Article

POLLEN SOURCE GATHERED BY MANAGED HONEY BEES AND UNMANAGED WILD BEES: IMPLICATIONS FOR WILD BEES' CONSERVATION IN THE INSULAR ECOSYSTEMS OF THE TUSCAN ARCHIPELAGO NATIONAL PARK

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Abstract—Insect pollination supports biodiversity in natural and agricultural systems. However, increasing beekeeping activity raises concerns about the impacts of managed *Apis mellifera* on wild bees, already threatened by land-use change, agricultural intensification, pesticides, climate change, and invasive species. Understanding interspecific interactions is therefore essential to inform wild bee conservation and management strategies. This study investigated pollen resource use and trophic niche overlap between managed honey bees and wild bee communities on Capraia, Elba, and Giglio islands, within the Tuscan Archipelago National Park, through morphological and molecular pollen analyses. Pollen-use overlap with managed honey bees was recorded in 58.7% of the interactions with wild bee species, with an overall medium–low niche overlap ($\alpha \leq 0.59$), while only 16.7% of interactions showed high overlap. Significant differences in pollen composition were detected between honey bees and the genera *Andrena*, *Bombus*, *Ceratina*, *Colletes*, *Heriades*, *Megachile* and *Seladonia*. These patterns may suggest limited trophic competition between honey bees and wild bees, but low niche overlap does not necessarily imply its absence. The negative relationship observed between honey bee density and pollen overlap suggests that wild bees may increasingly rely on alternative pollen sources under higher honey bee densities, indicating trophic repartition as a potential response to competitive pressure. Since National Parks play a key role in conserving pollinators, precautionary approaches towards a low-intensity beekeeping management and further research on the mechanisms underlying these interactions that may potentially threat the survival of wild bee communities are essential for their conservation.

Keywords—*Apis mellifera*, Apoidea, palynological analysis, protected area, trophic competition

INTRODUCTION

Insect pollination is a fundamental ecosystem service supporting biodiversity, ecosystem functioning, and agricultural production, with important ecological and economic value (Gill et al. 2016). Through the mutualistic plant-bees relationship, it ensures plant reproduction and contributes to the maintenance of both plant and bee diversity (Bascompte & Jordano 2007; Ollerton

2017; Hristov et al. 2020). In the context of global wild bee decline, mostly due to land-use change, agricultural intensification, pesticides, pollution, climate changes, invasive species introduction and parasites (Michez et al. 2026), their conservation is urgent (Hristov et al. 2020). The honey bee (*Apis mellifera*, L. 1758) is the most managed wild insect pollinator worldwide and is widely used for pollination purposes both in agricultural (Khalifa et al. 2021) and natural or semi-natural ecosystems (Hung et al. 2018). This led to an exponential increase of beekeeping activity and of the number of managed honey bee colonies, especially in some countries of the Mediterranean Basin. This phenomenon raises important concern about the gradual replacement of the natural populations of wild bees by *A. mellifera* (Herrera 2020), as well as the extinction of wild *A. mellifera* classified by the IUCN as endangered species in EU (Moro et al. 2025). Conservation concern about populations is heightened by the fact that the conservation status of most wild bee populations cannot be assessed populations, due to lack of data (Quaranta et al. 2018; Michez et al. 2026). In addition, high-intensity honey bee management could be detrimental to the maintenance of wild pollinator communities that, depending on inhabited ecosystem type, may have variable tolerance to different thresholds of honey bee colony densities (Abou-Shaara, 2025; Magrach et al. 2025). This last factor represents a relevant threat especially in insular ecosystems that are different from those of mainland and even more worthy of attention in natural protected areas for which biodiversity conservation is a priority. Insular ecosystems are characterized by unique biodiversity with isolated and endemic bee populations whose movement is spatially limited, and by limited floral resources (Kaiser-Bunbury et al. 2010; Manes et al. 2021; Pasquali et al. 2025). For these reasons, islands are more vulnerable to the introduction of alien species and/or human-managed organisms (Shavit et al. 2009; Lázaro et al. 2021). Competition is more likely under conditions such as: introduction of novel competitors (e.g., alien species with higher foraging efficiency) (Stout and Morales, 2009), environmental changes reducing floral resource availability (Ostwald et al., 2024), and high densities of highly competitive species (Magrach et al., 2025). Honey bees may compete with wild bees through direct and indirect negative interaction, i.e. interference and exploitative competition, respectively (Park 1962; Schoener 1983). Interference competition, involving direct aggressive interactions between individuals, appears to be relatively rare. Although pollen theft by honey bees from the bodies of wild bees has occasionally been documented (Jean, 2005), current evidence suggests that this type of competition is unlikely to have major effects on wild pollinator populations (Geslin et al., 2017). Conversely, exploitative competition occurs when different species share limited resources, potentially reducing the survival, fecundity, or abundance of one or more competitors (Park, 1962). Because honey bees and wild bees often overlap in their use of nectar and pollen resources, exploitative competition is considered the most likely mechanism through which managed honey bees may negatively affect wild bee populations (Mallinger et al., 2017; Iwasaki & Hogendoorn, 2022).

Interspecific trophic competition between wild bees and managed honey bees is frequently reported as one of the main threats for wild bees' conservation purposes (Mallinger et al. 2017; Iwasaki & Hogendoorn, 2022; Abou-Shaara 2025). Negative correlation between number of wild bees' species and beekeeping load has been recorded in the Greek and Italian islands suggesting that a high presence of honey bees may cause local extinctions in wild pollinators (Lázaro et al. 2021; Pasquali et al. 2025). Evidence for behavioural competition between honey bees and native bees has also been found in the Mediterranean region of Israel by Shavit et al. (2009), which recommended to prohibit the introduction of beehives in protected areas.

