. R. Soc. B Biol. Sci.*, 282(1809). DOI: 10.1098/rspb.2015.0299.
- Pauly, A. (2019). Les abeilles sauvages du Jardin Botanique “Jean Massart” à Bruxelles (Hymenoptera: Apoidea). *Belgian Journal of Entomology*, 78, 1–86.
- Petanidou, T., Kallimanis, A.S., Tzanopoulos, J., Sgardelis, S.P. & Pantis J.D. (2008). Long-term observation of a pollination network: fluctuation in species and interactions, relative invariance of network structure and implications for estimates of specialization. *Ecol. Lett.*, 11(6), 564–575. DOI: 10.1111/j.1461-0248.2008.01170.x.
- Petanidou, T. & Lamborn E. (2005). A land for flowers and bees: studying pollination ecology in Mediterranean communities. *Plant Biosyst.*, 139(3), 279–294. DOI: 10.1080/11263500500333941.
- Petanidou, T. & Potts S.G. (2006). Mutual use of resources in Mediterranean plant–pollinator communities: how specialized are pollination webs. In N.M. Wasser & J. Ollerton (Eds.), *Plant–pollinator interactions: from specialization to generalization* (pp. 220–244). Chicago: University of Chicago Press.
- Pierre, C., Dumbardon-Martial, E. & Singh C. (2017). Utilisation des bols colorés en Martinique (Antilles françaises): quelles possibilités pour l'inventaire et le suivi des Insectes pollinisateurs des agrosystèmes fruitiers. *Naturae*, 11, 1–16.
- Potts, S.G., Vulliamy, B., Dafni, A., Neëman, G. & Willmer P. (2003). Linking bees and flowers: how do floral communities structure pollinator communities. *Ecology*, 84(10), 2628–2642. DOI: 10.1890/02-0136.
- Potts, S.G., Vulliamy, B., Roberts, S., O'Toole, C., Dafni, A., Neëman, G. & Willmer P. (2005). Role of nesting resources in organising diverse bee communities in a Mediterranean landscape. *Ecol. Entomol.*, 30(1), 78–85. DOI: 10.1111/j.0307-6946.2005.00662.x.
- Rasmont, P. & Iserbyt S. (2012). *Atlas of the European Bees: genus Bombus*. STEP Project.
- Ricketts, T.H., Regetz, J., Steffan-Dewenter, I., Cunningham, S.A., Kremen, C., Bogdanski, A., Gemmill-Herren, B., Greenleaf, S.S., Klein, A.M., Mayfield, M.M., Morandin, L.A., Ochieng, A. & Viana B.F. (2008). Landscape effects on crop pollination services: are there general patterns. *Ecol. Lett.*, 11(5), 499–515. DOI: 10.1111/j.1461-0248.2008.01157.x.
- Rodríguez, S., Pérez-Giraldo, L.C., Vergara, P.M., Carvajal, M.A. & Alaniz A.J. (2021). Native bees in Mediterranean semi-arid agroecosystems: Unravelling the effects of biophysical habitat, floral resource, and honeybees. *Agric. Ecosyst. Environ.*, 307, 107188. DOI: 10.1016/j.agee.2020.107188.

- Roth, T., Coll, M. & Mandelik Y. (2023). The role of uncultivated habitats in supporting wild bee communities in Mediterranean agricultural landscapes. *Diversity*, 15(2), 294. DOI: 10.3390/d15020294.
- Rundlöf, M., Andersson, G.K., Bommarco, R., Fries, I., Hederström, V., Herbertsson, L., Jonsson, O., Klatt, B.K., Pedersen, T.R., Yourstone, J. & Smith H.G. (2015). Seed coating with a neonicotinoid insecticide negatively affects wild bees. *Nature*, 521, 77–80. DOI: 10.1038/nature14420.
- Saleem, M.S., Akbar, M.F., Javed, M.A. & Sultan A. (2023). Neonicotinoid pesticide applications affect pollinator abundance and visitation, leading to implications for sunflower production (*Helianthus annuus* L.). *Cogent Food, Agriculture*, 9(1), 2258773. DOI: 10.1080/23311932.2023.2258773.
- Samih, A., Petit, D., Maatouf, N., Fougrach, H., Hsaine, M. & Rohi L. (2025a). Complexity and dynamics of plant–pollinator (Hymenoptera: Apoidea) interaction networks: habitat fragmentation in the cork oak forest of Larache, Morocco. *Ann. Soc. Entomol. Fr.*, 62(1), 1–15. DOI: 10.1080/00379271.2025.2531817.
- Samih, A., Sentil, A., Maatouf, N., Habbaz, H., Fougrach, H., Hsaine, M., Petit, D. & Rohi L. (2025b). Knowledge of wild bees (Hymenoptera, Apoidea) in the Northwest region of Morocco. *Bol. Asoc. Esp. Entomol.*, 49 (3–4), 303–325. DOI: 10.70186/baeHTBD7118.
- Samih, A., Trócoli, S., Rohi, L., Fougrach, H., Hsaine, M. & Maatouf N. (2024a). Comparative study of the diversity and structure of plant–pollinator interactions in forest and agricultural landscapes in North-western Morocco. *European Journal of Entomology*, 121, 400–412. DOI: 10.14411/eje.2024.044.
