



Comparative study of the diversity and structure of plant-pollinator interactions in forest and agricultural landscapes in Northwestern Morocco

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Abstract. Fragmentation and destruction of natural habitats threaten essential plant-pollinator interactions. Despite their importance for biodiversity they remain understudied in the context of ecosystem functioning in Morocco. This study examines the influence of forest and agricultural landscapes in Northwestern Morocco on plant-pollinator interactions by analysing the structure and dynamics of their networks. Data were collected between mid-March and mid-July 2023 at eleven sites in different landscapes. The results show significantly higher richness and abundance of pollinators (Hymenoptera, Diptera and Coleoptera) in the cork oak forest of Larache compared to the Gharb plain. High plant diversity in forest landscapes promotes plant-pollinator interactions, enhancing network stability and resilience and the vulnerability of forest.

INTRODUCTION

The destruction and fragmentation of natural habitats, resulting from anthropogenic activities, pose threats to biodiversity and ecosystem functioning (Naeem et al., 2002; Thompson & Ronce, 2010). The loss of biodiversity can endanger crucial ecological interactions such as decomposition, parasitism, predation and pollination (Rollinson et al., 2012; Delmas et al., 2019). Plant-pollinator interactions, for example, are fundamental mutualistic associations crucial for the reproductive success of 88% of all flowering plants, and therefore the functioning of both forest and agricultural habitats (Ollerton et al., 2011; Ollerton, 2017). Conversely, plant-pollinator interactions are often analysed using a network framework, which provides a comprehensive view of their interrelationships (Palla et al., 2005; Pocock et al., 2016).

Using network analysis as an ecological indicator quantifies interactions between plant species and pollinators in natural areas, enhances our understanding of how environmental changes affect the stability and resilience of these networks (Forup & Memmott, 2005; Aizen et al., 2012). By identifying key species and sensitive metrics it is pos-

sible to assess their variations in response to environmental changes while maintaining ecosystem integrity (Dupont & Olesen, 2012; Soares et al., 2017). This information also helps determine community functionality and provides a powerful tool for determining its effects on structure (Janzen, 1974).

The northwestern region of Morocco, including the Larache cork oak forest (*Quercus suber* L.) and the Gharb plain, is a key area for studying cork oak woodlands along the Atlantic coast. This region is characterized by a mixture of cork oak forests and modern plantations (eucalyptus, sugarcane, sunflower) and is experiencing rapid urbanization and intensive agricultural development. These changes pose significant threats to local ecosystems, particularly by their adverse effects on pollinators and their host plants. Forest ecosystems include an abundant and diverse flora that provides essential food and nesting sites for pollinators (Milam et al., 2018; Urban-Mead et al., 2021), without which, they cannot survive or establish viable populations (Rader et al., 2016).

Although local studies have demonstrated the benefits of plant diversity for pollinators within specific agricultural

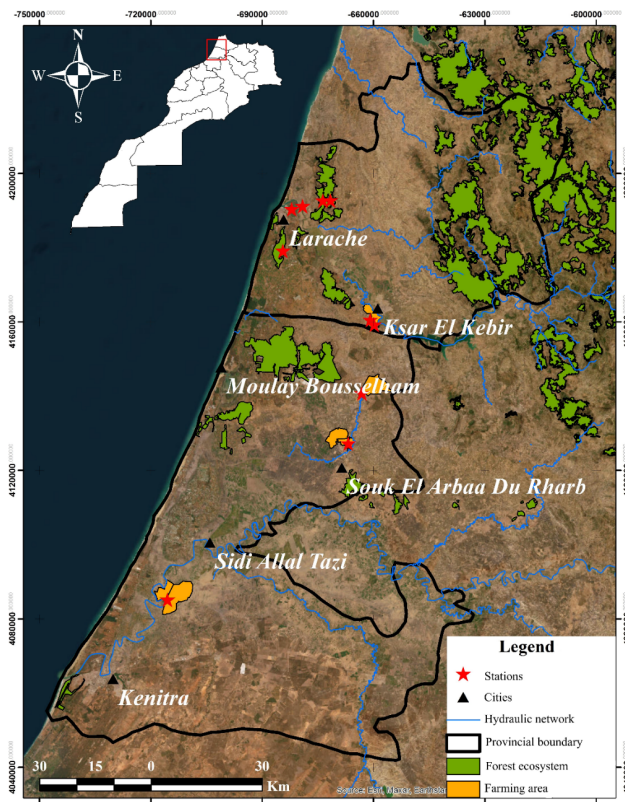


Fig. 1. Map of the Northwestern region of Morocco showing the locations of the sites sampled and the forest and agricultural landscapes.

plots (Sentil et al., 2021; 2022a; Bencharki et al., 2023), there is a critical gap in understanding how these effects translate to larger spatial scales. Specifically, there is a lack of knowledge about how agricultural and forest landscapes support pollinators differently and how these variations effect overall ecosystem functioning.

In this context, a study of plant-pollinator interactions was done in the Northwestern region of Morocco during the period from mid-March to mid-July 2023. This study aimed to address this gap by comparing forest landscapes, such as, the cork oak forest of Larache and agricultural landscapes on the Gharb plain. To achieve this, several hypotheses were proposed. H1: The abundance and species richness of pollinators will differ significantly in forest and agricultural landscapes, in which the former functions as a refuge for pollinators for agricultural landscapes in the Gharb plain, which experience different levels of anthropogenic effects. H2: The structure of plant-pollinator interactions networks will differ in these two landscapes, with forest predicted to be more stable and resilient due to less anthropogenic disturbance. H3: Certain ecological network metrics, such as, specialization, connectance, nestedness, link per species, network asymmetry and plant generality, will be more sensitive to environmental changes, and will reveal differences in network stability and species roles in the two landscapes.

MATERIAL AND METHODS

Study area

The study area is located in the northwestern region of Morocco (Fig. 1), featuring two distinct zones: the cork oak of Larache and the Gharb plain. The Cork oak forest of Larache, located in northwestern Morocco, around the Loukkos River plain, bordered by the Sahel and R'Mel plateaus to the north and south (Ballouche, 2013). This region has a Mediterranean climate. Bioclimatically, the area is classified as subhumid thermomediterranean, with mild to temperate winters. The regional vegetation consists mainly of cork oak forests, classified as “subhumid cork oak forests on sand” (Sauvage, 1961). The Gharb plain is one of the main agricultural areas in Morocco, benefiting from a network of rivers and irrigation canals flowing from the Oued Sebou and its tributaries (Zamrane, 2016). This region has a Mediterranean climate with mild winters and hot summers, and is suitable for intensive agriculture. Farmers in the region cultivate a wide variety of crops (such as, tomatoes, onions, zucchinis, carrots, peppers, oranges, lemons and oilseed) to meet the country's food needs and for export (Chbika & Aouane, 2021).

Choice of the sites sampled

Data was collected between March 15th and July 15th, 2023, at ten sites in contrasting habitats: forest edges, clearings, dense forest and in strips of flowering vegetation in agricultural areas (alongside sunflower and wheat fields). The selection of sites (Table 1) was based on availability of flowering plants, which resulted in an interesting diversity of local pollinating insects. This included five sites in the forest and five in the agricultural area.