Interspecific trophic competition remains yet a highly complex and very context-dependent biological phenomenon that needs to be fully investigated and understood through a conservation perspective (Abou-Shaara 2025; Pike & Rittschof, 2025). Focusing on these interspecific interactions is fundamental to fill the lack of information on Apoidea threat state and, consequently, to arrange action plans for the conservation of wild bee species and ecosystems. When trophic competition occurs, managed honey bees negatively impact on wild bee populations affecting different aspects of their biology, such as

the foraging behaviour, the fecundity, the abundance, the fitness and the survival of the populations (Paini 2004; Goulson & Sparrow 2009; Hudewenz & Klein 2015; Torné-Noguera et al. 2016; Lindstrom et al. 2016;). Nevertheless, there are still some gaps in the scientific literature that hamper the assessment of whether interspecific trophic competition represents a threat for wild bee populations. In particular, the real impact of honey bees on wild bee fitness is still poorly investigated, and most studies focus on only a few genera of wild bees, often assessing broad general trends rather than informing targeted conservation strategies (Pike & Rittschof, 2025). Furthermore, the feeding habits of some understudied wild bee species and the lack of evidence that overlapping trophic resource use strictly negatively impacts wild bee survival, still limit the possibility to identify the trend of the effect of honey bee presence on wild bees (Pike & Rittschof, 2025).

Interspecific trophic competition is more likely to occur whenever availability of floral resource is limited (Steffan-Dewenter & Tscharntke, 2000; Paini 2004). This makes protected island ecosystems particularly suitable and important contexts for investigating the potential impact of beekeeping activity on wild bees' conservation (Chowdhury et al. 2022). The aim of this study was to investigate pollen resource use and trophic niche overlap between managed honey bees and wild bee communities on Capraia, Elba, and Giglio islands within the Tuscan Archipelago National Park (Italy). Although trophic niche overlap cannot be considered a direct measure of interspecific competition, analysing pollen resource use is highly informative (Boni et al. 2025), as pollen constitutes the fundamental resource for bee reproduction and larval development, directly influencing population survival (Müller et al. 2006; Brodschneider et al. 2010; Nicolson 2011).In particular we aimed to: (i) characterize the composition and temporal dynamics of pollen resources exploited by managed honey bees and wild bees, combining palynological analysis and DNA metabarcoding; (ii) quantify the degree of trophic niche overlap between *A. mellifera* and wild bees at different taxonomic resolutions (species, genus, and community level) and across seasons, in order to assess how overlap varies among taxa, islands, and sampling periods; (iii) evaluate whether variation in managed honey bee colony density is associated with changes in pollen use overlap between honey bees and wild bees, as a first step toward assessing the potential role of beekeeping intensity in shaping resource partitioning within insular pollinator communities.

MATERIALS AND METHODS

STUDY AREAS AND POLLEN SAMPLINGS

The study was performed on Capraia and Giglio islands from 2021 to 2024 and on Elba Island from 2021 to 2022 in the Tuscan Archipelago National Park, Italy. The Tuscan Archipelago National Park, located in the Tyrrhenian Sea between the Tuscan coast and Corsica, includes also, from North to South, Gorgona, Pianosa, Montecristo and Giannutri islands, and covers 59% of the area of these islands (Fig. 1). On the three experimental islands, pollen from both managed honey bees and wild bees was sampled in a pre-determined area (Capraia: 43°03'14"N, 9°49'54"E; Elba: 42°47'53"N, 10°22'37"E; Giglio: 42°22'50"N, 10°53'34"E). Capraia Island (19.33 km²) is located approximately 60 km from the mainland and is characterized by a well-developed Mediterranean maquis dominated by strawberry tree (*Arbutus unedo*), tree heath (*Erica arborea*), mock privet (*Phillyrea* spp.), holm oak (*Quercus ilex*), mastic tree (*Pistacia lentiscus*), alatern (*Rhamnus alaternus*), myrtle (*Myrtus communis*), rockroses (*Cistus* spp.), everlasting flower (*Helichrysum* spp.), and spurges (*Euphorbia* spp.). Elba Island (223.24 km²), the largest island of the Tuscan Archipelago, is the closest island to the mainland (10 km) and the most heavily influenced by human activities, including tourism, agriculture, and historical mining. It hosts a high variety of habitats, including Mediterranean maquis, holm oak woodlands, chestnut forests, pine plantations, and coastal habitats. Mediterranean maquis is widespread at lower elevations and is mainly composed of strawberry tree, tree heath, mock privet, mastic tree, myrtle, rockroses, and other typical Mediterranean shrub species. Giglio Island (24.01 km²) is located approximately 17 km from the mainland. Mediterranean maquis is one of the island's dominant ecosystems and supports a high diversity of plant and animal species. Other important habitats include traditional agricultural terraces, holm oak woodlands, and pine forests. Since competition is expected to be highest when

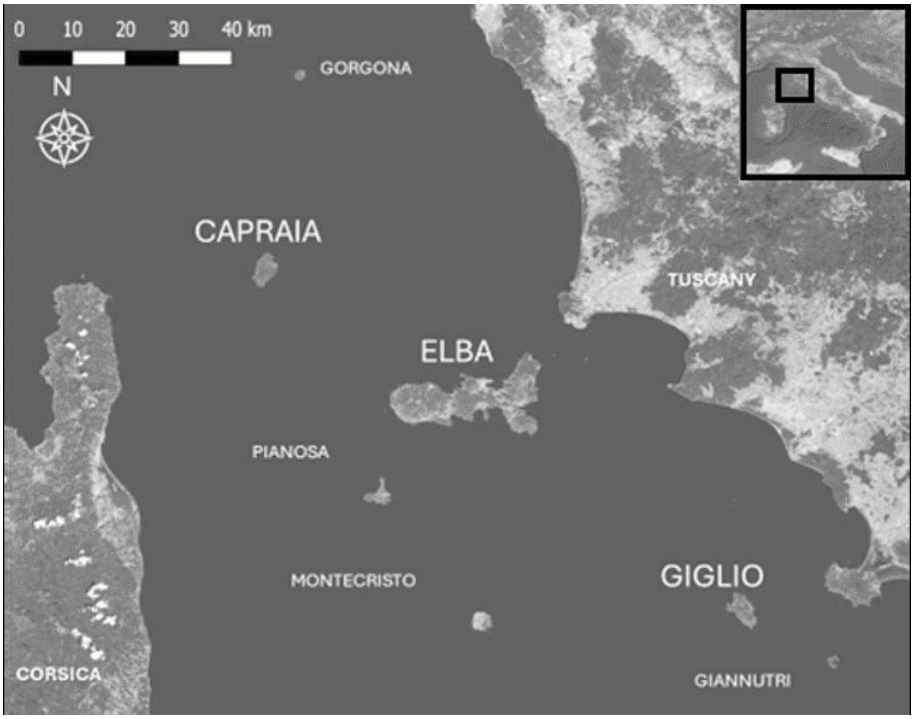


Figure 1. Map of the Tuscan Archipelago (Italy). Pollen samplings were performed on Capraia, Elba and Giglio Islands.

there is the greatest overlap in niche space (Wojcik et al. 2018) and at a distance of 0.6-1.1 km from apiaries (Henry & Rodet, 2018, 2020), sampling areas of approximately 0.5 km^2 were characterised by the presence of an apiary at a maximum distance of 1 km set up in a mixed-heterogeneous habitat.