- Samih, A., Rohi, L., Soldati, F. & Maatouf N. (2024b). Response of beetle communities and functional groups to changes in structural and compositional biodiversity of cork oak forest and agricultural landscapes in the northwest of Morocco. *Arxius de Miscel·lània Zoològica*, 22(1), 169–183. DOI: 10.32800/amz.2024.22.0169.
- Sauvage, C. (1961). Recherches géobotaniques sur les subéraies marocaines. *Travaux de l'Institut Scientifique Chérifien, série Botanique*, 21, 1–452.
- Schindler, M., Diestelhorst, O., Haertel, S., Saure, C., Scharnowski, A. & Schwenninger R. (2013). Monitoring agricultural ecosystems by using wild bees as environmental indicators. *BioRisk*, 8, 53–71. DOI: 10.3897/biorisk.8.3600.
- Sentil, A., Fiordaliso, W. & Michez D. (2024). Relation between honey bee abundance and wild bee communities in Moroccan agro-ecosystems. *Biodivers. Conserv.*, 34(1), 299–314. DOI: 10.1007/s10531-024-02972-0.
- Sentil, A., Reverté, S., Lhomme, P., Bencharki, Y., Rasmont, P., Christmann, S. & Michez D. (2022a). Wild vegetation and ‘farming with alternative pollinators’ approach support pollinator diversity in farmland. *J. Appl. Entomol.*, 146(9), 1155–1168. DOI: 10.1111/jen.13060.
- Sentil, A., Wood, T.J., Lhomme, P., Hamroud, L., El Abdouni, I., Ihsane, O., Bencharki, Y., Rasmont, P., Christmann, S. & Michez D. (2022b). Impact of the “Farming With Alternative Pollinators” Approach on Crop Pollinator Pollen Diet. *Frontiers in Ecology and Evolution*, 10, 824474. DOI: 10.3389/fevo.2022.824474.
- Sentil, A., Lhomme, P., Michez, D., Reverté, S., Rasmont, P. & Christmann S. (2022c). Farming with Alternative Pollinators approach increases pollinator abundance and diversity in faba bean fields. *J. Insect Conserv.*, 26, 401–414. DOI: 10.1007/s10841-021-00351-6.
- Stanley, D.A., Garratt, M.P.D., Wickens, J.B., Wickens, V.J., Potts, S.G. & Raine N.E. (2015). Neonicotinoid pesticide exposure impairs crop pollination services provided by bumblebees. *Nature*, 528(7583), 548–550. DOI: 10.1038/nature16167.
- Thompson, J.D. (2005). *Plant Evolution in the Mediterranean*. Oxford: Oxford University Press.
- Thomson, J.D. & Wilson P. (2008). Explaining evolutionary shifts between bee and hummingbird pollination: convergence, divergence, and directionality. *Int. J. Plant Sci.*, 169(1), 23–38. DOI: 10.1086/523361.
- Tsiakiris, R., Stara, K., Kazoglou, Y., Kakouros, P., Bousbouras, D., Dimalexis, A., Dimopoulos, P., Fotiadis, G., Gianniris, I., Kokkoris, I. P., Mantzanas, K., Panagiotopoulou, M., Tzortzakaki, O., Vlami, V. & Vrahnakis M. (2024). Agroforestry and the Climate Crisis: Prioritizing Biodiversity Restoration for Resilient and Productive Mediterranean Landscapes. *Forests*, 15(9), 1648. DOI: 10.3390/f15091648.
- Ulyshen, M., Urban-Mead, K.R., Dorey, J.B. & Rivers J.W. (2023). Forests are critically important to global pollinator diversity and enhance pollination in adjacent crops. *Biol. Rev.*, 98(4), 1118–1141. DOI: 10.1111/bvr.12947.
- Wcislo, W.T. (1987). The roles of seasonality, host synchrony, and behaviour in the evolutions of host specificity in cleptoparasitic bees. *Biol. J. Linn. Soc.*, 30(4), 373–394. DOI: 10.1111/j.1095-8312.1987.tb00305.x.
- Wood, T.J. & Cross I. (2017). Specialist bee foraging on Asteraceae in Mediterranean landscapes: evidence from pollen analysis. *Apidologie*, 48(3), 327–339. DOI: 10.1007/s13592-016-0474-0.
- Woodcock, B.A., Bullock, J.M., Shore, R.F., Heard, M.S., Pereira, M.G., Redhead, J., Ridding, L., Dean, H., Sleep, D., Henrys, P., Peyton, J., Hulmes, S., Hulmes, L., Sárospataki, M., Saure, C., Edwards, M., Genersch, E., Knäbe, S. & Pywell R.F. (2017). Country-specific effects of neonicotinoid pesticides on honey bees and wild bees. *Science*, 356(6345), 1393–1395. DOI: 10.1126/science.aaa1190.
- Zamrane, Z. (2016). *Recherche d'indices de variabilité climatique dans des séries hydroclimatiques au Maroc: identification, positionnement temporel, tendances et liens avec les fluctuations climatiques: cas des grands bassins de la Moulouya, du Sebou et du Tensift*. Sciences de la Terre et de l'Eau, Université Cadi Ayyad, Marrakech, 197.
- Zayed, A. & Packer L. (2005). Complementary sex determination substantially increases extinction proneness of haplodiploid populations. *Proc. Natl. Acad. Sci. USA*, 102(30), 10742–10746. DOI: 10.1073/pnas.0502271102.