Sampling protocol

Before this study, the region was surveyed in 2021 and 2022 in order to identify potential sample sites based on ecological characteristics and the availability of flowering plants. The focus was on the Larache cork oak forest and the Gharb plain, which differed greatly in terms of biodiversity, extent of agriculture and habitat disturbance. The cork oak forest is a relatively intact habitat with a rich biodiversity, whereas the Gharb plain, is characterized by intensive agriculture and highlights the effect of such practices on pollinators. The sites sampled were rich in flowering plants and attractive to local pollinators. Specific ecological features, along with results from the preliminary surveys and previous studies on functional entomofauna, guided the selection process aimed at including various types of habitat and environmental conditions.

The sampling involved surveying pollinators on flowering plants at different sites, over 4 consecutive days per month (mid-March to mid-June 2023). The sampling of interactions between plants and pollinators was done by walking along 4 transects (150 m long and 2 m wide) per site. In addition, the time spent walking along each transect was standardized in order to ensure consist-

Table 1. Satellite coordinates of the sites sampled.

Landscapes	Sites	Latitude	Longitude
Forest	S1	35.21125	-6.03254
	S2	35.208901	-6.057496
	S3	35.200616	-6.099863
	S4	35.194685	-6.126354
	S5	35.111676	-6.147248
Agricultural	S6	34.975211	-5.936347
	S7	34.965498	-5.926937
	S8	34.828096	-5.961945
	S9	34.729699	-5.990363
	S10	34.418241	-6.428204

ency and comparability of the data between sites. Each transect was surveyed for a fixed period of 30 min at all sites in order to avoid any bias in the data collected. This procedure was rigorously followed during each survey to maintain consistency. By walking slowly along each transect and capturing the insects visiting the flowers, using a sweep net (to capture flying insects that move quickly between flowers) or bottle (to collect pollinators directly from the flowers), from 9:00 AM to 4:00 PM provided data was for calculating visitation rates. This time interval includes the period when the pollinators are most active (Gezon et al., 2015; Fijen & Kleijn, 2017). The collection consisted mainly of insects belonging to three groups: Hymenoptera, Diptera and Coleoptera. These groups were chosen as they are known to be important pollinators (Kevan & Baker, 1983; Terzo & Rasmont, 2007; Ouvrard et al., 2018). After collection, specimens were placed in 15 ml centrifuge tubes. Each tube was labelled with the site, transect, date, time and species of plant on which the pollinator was captured. In addition, samples of each plant visited were collected and handed over to botanists (Fougrach Hassan and Hsaine Mohammed) for accurate identification and inclusion in an herbarium for scientific documentation purposes.

Specimens of Hymenoptera were classified to 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 identification was conducted by a team of taxonomists, including: Ahlam Sentil and William Flordaliso did general identification and other families. Pierre Rasmont focused on *Bombus* and *Anthophora*, while Simone Flaminio specialized in *Lasioglossum*. Thomas James Wood was responsible for *Andrena*, *Osmia*, *Megachile* and additional genera including *Nomiapis* and *Sphecodes*. Achik Dorchin identified *Eucera*, Guillaume Ghisbian worked on *Dasygaster*, and Romain Le Divelec focused on *Hylaeus*. Michael Terzo, Max Kasperek and Andreas Muller identified other families. The collected Diptera and Coleoptera were examined in the laboratory, identified to genus and/or species level using a binocular microscope and various identification keys and catalogues. For species confirmation, they were compared with specimens in the museum's collections of the CIRF (Center for Innovation, Research and Training) and the Museum of the Scientific Institute of Rabat (Morocco).

Data analysis

Abundance and diversity analysis of the three groups of pollinators

The Tukey's test (PAST 4.13) was used to compare the abundance and species richness of the three pollinator groups (Hymenoptera, Coleoptera and Diptera) in forest and agricultural landscapes. This choice was based on preliminary analyses that confirmed the data met the assumptions for parametric testing. Specifically, for abundance data, Hymenoptera had homogeneous variances (Levene's test: $F = 28.88$, $p = 0.06$) and a normal distribution (Shapiro-Wilk test: $W = 0.93$, $p = 0.62$). Coleoptera had similar results, with homogeneous variances (Levene's test: $F = 30.58$, $p = 0.07$) and a normal distribution (Shapiro-Wilk test: $W = 0.95$, $p = 0.73$). For Diptera, the variances were also homogeneous (Levene's test: $F = 34.41$, $p = 0.08$) and the data normally distributed (Shapiro-Wilk test: $W = 0.96$, $p = 0.78$). Regarding species richness, the data for Hymenoptera again had homogeneous variances (Levene's test: $F = 16.48$, $p = 0.26$) and a normal distribution (Shapiro-Wilk test: $W = 0.87$, $p = 0.2$). Coleoptera followed the same pattern, with variances confirmed as homogeneous (Levene's test: $W = 8.33$, $p = 0.7$) and a normal distribution (Shapiro-Wilk test: $W = 0.86$, $p = 0.27$). Finally, Diptera also had homogeneous variances (Levene's test: $F = 8.10$, $p = 0.2$) and was normally distributed (Shapiro-Wilk test: $W = 0.94$, $p = 0.68$).

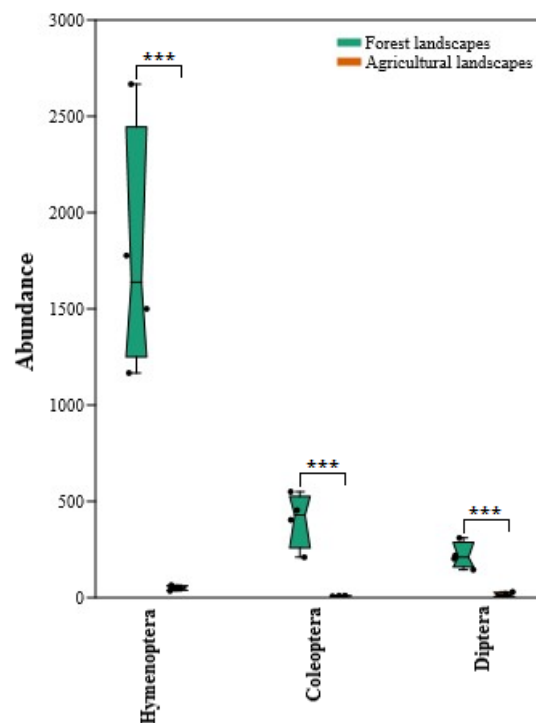


Fig. 2. Difference in the mean abundance of three pollinator groups in the two landscapes: Forest and agricultural. The boxplots illustrate the median, quartiles and outliers, with significant differences indicated by Tukey's test (** $p \leq 0.001$).

These results validated the use of Tukey's test for analysing and comparing both the abundance and species richness of the pollinators in the different landscapes.

A heatmap was constructed using the OriginPro 2023, utilizing the "Matrix plot", to visualize interactions between different families of pollinators and plant families. This was done using the number of visits by each family to plants in forest and agricultural landscapes.