During the study period, four sessions (February-March, April-May, June-July, September-October) of pollen sampling were performed yearly on each island. During each sampling session (lasting 1 hour i.e., from 12:00 to 13:00), five to ten female wild bees carrying pollen were opportunistically captured with an entomological net, placed in a 50 ml plastic tube, and killed by freezing (-20°C). At the same time, 2 g of pollen gathered by one colony of honey bees were collected from pollen trap set up on one hive in the apiary at least a day before and placed in a plastic tube. During field sampling, a list of flowering species present in the surroundings of sampling areas and flower species on which wild bees were captured were also recorded. Each sample was stored at -20°C until analysis.

For each sampling session (N = 38 on Capraia Island; N = 28 on Elba Island; N = 48 on Giglio Island), the density of honey bees (number of hives/km^2) for each Island was extracted from the Italian national beekeeping registry (https://www.vetinfo.it/j6_statistiche/#/report-pbi/45). The geographic locations of registered apiaries are not publicly available for privacy reasons. Consequently, although the exact number of hives was known for the apiary from which honey bee pollen samples were collected, the presence of honey bees from the surrounding apiaries within each study area could not be excluded, particularly given the limited spatial extent of the study islands. To account for the overall beekeeping pressure, honey bee density was therefore estimated using municipality-level data from the registry. Specifically, data from the municipalities of Isola di Capraia and Giglio Porto, each corresponding to the entire island, were used for Capraia and Giglio, respectively, whereas data from the municipality of Portoferraio were used for Elba, as the focal apiary was located within this municipality. Therefore, municipality-level hive density was used as a macro-scale screening indicator of overall extent of beekeeping activity, rather than a precise measure of honey bee colony density within the individual sampling areas.

Palynological analysis and taxonomic identification of wild bees

Morphological pollen analysis was performed following the methodology described in Louveaux et al. (1978), Ricciardelli D'Albore (1978), Ricciardelli D'Albore (1997), Ricciardelli D'Albore

(1998) and Palmieri et al. (2017). Pollen loads of each pollen sample gathered by honey bees were divided based on the colour and each group was weighted. For each colour, two pollen loads were suspended in 3 ml of sterile water and homogenized using a Pasteur-pipette. A microscope slide for each colour group was prepared by using 200 µl of pollen suspension and glycerin jelly for permanent preparations. Pollen grains identification was performed by observation via the optical microscope OBN 132 Transmitted light laboratory microscope (KERN, Albstadt, Ebingen, Germany) with total magnification of 400x, 600x and 1000x. Pollen grains were identified by using a reference collection from Pisa University and morphology guides (Ricciardelli D'Albore & Persano 1978; Ricciardelli D'Albore 1997, 1998, 2007; Palmieri et al. 2017, PalDat.org). The frequency of each pollen type in the blend was determined as percentage on a total of 2 grams of the analysed mixture. Pollen gathered by wild bees was removed from every specimen using a steel spatula or by washing the entire insect in 3 ml of sterile water. A microscope slide for each pollen mixture gathered by wild bees was prepared using the same procedure described above. Pollen grains were counted to determine the relative abundance (%) of each type for each slide. The nomenclature of each pollen types was assigned in accordance with Persano Oddo & Ricciardelli D'Albore (1989). Whenever necessary, to increase the identification of pollen grain at a fine taxonomic resolution, a DNA-metabarcoding analysis was also performed at Zooplant Lab (Milano, Italy) on honey bee pollen samples (Tommasi et al. 2021).

Captured wild bees were subsequently subjected to taxonomic recognition through analysis of diagnostic morphological traits in the entomological laboratory of CREA (Bologna, Italy), as well as using diagnostic keys (Rasmont et al. 2021) and/or DNA-barcoding analysis whenever necessary. DNA for DNA-barcoding was extracted from single legs of captured specimens following the HotSHOT method (Lunt 2017). The subsequent amplification targeting the 658 bp region of the mitochondrial cytochrome c oxidase (cox1) gene (Hebert et al. 2003) was performed using the Qiagen *Taq* PCR Master Mix Kit (QIAGEN, Hilden, Germany) and Folmer primers (Folmer et al. 1994). Sequencing was carried out on Nanopore GridION using MinION and Flongle flowcells (Oxford Nanopore Technologies, Oxford, United Kingdom).

Data analysis

Pollen networks and pollen use overlap between honey bees and wild bees

Pollen network graphs were generated with the composition of pollen (i.e., the relative abundance of pollen types) for each island and each sampling session, and for three different taxonomical levels of wild bee: species, genera and the general level "wild bees", by using the R-package bipartite (R Core Team 2022) (Dormann et al. 2009). In each network, the two sets of nodes represented bee taxa and plant taxa identified through palynological analyses, whereas links represented bee–plant interactions weighted by the relative abundance (%) of each pollen type in the corresponding pollen loads.

To test whether the composition of pollen gathered by honey bees significantly differed from the pollen gathered by wild bees, a permutational multivariate analysis of variance (PERMANOVA, 999 permutations) based on Bray–Curtis dissimilarity matrices was applied. Prior to PERMANOVA, the assumption of homogeneity of multivariate dispersions was tested using a permutation test on Bray–Curtis distances (betadisper; vegan R package). All tests were non-significant, indicating comparable within-group dispersion and supporting the validity of PERMANOVA results. These analyses were performed separately for each sampling session and each island, by comparing honey bee pollen to the pollen gathered by wild bee genera, represented at least by three individuals. The dissimilarities were visualized through a Principal Coordinates Analysis (PCoA). Both PERMANOVA and PCoA analyses were performed using the vegan R package.

Pianka index (1973), applied to the relative abundance of pollen types gathered by each bee species, was used to assess the niche overlap between honey bees and a wild bee within the same sampling session and on the same island:

$$\alpha jk = \frac{\sum_i^n Pij * Pik}{\sqrt{\sum_i^n Pij^2 \quad \sum_i^n Pik^2}}$$

where αjk is Pianka index of niche overlap between bee species *j* and bee species *k*, P*ij* is the proportion of plant taxa i^{th} on the total resources used by bee species *j*, P*ik* is the proportion of plant taxa i^{th} on the total resources used by bee species *k*. The index ranges from 0 to 1, indicating a low and a high degree of niche overlap, respectively. As Pianka index has no universally accepted interpretative thresholds, a value of ≥0.6 was adopted as an operational criterion to identify bee pairs showing relatively high trophic overlap. This threshold was selected to represent substantial overlap on the 0–1 scale of the index and was used solely to facilitate the interpretation and comparison of the results. To verify whether the overlap in pollen use may vary depending on the taxonomic group of wild bees considered, Pianka index was calculated for each sampling session and for each island, for three different taxonomical levels of wild bee: species, genera and the general level "wild bees". To assess the reliability of Pianka index calculated for each interaction *A. mellifera* – wild bee species, a bootstrap resampling (1000 iterations) was applied. To ensure sufficient data for the variability assessment, this analysis was restricted to genera and species represented by at least three samples. For each interaction, the 95% confidence interval (CI) of Pianka index was calculated from the bootstrap distribution, and the width of the intervals were interpreted as a measure of the estimate reliability (Fischer 2019). As no universally accepted threshold exists for the interpretation of bootstrap confidence interval widths for Pianka's index, a conservative operational threshold of 0.4 was adopted to identify estimates with relatively high precision and CI width <0.4 was then considered as reliable.

Effects of honey bee densities on wild bee pollen use

Relationships between the honey bee densities and the overlap of pollen use with wild bees, were analysed by using beta regression, with Pianka indices as response variables. Since indices included values equal to 0 and 1, a Smithson-Verkuilen transformation (Smithson & Verkuilen, 2006) was applied prior to model fitting to map the response variable to the open interval (0,1). All analyses and visualizations were performed in R (v.4.3), using the *betareg*, *ggplot2*, and *patchwork* packages.

RESULTS

From palynological analysis of wild bee and honey bee pollen a total of 122 plant taxa, of which 18 at species level, 92 at genus level, and 12 at family level, were identified (Supplementary Table 1).

Overall, a total of 268 wild bees, belonging to 18 genera and 51 species, were captured on the three islands during the sampling period (Supplementary Table 2).

At the species level, a total of 92 interactions between the pollen collected by honey bees and that collected by wild bees were observed (Fig. 2 - 4). Of these, 54 (58.7%) showed pollen use overlap with honey bees ($\alpha > 0$) (Table 1) while the absence of overlap was recorded in the remaining 41.3% (38/92) of interactions, all represented by only one or two individuals per species. At genus level, a total of 43 interactions between the pollen collected by honey bees and that collected by wild bees were performed (Fig. 2 - 4). Of these, 41 (95.3%) showed pollen use overlap with honey bees ($\alpha > 0$) (Table 1). By applying PERMANOVA analyses significant differences in pollen gathered by honey bees and wild bees were detected for 26.67% (8/30) of the wild bee genera analysed: on Capraia for *Andrena* (PERMANOVA, $R^2 = 0.5$; $F = 6.12$; $P = 0.024$) and *Bombus* (PERMANOVA, $R^2 = 0.2$; $F = 6.26$; $P = 0.001$) in April-May, on Elba for *Bombus* (PERMANOVA, $R^2 = 0.2$; $F = 2.77$; $P = 0.011$) and *Seladonia* (PERMANOVA, $R^2 = 0.4$; $F = 4.65$; $P = 0.015$) in April-May and June-July, respectively, and on Giglio for *Bombus* (PERMANOVA, $R^2 = 0.2$; $F = 2.31$; $P = 0.046$) in February-March, for *Andrena* (PERMANOVA, $R^2 = 0.3$; $F = 6.16$; $P = 0.002$) and *Colletes* (PERMANOVA, $R^2 = 0.4$; $F = 4.3$; $P = 0.003$) in April-May, and for *Seladonia* (PERMANOVA, $R^2 = 0.1$; $F = 1.86$; $P = 0.048$) and *Ceratina* (PERMANOVA, $R^2 = 0.4$; $F = 4.77$; $P = 0.011$) in June-July (Supplementary Fig. 1).

The Pianka niche overlap index (Pianka 1973) was applied to the relative abundance of pollen types, where α ranges from 0 (no overlap) to 1 (complete overlap); values $\alpha > 0.6$ were considered high overlap. Pianka indices applied to the pollen composition gathered by honey bees and "wild bee" group indicated the occurrence of a high niche overlap (i.e. $\alpha > 0.6$) only on Capraia Island in June-July ($\alpha = 0.603$), while values recorded