Plant-pollinator networks

Interaction data were structured as a quantitative matrix. For each landscape, a quantitative matrix was created with species of plants in rows and pollinators in columns. The cells indicate the number of individuals of pollinator species 'I' visiting plant species 'J'. This statistical analysis of plant-pollinator interaction networks was carried out for both forest and agricultural landscapes. This approach is considered to be the most informative and precise for analysing interaction networks (Blüthgen & Klein, 2011; Dormann & Strauss, 2014). Network analyses were done using the "bipartite" package (Dormann et al., 2008, 2017) in R statistical software version 4.2.1. This package is specifically designed for bipartite network analysis and includes the main function "networklevel" (Dormann et al., 2008) for calculating network-level indices, making it the appropriate tool for this study. To thoroughly explore the interaction network data, six metrics were selected that are sensitive to changes in environmental quality (Albrecht et al., 2007; Soares et al., 2017):

Connectance (C). Indicates the number of realized links out of all possible links in the network studied (Bersier et al., 2002; Dormann et al., 2009). Its values range from 0 to 1, with higher values indicating more realized interactions (Vizentin-Bugoni et al., 2018).

Specialization index (H2'). Evaluates the specialization of interactions between species in the network by measuring how specific or generalist the interactions are (Blüthgen et al., 2006;

Table 2. Number of different species recorded visiting flowers of the three groups of pollinators in forest and agricultural landscapes in the Northwest region of Morocco.

Landscape	Group	Family	Genus / Species	Number
Forest	Hymenoptera	Andrenidae	<i>Andrena antigana</i> (Pérez, 1895)	28
			<i>Andrena avara</i> (Warncke, 1967)	451
			<i>Andrena bellidis</i> (Pérez, 1895)	64
			<i>Andrena djelfensis</i> (Pérez, 1895)	15
			<i>Andrena flavipes</i> (Panzer, 1799)	281
			<i>Andrena fulvicornis</i> (Schenck, 1853)	7
			<i>Andrena insignis</i> (Warncke, 1974)	338
			<i>Andrena labialis</i> (Kirby, 1802)	74
			<i>Andrena lagopus</i> (Latreille, 1809)	19
			<i>Andrena morio</i> (Brullé, 1832)	82
			<i>Andrena oraniensis</i> (Lepelletier, 1841)	18
			<i>Andrena orbitalis</i> (Morawitz, 1871)	113
			<i>Andrena poupillieri</i> (Dours, 1872)	38
			<i>Andrena propinqua</i> (Schenck, 1853)	37
			<i>Andrena ranunculi</i> (Schmiedeknecht, 1883)	125
			<i>Andrena rhyssnata</i> (Pérez, 1895)	45
			<i>Andrena simontornyiella</i> (Noskiewicz, 1939)	15
			<i>Andrena spreta</i> (Pérez, 1895)	172
			<i>Andrena vulcana</i> (Dours, 1873)	229
		Apidae	<i>Anthophora blanda</i> (Percz, 1812)	12
			<i>Apis mellifera</i> (Linnaeus, 1758)	1568
			<i>Bombus terrestris</i> (Linnaeus, 1758)	18
			<i>Eucera collaris</i> (Dours, 1873)	262
			<i>Eucera elongatula</i> (Vachal, 1907)	29
			<i>Eucera grisea</i> (Fabricius, 1793)	29
			<i>Eucera nadigi</i> (Friese, 1924)	53
			<i>Heliothia</i> (<i>Anthophora</i>) sp. (Klug, 1807)	41
			<i>Nomada accentifera</i> (Pérez, 1895)	20
			<i>Nomada numida</i> (Lepelletier, 1841)	17
			<i>Nomada panurginoides</i> (Saunders, 1908)	13
			<i>Nomada stigma</i> (Fabricius 1804)	19
		Colletidae	<i>Hylaeus cornutus</i> (Curtis, 1831)	53
			<i>Hylaeus purpurissatus</i> (Vachal, 1895)	42
		Halictidae	<i>Halictus scabiosae</i> (Rossi, 1790)	53
			<i>Lasioglossum algericolellum</i> (Strand, 1909)	368
			<i>Lasioglossum callizonium</i> (Pérez, 1895)	189
			<i>Lasioglossum glabriusculum</i> (Morawitz, 1872)	170
			<i>Lasioglossum immunitum</i> (Vachal, 1895)	167
			<i>Lasioglossum malachurum</i> (Kirby, 1802)	219
			<i>Lasioglossum mediterraneum</i> (Blüthgen, 1925)	401
			<i>Lasioglossum pauperatum</i> (Brullé, 1832)	132
			<i>Lasioglossum prasinum</i> (Smith, 1848)	267
			<i>Nomioides minutissimus</i> (Rossi, 1790)	29
			<i>Seladonia gemmea</i> (Dours, 1872)	47
		Megachilidae	<i>Anthidiellum strigatum</i> (Panzer, 1805)	5
			<i>Megachile ericetorum</i> (Lepelletier, 1841)	70
		Melittidae	<i>Megachile sicula</i> (Rossi, 1792)	61
			<i>Osmia submicans</i> (Morawitz, 1870)	23
		Scoliidae	<i>Dasypoda maura</i> (Pérez, 1896)	70
			<i>Dasypoda visnaga</i> (Rossi, 1790)	54
		Sphecidae	<i>Megascolia maculata</i> (Drury, 1773)	19
			<i>Scolia hirta</i> (Schrank, 1781)	20
		Buprestidae	<i>Ammophila</i> sp. (W. Kirby, 1798)	17
			<i>Anthaxia scutellaris</i> (Gené, 1839)	87
		Cerambycidae	<i>Anthaxia umbellatarum</i> (Fabricius, 1787)	71
			<i>Stenopterus ater</i> (Linnaeus, 1767)	76
		Meloidae	<i>Stenopterus rufus</i> (Linnaeus, 1767)	100
			<i>Stictoleptura fontenayi</i> (Mulsant et Rey, 1839)	15
		Melyridae	<i>Chlorophorus sexguttatus</i> (Lucas, 1849)	18
			<i>Cerocoma vahli vahli</i> (Fabricius, 1787)	21
		Melyridae	<i>Croscherichia paykulli</i> (Billberg, 1813)	52
			<i>Hycleus duodecimpunctatus</i> (Olivier, 1811)	92
		Melyridae	<i>Hycleus rufipalpis</i> (Escalera, 1909)	96
			<i>Psilothrix viridicoerulea</i> (Geoffroy, 1758)	63
Forest	Coleoptera	Oedemeridae	<i>Chitona connexa</i> (Fabricius, 1798)	190
			<i>Oedemera barbara</i> (Fabricius, 1792)	39
			<i>Oedemera femorata</i> (Scopoli, 1763)	13
		Scarabaeidae	<i>Anthoplia floricola</i> (Fabricius 1787)	14
			<i>Anthypna meles</i> (Fabricius, 1792)	6
			<i>Blitopertha lineata</i> (Fabricius, 1798)	72
			<i>Eulasia goudoti</i> (Laporte, 1840)	427
			<i>Hoplia bilineata</i> (Fabricius, 1801)	53
			<i>Oxythrea funesta</i> (Poda, 1761)	39
			<i>Paratriodonta</i> sp. (Baraud, 1962)	49
			<i>Phyllopertha horticola</i> (Linnaeus, 1758)	16
			<i>Trichius zonatus</i> (Germar, 1831)	6
			<i>Tropinota squalida</i> (Brullé, 1832)	117
		Tenebrionidae	<i>Gasthraema rufiventris</i> (Waltl, 1835)	101
			<i>Heliotaurus ruficollis</i> (Fabricius, 1781)	167
		Bombyliidae	<i>Bombylius major</i> (Linnaeus, 1758)	8
		Calliphoridae	<i>Chrysomya</i> sp. (Robineau-Desvoidy, 1830)	9
		Conopidae	<i>Thecophora atra</i> (Fabricius, 1775)	13
		Conopidae	<i>Myopa dorsalis</i> (Fabricius, 1775)	17
		Sarcophagidae	<i>Miltogramma oestracea</i> (Fallén, 1820)	21
		Stratiomyidae	<i>Odontomyia flavissima</i> (Rossi, 1790)	24
	Diptera	Syrphidae	<i>Eupeodes corollae</i> (Fabricius, 1794)	5
			<i>Sphaerophoria scripta</i> (Linnaeus, 1758)	95
			<i>Sphaerophoria taeniata</i> (Meigen, 1822)	107
			<i>Episyrphus balteatus</i> (De Geer, 1776)	344
			<i>Eristalinus taeniops</i> (Wiedemann, 1818)	57
			<i>Eristalis tenax</i> (Linnaeus, 1758)	117
			<i>Ceriana vespiformis</i> (Latreille, 1809)	9
			<i>Atylotus</i> sp. (Osten Sacken, 1876)	13
		Tabanidae	<i>Silvius alpinus</i> (Scopoli, 1763)	11
			<i>Tabanus atratus</i> (Fabricius, 1775)	12
		Tachinidae	<i>Gymnosoma clavatum</i> (Rohdendorf, 1947)	14