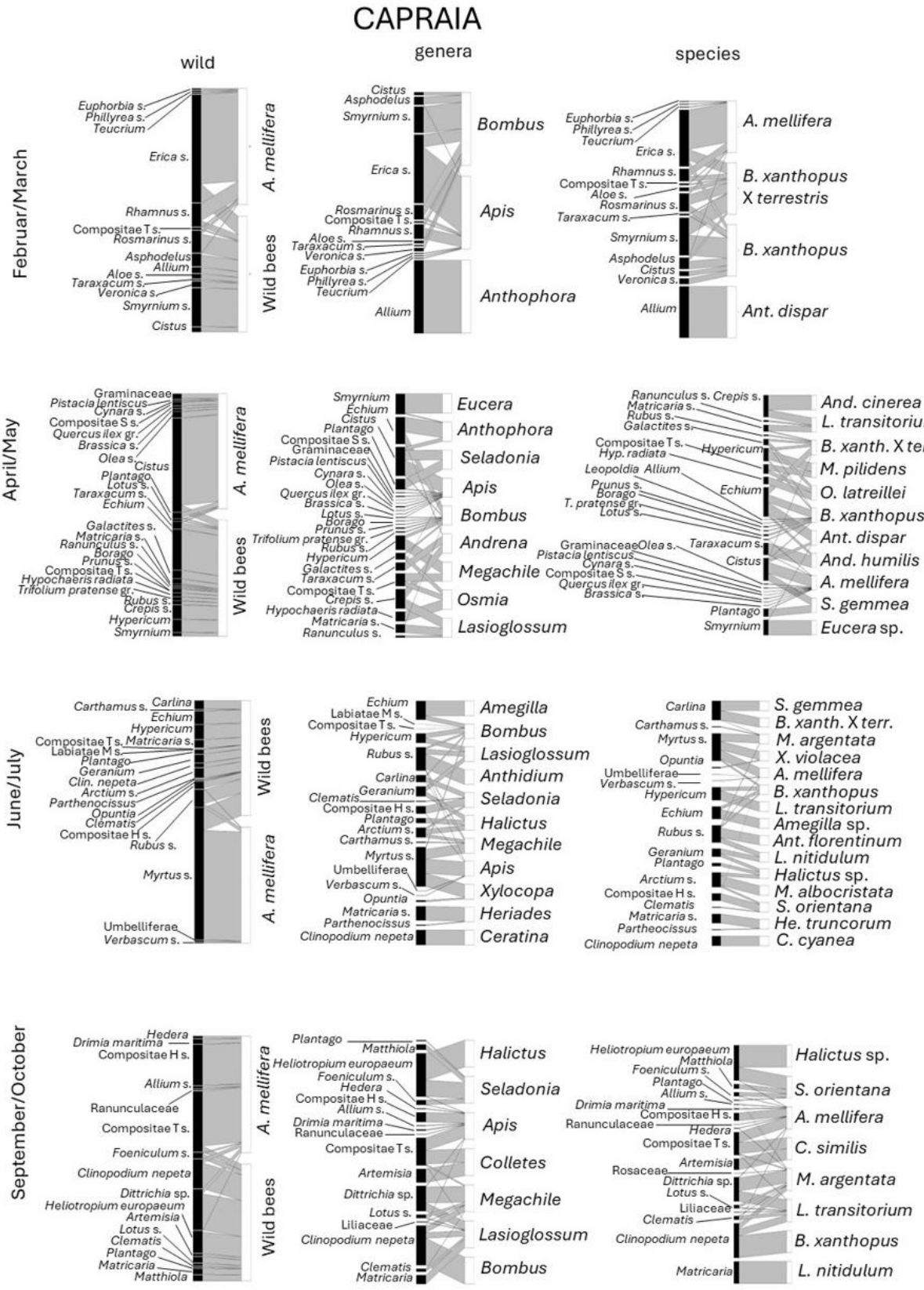


Figure 2. Pollen networks of bees sampled in Capraia Island in each sampling session for three different taxonomical levels of wild bee: the general level "wild bees" (left), genera (center) and species (right). Black bar height indicates the relative abundance (%) of pollen grains gathered per plant taxa across bee species (white bar). (HB: honey bees; s: shape; gr: group).

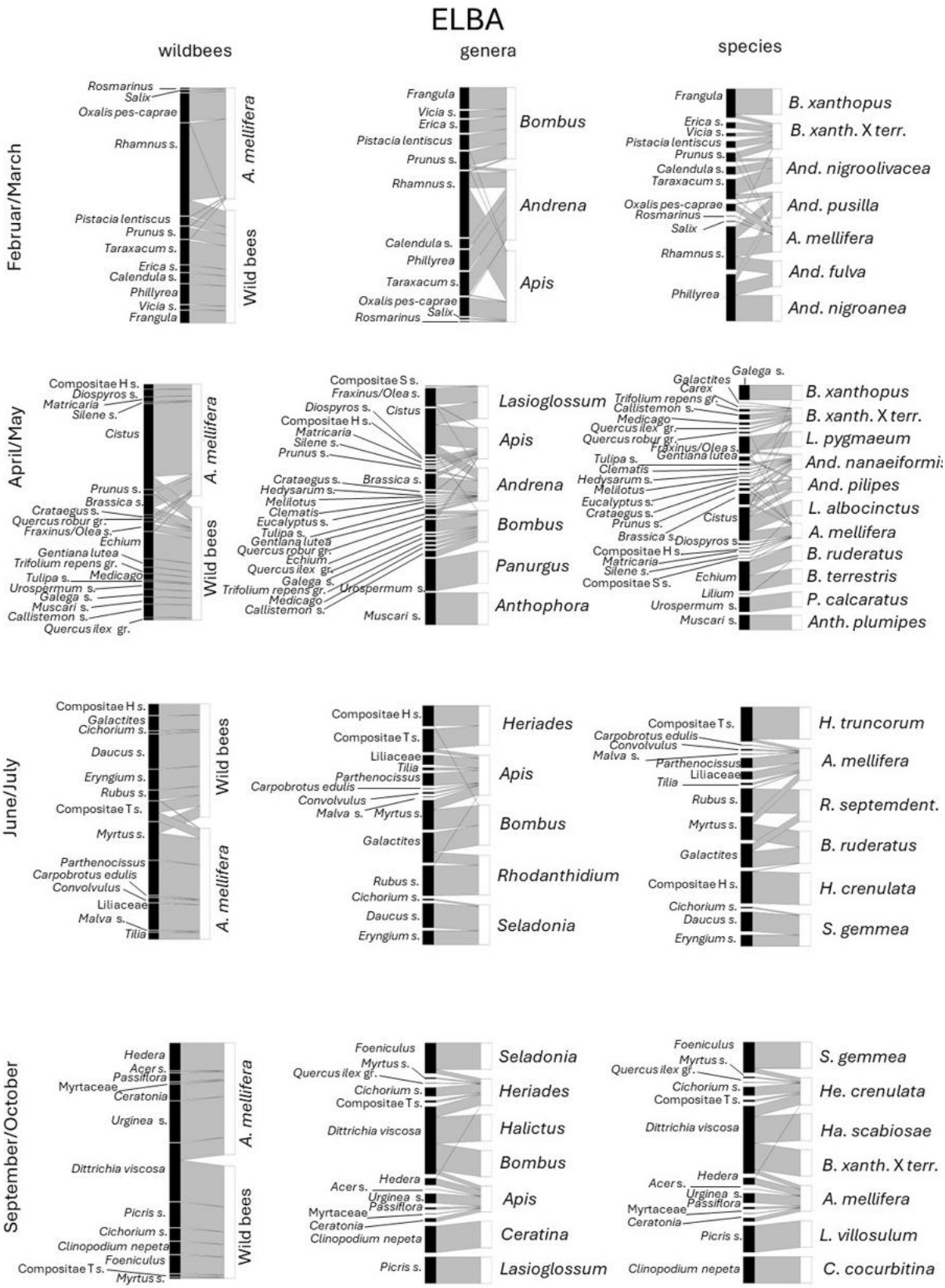


Figure 3. Pollen networks of bees sampled in Elba Island in each sampling session for three different taxonomical levels of wild bee: the general level "wild bees" (left), genera (center) and species (right). Black bar height indicates the relative abundance (%) of pollen grains gathered per plant taxa across bee species (white bar). (HB: honey bees; s: shape; gr: group).

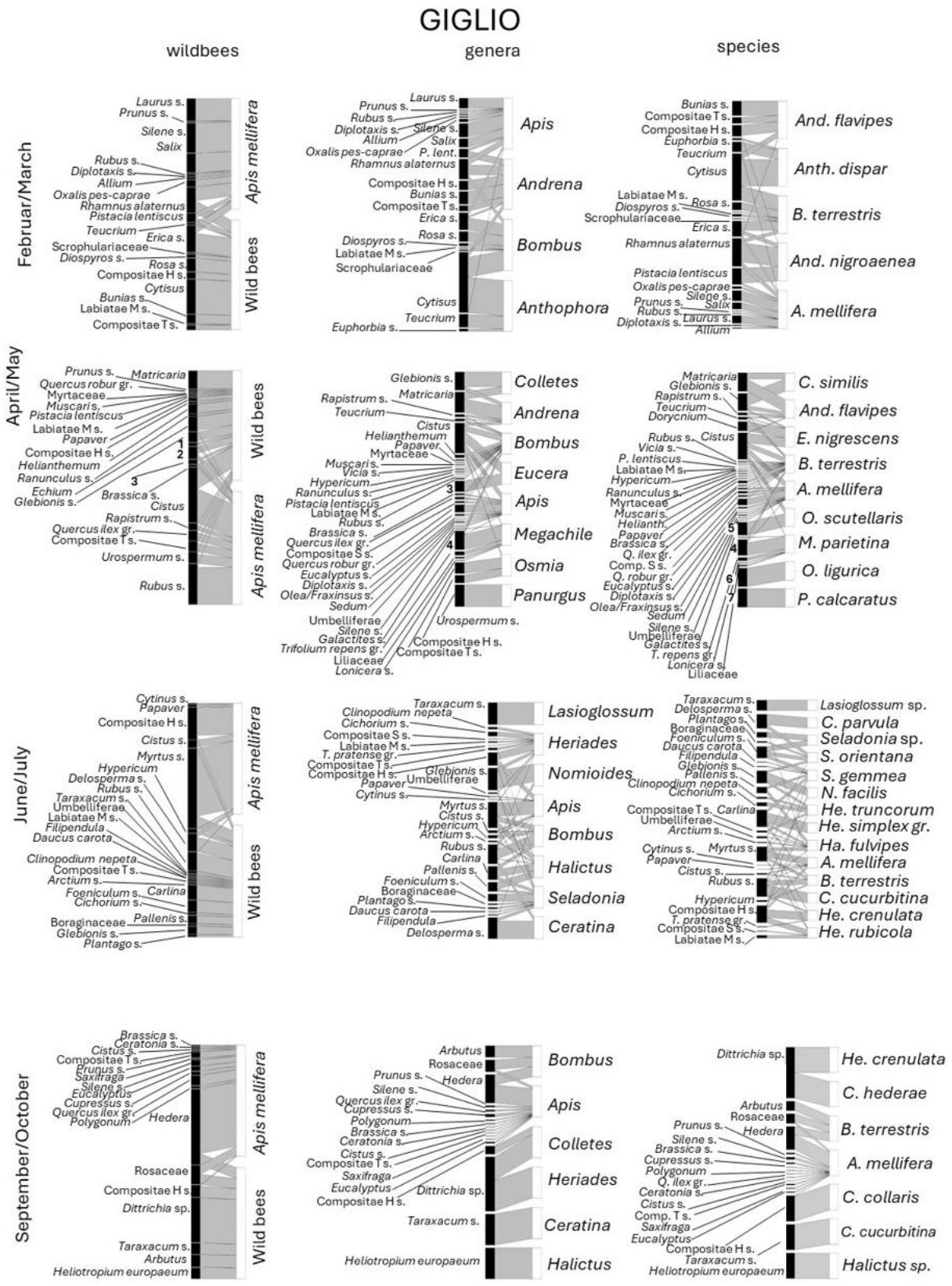


Figure 4. Pollen networks of bees sampled in Giglio Island in each sampling session for three different taxonomical levels of wild bee: the general level "wild bees" (left), genera (center) and species (right). Black bar height indicates the relative abundance (%) of pollen grains gathered per plant taxa across bee species (white bar). (HB: honey bees; 1: *Hypericum*; 2: *Teucrium*; 3: *Dorycnium*; 4: *Echium*; 5: Compositae H shape; 6: Compositae T shape; 7: *Urospermum* shape; s: shape; gr: group).

Table 1. Pianka indices, for each island and each sampling session, of all wild bees for which an overlap in pollen use with honey bees was recorded. Indices are reported for three different taxonomical levels of wild bee: the general level "wild bees", genera and species (*N* = number of individuals). In bold, Pianka indices indicating high pollen use overlap.