Table 2 (continued).

Landscape	Group	Family	Genus / Species	Number
Agricultural	Hymenoptera	Andrenidae	<i>Andrena aerinifrons</i> (Dours, 1873)	5
			<i>Andrena bellidis</i> (Pérez, 1895)	9
			<i>Andrena flavipes</i> (Panzer, 1799)	34
			<i>Andrena fulvicornis</i> (Schenck, 1853)	11
			<i>Andrena miegiella</i> (Dours, 1873)	7
		Apidae	<i>Apis mellifera</i> (Linnaeus, 1758)	65
			<i>Eucera nadigi</i> (Friese, 1924)	5
			<i>Eucera nigrilabris</i> (Lepeletier, 1841)	1
			<i>Eucera oblitterata</i> (Pérez, 1895)	7
			<i>Nomada bifasciata</i> (Olivier, 1811)	5
	Colletidae	<i>Hylaeus cornutus</i> (Curtis, 1831)	7	
		Halictidae	<i>Lasioglossum pauperatum</i> (Brullé, 1832)	4
	<i>Nomiapis rufiventris</i> (Lepeletier, 1841)		13	
	<i>Sphecodes rubicundus</i> (Hagens, 1875)		7	
	Coleoptera	Megachilidae	<i>Osmia notata</i> (Fabricius, 1804)	17
		Cerambycidae	<i>Certallum ebulinum</i> (Linné, 1767)	9
		Meloidae	<i>Lytta vesicatoria</i> (Linnaeus, 1758)	11
		Melyridae	<i>Melyris abdominalis</i> (Fabricius, 1787)	2
			<i>Psilothrix viridicoerulea</i> (Geoffroy, 1758)	9
		Scarabaeidae	<i>Blitopertha lineata</i> (Fabricius, 1798)	4
Bombyliidae		<i>Bombylius major</i> (Linnaeus, 1758)	4	
Stratiomyidae		<i>Odontomyia annulata</i> (Meigen, 1822)	4	
Diptera		Syrphidae	<i>Brachypalpus valgus</i> (Panzer, 1797)	3
			<i>Sphaerophoria taeniata</i> (Meigen, 1822)	6
	<i>Episyrphus balteatus</i> (De Geer, 1776)		21	
	<i>Eristalinus megacephalus</i> (Rossi, 1794)		6	
	<i>Eristalis tenax</i> (Linnaeus, 1758)		6	
	Tachinidae	<i>Melanostoma mellinum</i> (Linnaeus, 1758)	3	
		<i>Cylindromyia brassicaria</i> (Fabricius, 1775)	8	
TOTAL			9877	

Miranda et al., 2019). Specialization values range from 0 to 1, with higher values indicating greater specialization and lower values indicating the opposite (Dzekashu et al., 2023).

Nestedness (wNODF). Measures the degree of hierarchy in the network. It describes a non-random pattern in which links from specialist species primarily connect with generalist species. Niche values range from 0 to 100, where 0 indicates fully nested networks (Classen et al., 2020) and 100 random networks (Almeida-Neto & Ulrich, 2011; Petanidou et al., 2018).

Links per species. The average number of qualitative links for all species in the network. It is simply the average of the number of species from the other group with which each animal or plant species in the network interacts (Fonkalsrud, 2014).

Network asymmetry. Shown to correlate with asymmetry in the specialization between plants and pollinators, such that the less abundant group is more specialized “positive number would indicate more pollinator species than plant species” (Blüthgen et al., 2007).

Plant generality. The weighted average number of pollinator species per plant species. Equivalent to vulnerability in trophic networks (Bersier et al., 2002).

RESULTS

In total, 9877 flower visitors were collected in this study, belonging to 108 species and 63 genera in the three groups of pollinators (Hymenoptera, Coleoptera, and Diptera), in both the forest and agricultural landscapes (Table 2).

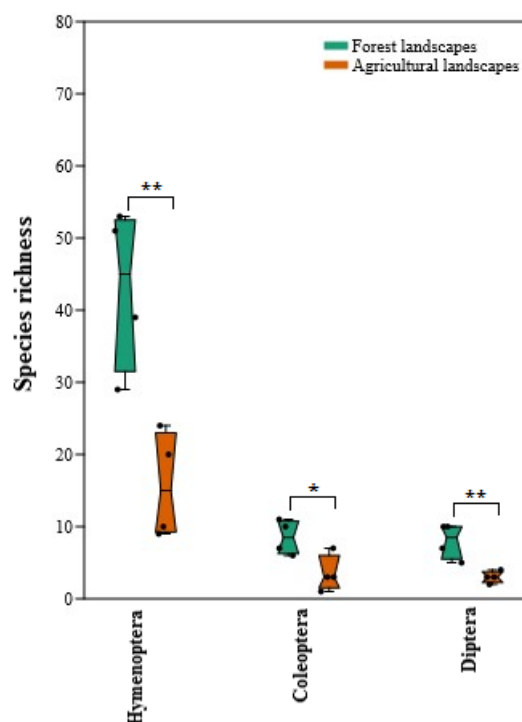


Fig. 3. Difference in species richness of the three groups of pollinators in the two landscapes: Forest and agricultural. The boxplots illustrate the median, quartiles and potential outliers, with significant differences indicated by Tukey's test (* $p \leq 0.05$; ** $p \leq 0.01$).

Table 3. Descriptive statistics of pollinator abundance in forest and agricultural landscapes.