Island	Sampling Session	Pianka Index on "wild bees" group	Genus	*N*	Pianka Index	Species	*N*	Pianka Index
Capraia	Feb-March	0.4	*Bombus*	20	0.401	*Bombus xanthopus*	9	0.265
						Bombus xanthopus x *terrestris*	11	0.494
	April-May	0.147	*Andrena*	4	0.009	*Andrena humilis*	2	0.014
			Anthophora	1	0.226	*Anthophora dispar*	1	0.226
			Bombus	21	0.114	*Bombus xanthopus*	12	0.123
						Bombus xanthopus x *terrestris*	9	0.098
			Seladonia	**1**	**0.74**	***Seladonia gemmea***	**1**	**0.74**
	June-July	**0.603**	*Anthidium*	1	0.032	*Anthidium florentinum*	1	0.032
			Bombus	8	0.347	*Bombus xanthopus*	7	0.359
			Lasioglossum	3	0.018	*Lasioglossum nitidulum*	2	0.022
			Megachile	**5**	**0.95**	***Megachile argentata***	**3**	**0.992**
			Seladonia	3	0.008	*Seladonia orientana*	2	0.01
			Xylocopa	**1**	**0.994**	***Xylocopa violacea***	**1**	**0.993**
	Sept-Oct	0.166	*Bombus*	2	0.051	*Bombus xanthopus*	2	0.051
			Colletes	1	0.563	*Colletes similis*	1	0.563
			Halictus	1	0.017	*Halictus* sp.	1	0.017
			Lasioglossum	3	0.077	*Lasioglossum transitorium*	2	0.102
			Megachile	10	0.138	*Megachile argentata*	10	0.138
			Seladonia	5	0.02	*Seladonia orientana*	5	0.04
Elba	Feb-March	0.387	*Andrena*	8	0.418	***Andrena fulva***	**1**	**0.664**
						Andrena nigroolivacea	4	0.014
						Andrena pusilla	**3**	**0.756**
			Bombus	4	0.053	*Bombus xanthopus* x *terrestris*	4	0.067
	April-May	0.391	***Andrena***	**3**	**0.731**	***Andrena cf. nanaeiformis***	**1**	**0.773**
						Andrena pilipes	**2**	**0.631**
			Bombus	11	0.035	*Bombus ruderatus*	1	0.016
						Bombus terrestris	3	0.016
						Bombus xanthopus x *terrestris*	6	0.038
						Bombus xanthopus	1	0.01
			Lasioglossum	**2**	**0.707**	***Lasioglossum albocinctus***	**1**	**0.974**
						Lasioglossum pygmaeum	1	0.029
	June-July	0.166	*Bombus*	2	0.353	*Bombus ruderatus*	2	0.353
			Heriades	1	0.126	*Heriades truncorum*	1	0.179
			Rhodanthidium	1	0.022	*Rhodanthidium septemdentatum*	1	0.022

Table 1 continued.

Island	Sampling Session	Pianka Index on "wild bees" group	Genus	*N*	Pianka Index	Species	*N*	Pianka Index
Elba	Sept-Oct	0.235	*Bombus*	1	0.307	*Bombus xanthopus* x *terrestris*	1	0.307
			Halictus	1	0.022	*Halictus scabiosae*	1	0.022
			Heriades	3	0.23	*Heriades crenulata*	3	0.23
Giglio	Feb-March	0.16	*Andrena*	6	0.179	*Andrena flavipes*	4	0.023
						Andrena nigroaenea	2	0.313
			Bombus	11	0.132	*Bombus terrestris*	11	0.132
	April-May	0.5	*Andrena*	11	0.117	*Andrena flavipes*	10	0.027
						Andrena nigroaenea	**1**	**0.64**
			Bombus	27	0.484	*Bombus terrestris*	27	0.484
			Megachile	1	0.075	*Megachile parietina*	1	0.075
			Osmia	1	0.153	*Osmia scutellaris*	1	0.252
	June-July	0.418	*Bombus*	13	0.406	*Bombus terrestris*	13	0.406
			Ceratina	4	0.044	*Ceratina parvula*	4	0.045
			Halictus	5	0.435	*Halictus fulvipes*	5	0.515
			Heriades	4	0.358	*Heriades rubicola*	1	0.56
						Heriades truncorum	3	0.112
			Seladonia	13	0.13	*Seladonia gemmea*	7	0.219
						Seladonia orientana	6	0.029
	Sept-Oct	0.21	*Colletes*	4	0.005	*Colletes collaris*	1	0.017
			Bombus	3	0.551	*Bombus terrestris*	3	0.551

from all islands among different seasons ranged between 0.147 and 0.603 (Table 1). Overall, a pollen use overlap between honey bees and 41 genera interactions and 54 species interactions, with Pianka index values respectively ranging from 0.005 to 0.994 and from 0.01 to 0.993, with high niche overlap recorded in only 12.2% (5/41) and 16.7% (9/54) of the observed interactions (Table 1).

Based on sample size ($N > 3$), the reliability of Pianka indices was assessed for the 65% (26/41) of honey bee interactions with wild bees at genus level and for the 46.29% (25/54) of interactions with wild bees at species level. Among Pianka indices analysed for reliability, high levels of niche overlap were recorded for only 4 honey bee-wild bee interactions, two at genus level and two at species level. Of these, only the interaction between honey bees and *Andrena pusilla* in February-March on Elba Island resulted reliable with bootstrap resampling (CI 95% = 0.2) (Fig. 5A, B). Pianka reliability was also ascertained for 14 out of 26 (53.8%) honey bee-wild bee genera interactions and for 14 out of 25 (56%) honey bees-wild bee species interactions (Fig. 5A, B). All these reliable Pianka indices resulted with medium-low values (i.e. $\alpha \leq 0.59$) (Table 1).

The honey bee density ranged between 6.07 hives/km^2 in September 2021 and 10.75 hives/km^2 in 2024 on Capraia Island, 3.26 hives/km^2 in May 2021 and 6.19 hives/km^2 in July and September 2022 on Elba Island, and between 1.56 hives/km^2 in July and September 2023 and 8.21 hives/km^2 in 2021 on Giglio Island.