Pollinators	Landscapes	Abundance	Mean \pm S.E.	Min	Max	Q2	Q1	Q3
Hymenoptera	Forest	6707	1777.75 \pm 321.57	1167	2667	1638.5	1250.25	2444.5
	Agricultural	197	49.25 \pm 6.14	35	65	48.5	38.25	61
Coleoptera	Forest	2000	404.5 \pm 71.56	210	550	429	258.5	526
	Agricultural	35	8.75 \pm 0.75	7	10	9	7.25	10
Diptera	Forest	876	219 \pm 34.21	145	310	210.5	159.25	287.25
	Agricultural	61	15.25 \pm 5.99	5	30	13	5.25	27.5

Q1: 25th (First quartile), Q2: Median, Q3: 75th (Third quartile).

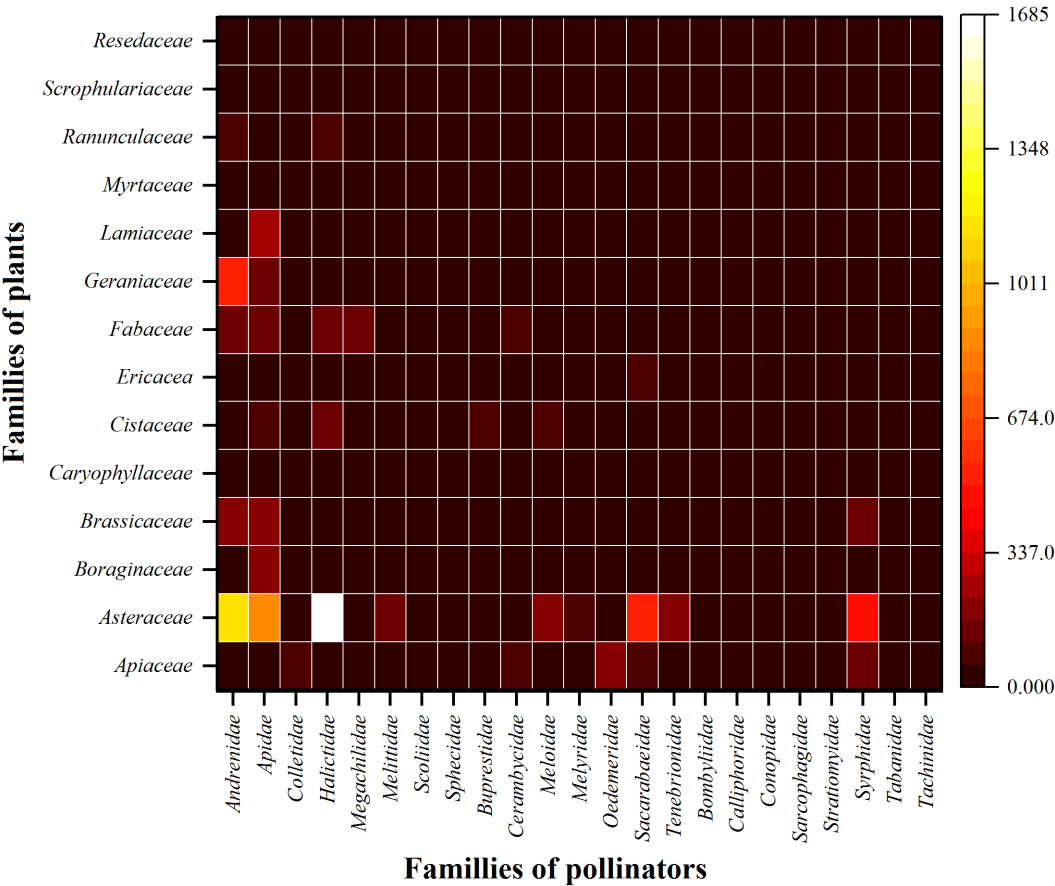


Fig. 4. Heatmap showing the insect families pollinating each plant family in the forest landscape.

Abundance and diversity of pollinators

The results showed a highly significant difference in the abundance of the three pollinator groups in the forest and agricultural landscapes (Fig. 2). Hymenoptera was the most abundant group in both landscapes, but were significantly ($P = 0.001$) more abundant in the forest (6708 individuals) than in agricultural landscapes (197 individuals). Similarly, Coleoptera were much more abundant in the forest (2000 individuals) than in the agricultural landscape (35 individuals) ($P = 0.001$). Diptera followed the same trend, with a higher abundance in forest (876 individuals) than in the agricultural landscape (293 individuals) ($P = 0.001$). Table 3 presents detailed descriptive statistics of abundance for each group of pollinators in forest and agricultural landscapes.

In terms of species richness (Fig. 3), Hymenoptera was significantly more diverse in the forest landscape, with 53

species recorded, compared to only 15 species in the agricultural landscape ($P = 0.006$). Similarly, for Coleoptera there were 26 species in the forest landscape and only five in the agricultural landscape ($P = 0.02$). There was also a greater richness of Diptera in the forest landscape, with 17 species recorded compared to nine in the agricultural landscape, and this difference is highly significant ($P = 0.008$). Table 4 presents detailed descriptive statistics of species richness for each group of pollinators in forest and agricultural landscapes.

Plant-pollinator interactions

In the forest landscape a total of 9584 interactions between 38 species of flowering plants, belonging to 14 families, and 96 species of pollinator were recorded (Fig. S1). Among these interactions, Hymenoptera were the most active pollinators, accounting for 6708 interactions, followed by beetles with 2000 and flies only 876 visits.

Table 4. Descriptive statistics of species richness of pollinators in forest and agricultural landscapes.

Pollinators	Landscapes	Species richness	Mean \pm S.E.	Min	Max	Q2	Q1	Q3
Hymenoptera	Forest	53	43 \pm 5.59	29	53	45	32	52.5
	Agricultural	15	15.75 \pm 3.70	9	24	15	9.3	23
Coleoptera	Forest	26	8.5 \pm 1.19	6	11	9	6.3	10.8
	Agricultural	5	3.5 \pm 1.25	1	7	3	1.5	6
Diptera	Forest	17	8 \pm 1.22	5	10	9	5.5	10
	Agricultural	9	3 \pm 0.40	2	4	3	2.3	3.75

Q1: 25th (First quartile), Q2: Median, Q3: 75th (Third quartile).

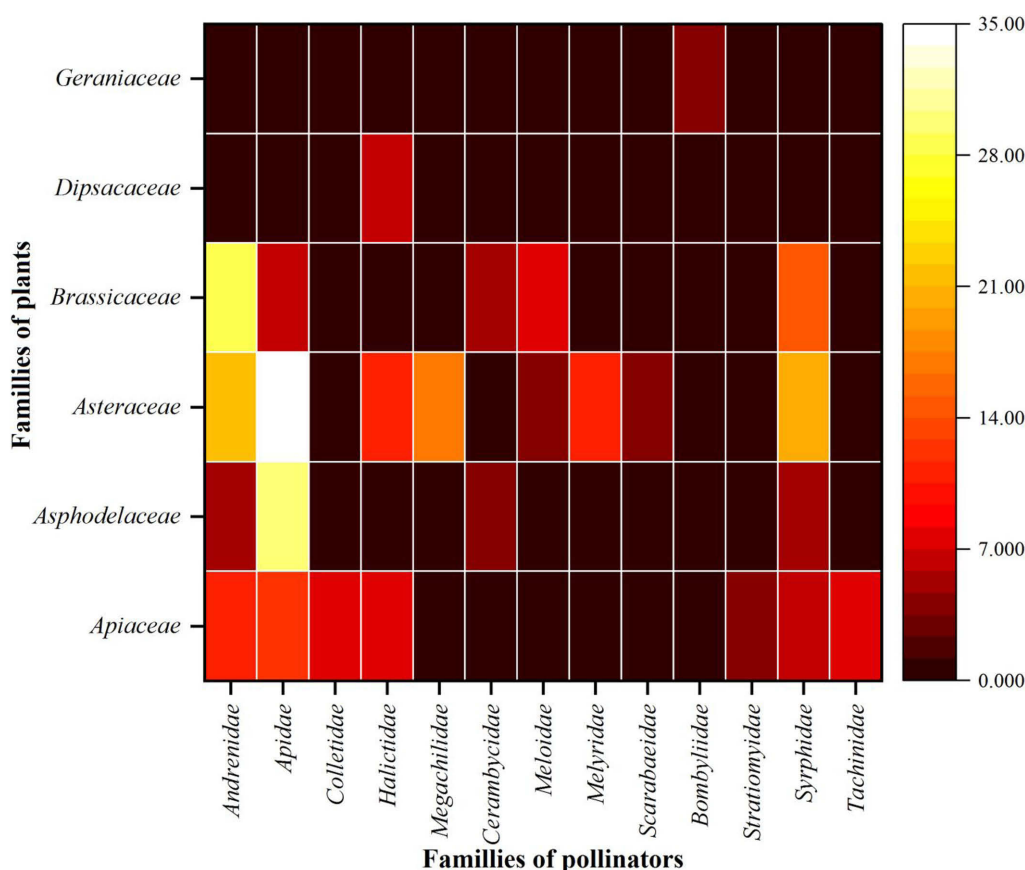


Fig. 5. Heatmap showing insect families pollinating each plant family in the agricultural landscape.

Examining the different pollinator families more closely (Fig. 4), Andrenidae, Apidae and Halictidae were the most frequently recorded Hymenoptera, with 2151 (32.1%), 2081 (31.02%) and 2042 (30.44%) visits, respectively. For Coleoptera, Scarabaeidae was the most represented, with 799 interactions, accounting for 39.95% of the total recorded visits. Diptera were mainly represented by Syrphidae, with 734 visits, or 79% of the total visit by flies.

In the agricultural landscape, fewer interactions (293) between 12 species of flowering plants, belonging to 6 different families, and 29 species of pollinator were recorded (Fig. S2). Hymenoptera were the most active pollinators, accounting for 197 interactions, followed by flies with 61 visits and beetles with only 35 visits.

Based on the most frequent interactions (Fig. 5), Apidae and Andrenidae were the most frequently observed, with 83 (42.13%) and 66 (33.50%) visits, respectively. Syrphidae was the most represented of the Diptera, contributing 73.77% with 45 interactions of the total number of visits.

Table 5. The community-level network indices calculated for the forest and agricultural landscapes.

Network description	Forest landscape	Agricultural landscape
Specialisation (H^2)	0.52	0.71
Connectance (C)	0.07	0.12
Nestedness (wNODF)	9.78	7.58
Link per species	2.09	1.04
Asymmetry	0.43	0.41
Pollinator generality	7.65	2.01
Vulnerability (V)	10.15	4.35

Among Coleoptera, the Meloidae and Melyridae were the most active, each accounting for 11 (31.42%) interactions.

Descriptors of plant-pollinator interaction networks

The calculated indices (Table 5) describe the various properties of the plant-pollinator interaction networks in both forest (Fig. S1) and agricultural landscapes (Fig. S2). In the forest landscape, network specialization is lower ($H^2 = 0.52$) than in the agricultural landscape ($H^2 = 0.71$). Network connectance is also lower in the forest landscape ($C = 0.07$) than in the agricultural landscape ($C = 0.12$), indicating fewer recorded interactions relative to all possible potential interactions. However, despite the lower connectance, nestedness is higher in the forest (wNODF = 9.78) than in the agricultural landscape (wNODF = 7.58). In addition, each species is associated with a greater number of links on average in the forest (2.09) than in the agricultural landscape (1.04). Network asymmetry is similar in both landscapes. Regarding pollinator generality, it is much higher in the forest (7.65) than the agricultural landscape (2.01). Finally, vulnerability is higher in the forest (10.15) than in the agricultural landscape (4.35).

DISCUSSION

Comparison of the pollinators of the flowering plants in agricultural and forest landscapes

Forest landscape

There was a significantly higher richness and abundance of pollinators (Hymenoptera, Diptera, and Coleoptera) in

the Larache cork oak forest than in the agricultural landscape. This can be attributed to the greater floral and structural diversity in the forest, which provide a greater variety of niches and food resources for pollinators (Potts et al., 2006; Christmann et al., 2021b).

Hymenoptera. Hymenoptera are predominantly represented by bees in oak forests (Potts et al., 2006). The most frequently observed bees in the forest landscape belonged to the families Andrenidae, Apidae and Halictidae. Forests provide numerous nesting and foraging opportunities for a wide range of species of bees (Perlik et al., 2024). Studies indicate that the soil is an ideal substrate for solitary bee nests, particularly species of *Lasioglossum* (Halictidae) and *Andrena* (Andrenidae) (Christmann et al., 2021a). This is, accounted for by the fact that the majority of these species nest in the soil, and therefore cork oak forest is a nesting resource for these species. The Andrenidae, primarily represented by species of the genus *Andrena*, recorded 2151 visits (32.06%). Among the plants visited, species of Asteraceae, such as *Leontodon maroccanus*, are frequently visited by *Andrena insignis* (Warncke, 1974) and *Andrena avara* (Warncke, 1967) with 176 and 137 visits, respectively. The strong attractiveness of Asteraceae to Andrenidae can be attributed to their abundance, diversity and easy access to nectar and pollen (Larkin et al., 2008). The Apidae, with 2081 visits (31.02%), were mainly recorded in the forest landscape. *Apis mellifera* (Linnaeus, 1758), the domestic honeybee, accounted for the highest number of visits with 1568 interactions, reflecting its generalist behaviour and ability to feed on a great diversity of nectar and pollen sources (Klein et al., 2007). *Eucera collaris* (Scopoli, 1770) with 262 visits, primarily with species of Asteraceae, particularly *Otospermum glabrum* (129 visits) and *Glebionis coronaria* (56 visits), most likely because they are an abundant and rich nutritional resource in Mediterranean habitats (Potts et al., 2006). The Halictidae with 2042 visits (30.44%), which highlights their importance in forest pollination networks. Species of the genus *Lasioglossum* were particularly active, foraging a wide variety of species of Asteraceae, indicating they are also likely to be important pollinators in Morocco (Bencharki et al., 2023). *Lasioglossum mediterraneum* (Blüthgen, 1926) with 401 interactions, highlights the strong attraction of Asteraceae for this genus. Polidori et al. (2010) notes that *Lasioglossum* is particularly attracted to the colour yellow, which is the colour of the flowers of Asteraceae, which are frequently visited by these pollinators.

Coleoptera. The diversity of beetles in forest ecosystems is enhanced by the larvae of many of them being saproxylic and develop in dead wood and plant debris, aiding nutrient decomposition and recycling (Jonsson et al., 2005). Beetles, particularly Scarabaeidae, had the highest number of interactions, with 799 visits, making up 39.95% of total visits. Some plants in the Eastern Mediterranean basin are pollinated by hairy beetles of this family (Dafni et al., 1990). Many species of Scarabaeidae forage on a broad range of flowering plants, but have a marked preference for Asteraceae. *Eulasia goudotti* (Boisduval, 1833), with 427

interactions, had a strong affinity for *Hypochaeris glabra* (221 visits) and *Glebionis coronaria* (166 visits). Studies report that Scarabaeidae are important pollinators of Asteraceae, as its pollen makes up a high percentage of their pollen loads (Mayer et al., 2006). Beetles are only effective pollinators for a few plants (Dafni et al., 1990).

Diptera. In the forest landscape, Syrphid flies are predominant and account for 734 interactions, or 79% of all-visits by flies. The high abundance of Syrphidae is linked to their larvae developing in decaying wood and organic matter, which are abundant in cork oak forests. This habitat provides essential resources for both larval development and adult foraging (Ricarte et al., 2009). Syrphidae are strongly attracted to the flowers of *Ammi majus* of the Apiaceae, a plant with small flowers (Tooker, 2006; Wojciechowicz-Żytka, 2019). This species was visited by almost all of the hoverflies. *Episyrphus balteatus* (De Geer, 1776) stands out as the hoverfly with the highest number of visits, totaling 344 interactions.

Agricultural landscapes

In contrast, in the agricultural landscape there were far fewer interactions between pollinators and flowering plants, with only 12 plant species belonging to 7 different families and a total of 29 visitors. This can be attributed to various anthropogenic factors, including landscape simplification, monocultures, and intensive use of pesticides and herbicides, which limit food resources for pollinators and alter plant communities (Potts et al., 2010; Goulson, 2013).

Hymenoptera. Agricultural landscapes, with their more uniform and disturbed conditions, offer fewer resources and nesting sites, which limits diversity and abundance of Hymenoptera (197 visits). The families Apidae and Andrenidae were the most frequently recorded, which account for 83 (42.13%) and 66 (33.50%) of the total visits, respectively. The highest number of interactions were recorded for *Apis mellifera* (65 visits), followed by *Andrena flavipes* (Panzer, 1799) with 34 interactions. However, these numbers are lower than those recorded in the forest landscape, where the diversity of flowering plants is higher. Bees relying on a narrow range of pollen sources or non-preferred host plants are not likely to thrive (Kleijn & Raemakers, 2008; Sentil et al., 2022b). Furthermore, the absence of ecological niches for ground-nesting species prevents them from becoming established. For example, Halictidae are less prevalent (12.18%), as they require undisturbed soil, which is rare in agricultural landscapes due to intensive plowing.

Diptera. Among flies (61 visits), hoverflies were the most frequently recorded, with 45 interactions, accounting for 73.77% of total visits within this group. However, this is lower than in the forest landscape, indicating that its structural complexity and floral diversity provide more favourable conditions for Syrphidae. Specifically, *Episyrphus balteatus* (De Geer, 1776) was the dominant species, with 21 visits. In addition, the agricultural landscape lacked niches for saproxylic larvae, which accounts for the lower abundance of Syrphidae in this environment, where resources and shelters for larval stages are limited.

Coleoptera. For beetles (35 visits), the situation is similar. The larval stages of many species of beetle are saproxylic, but there is little or no dead wood in agricultural landscapes. The families Meloidae and Melyridae were the most active, each contributing 11 interactions (31.42% of total visits). While they frequently visit flowers, their short tongues limit their ability to feed on those with exposed nectaries, making them poor pollinators (Davies, 2012). For example, *Psilothrix viridicoerulea* (Geoffroy, 1785) had the highest number of visits (nine interactions) but is also recognized as a poor pollinator (Bartomeus et al., 2008), as it occupies certain flowers, reducing accessibility for bees and hoverflies (Barbir et al., 2015).

Structure and dynamics of plant-pollinator interactions

The interaction specialization index is lower in forest ($H' = 0.52$) compared to agricultural landscapes ($H' = 0.71$), indicating greater interaction diversity within the cork oak habitat, where many species of plants are pollinated by a wide range of pollinators. This indicates that plant-pollinator interactions in the forest landscape are less specific and more generalized (Gómez et al., 2010), which is in accord with higher plant generality in forest (7.65) than in agricultural landscapes (2.01). In agricultural areas, habitat simplification and environmental disturbances lead to more specific and less diverse interactions. In contrast, in forest ecosystems there is a high diversity of plants, many habitats and resource stability, facilitating generalized and diverse interactions between plants-pollinators (Klein et al., 2007; Winfree et al., 2011). For instance, Santamaría et al. (2018) report similar patterns in other Mediterranean habitats, where generalized networks support a greater diversity of interactions. Furthermore, the interaction network in the forest landscape is less connected ($C = 0.07$) than in the agricultural landscape ($C = 0.12$). Higher connectance indicates a network where a greater number of interactions among species (Jordano et al., 2006). In forest landscapes, lower connectance may result from several factors. High structural and floral complexity can lead to incomplete sampling of interactions due to species diversity and abundance. In addition, ecological factors like predation can disrupt plant-pollinator relationships, limiting interactions. This lower connectance may indicate higher specialization or many underrepresented interactions in the data. Thus, while connectance can signal stability (Thébault & Fontaine, 2010), nevertheless, a network with low connectance might still be resilient if species are functionally diverse and adaptable (Fortuna & Bascompte, 2006). Although the connectance of the interaction network in the forest landscape was lower, and even though the total number of potential interactions was not fully realized, the nestedness of the network is much higher ($wNODF = 9.78$). Although realized potential interactions are fewer in the forest landscape, each species is more likely to engage with a diverse range of partners (Bascompte et al., 2003). This is due to the high species diversity, availability of many ecological niches, and relative habitat stability in forest ecosystems (Blüthgen & Klein, 2011). In the agricultural landscape,

although the total number of interactions was higher, the nestedness is lower ($wNODF = 7.58$), this means that while more potential interactions occur, they involve fewer species. Habitat simplification may reduce both species diversity and interactions within the ecological network (Garibaldi et al., 2013). Each species was associated with a greater number of links on average in the forest (2.09) than in the agricultural landscapes (1.04). This difference suggests closer cooperation among species in forest than in agriculture landscapes. In forest landscapes, the high diversity of plant and animal species results in numerous interactions, fostering greater cooperation and interdependence (Memmott et al., 2004).

The forest landscape is much more vulnerable (10.15) than the agricultural landscape (4.35), which may indicate a greater fragility of the interaction networks in the forest, where species are more dependent on each other. In other words, the agricultural habitat has already been simplified, so there is nothing left to simplify. Therefore, the perceived vulnerability of the forest landscape simply reflects the fact that it is more complex. However, the loss of a pollinator species could have significant repercussions on the reproduction of the plants associated with it, jeopardizing the stability of the network (Fortuna & Bascompte, 2006).

CONCLUSION

This study underscores the need for rigorous analysis of plant-pollinator networks, especially in forest landscapes, where interactions are often underestimated. Biases in sampling between forest and agricultural landscapes highlight the necessity for more precise methods to understand connectance and its ecological implications. The cork oak forest of Larache is particularly vulnerable to environmental disturbance; the loss of key pollinators could trigger cascading effects that threaten ecosystem stability. This interdependence makes forest habitats sensitive to climate change and human pressures.

This research presents a new record for *Nomada stigma* (Fabricius, 1804), which is absent from the recent checklist of Moroccan bees. Additional studies are needed to refine the taxonomy of complex genera like *Nomada*. These findings reveal gaps in our knowledge about the distribution of this species, suggesting it may have been misidentified or undocumented in the region studied due to the complexity of this genus. Moreover, this species was found in samples from the cork oak forests of Larache, highlighting the role of forest ecosystems as refuges for potentially rare and threatened species. Thus there is a need to increase sampling in these areas in order to better record the biodiversity and implement effective conservation measures.

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Supplementary Figs S1 and S2 follow on next page.

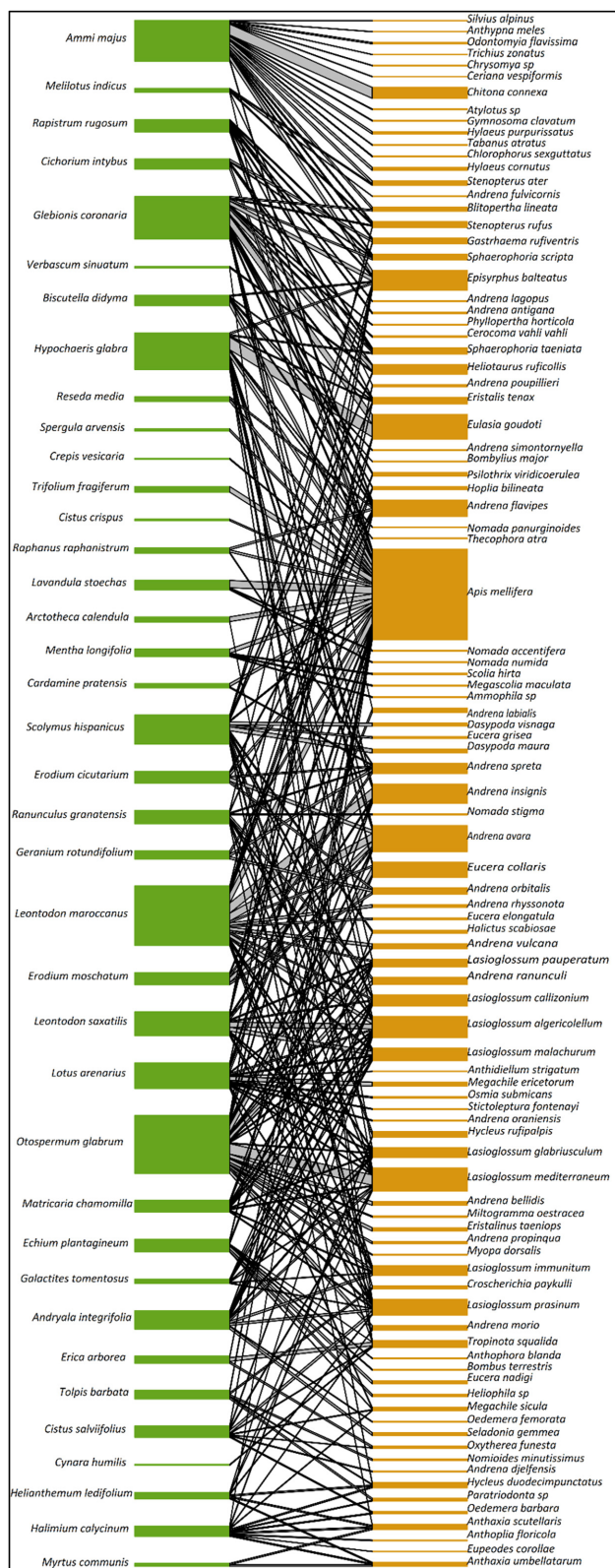


Fig. S1. Plant-pollinator interaction network in the forest landscape (Cork oak of Larache).

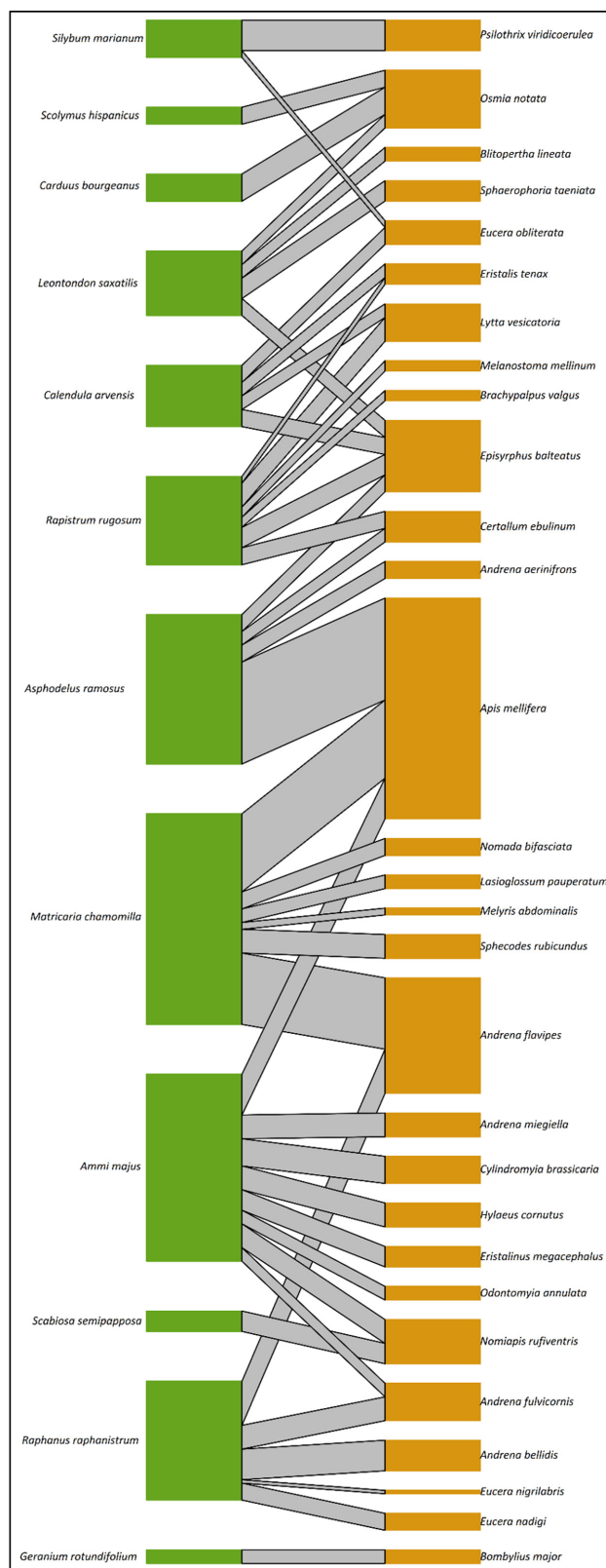


Fig. S2. Plant-pollinator interaction network in the agricultural environment (Gharb plain).