Honey bee density showed a significant negative effect on pollen use overlap on Capraia Island (β = -0.263, *pseudo-*R^2 = 0.181, P = 0.023) (Fig. 6A), whereas a similar negative trend was

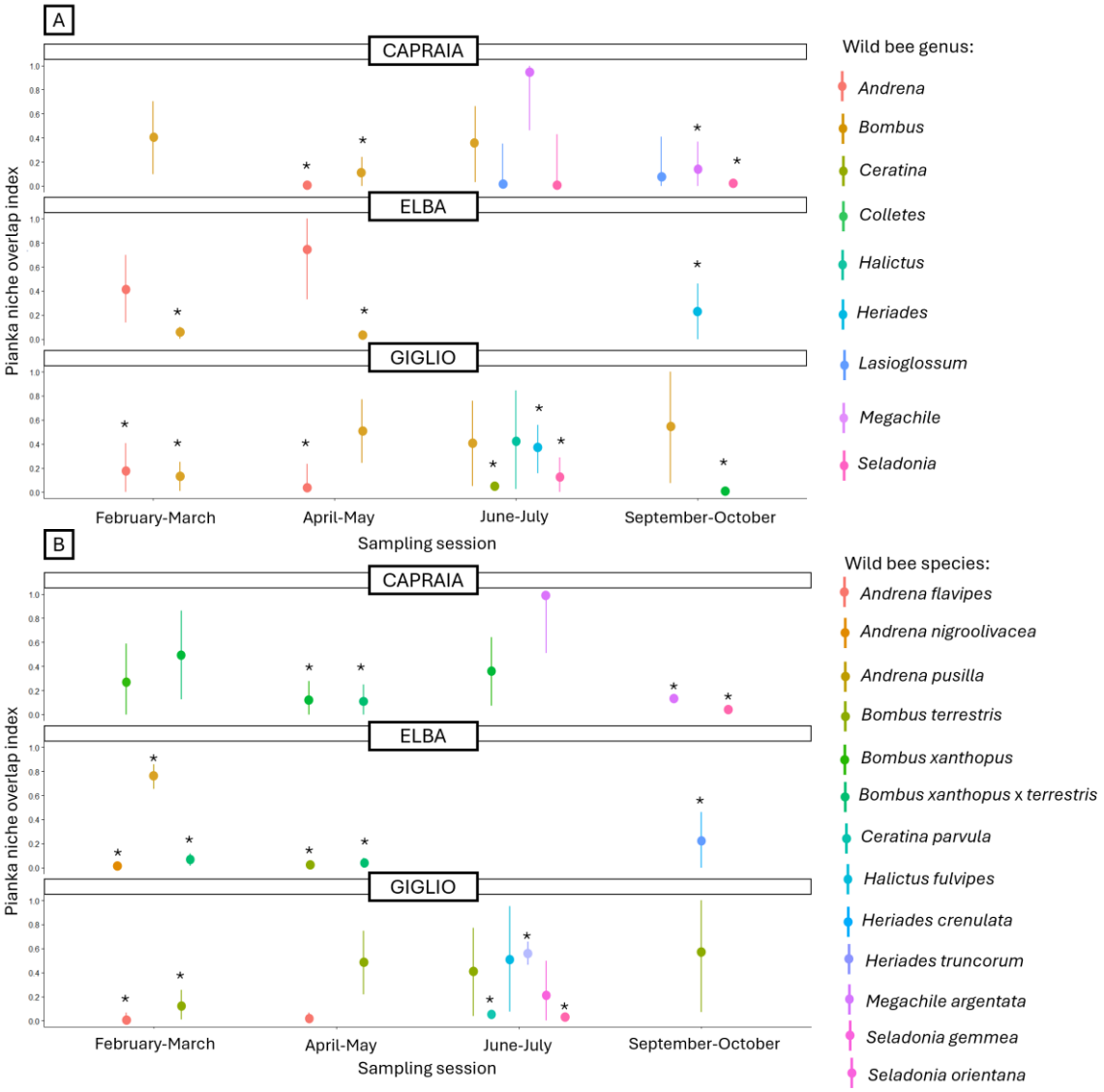


Figure 5. Pianka Index applied to the composition of the pollen gathered by (A) honey bees and wild bee genera and (B) honey bees and wild bee species across different sampling sessions for Capraia, Elba and Giglio Isalnds. Points represent Pianka index calculated for each wild bee species composed of at least three samples; vertical bars indicate the 95% bootstrap confidence intervals. Asterisks (*) indicate estimates with a CI width <0.4, considered of high reliability.

observed on Elba Island but was only marginally significant (β = -0.420, *pseudo-*R^2 = 0.229, P = 0.054) (Fig. 6B). No significant relationship was detected on Giglio Island (β = 0.042, *pseudo-*R^2 = 0.018, P = 0.548) (Fig. 6C).

Discussion

Trophic interactions between managed honey bees and wild bee communities of three islands of the Tuscan Archipelago National Park were here investigated by focusing on pollen resource use. As pollen is essential for larval development and reproduction, it represents a more informative proxy than nectar for evaluating potential trophic competition and its long-term ecological implications (Müller et al. 2006; Nicolson 2011; Boni et al. 2025). By using palynological analysis, we achieved a characterization of trophic niches and pollen diets of bees across seasons and islands. Pollen use overlap was quantified using the Pianka index, and analyses were conducted at different taxonomic levels, considering wild bees at species and genus levels and as a group, in order to obtain a wider overview of pollen niche partitioning, i.e. the differentiation in pollen resource use among coexisting taxa. Overall, our results showed that, independently of the level of analysis, strong

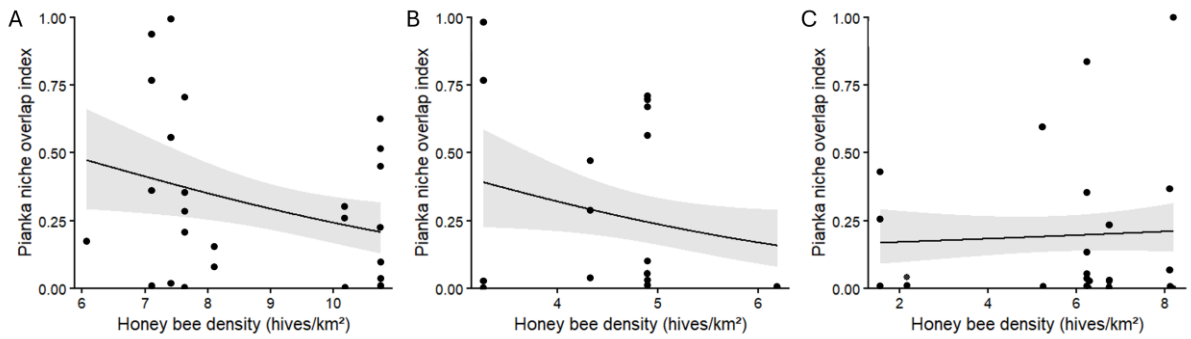


Figure 6. Relationship between honey bee density and pollen resource overlap (Pianka niche overlap index) between honey bees and wild bees in the three investigated islands: A) Capraia, B) Elba, C) Giglio. Points represent observed Pianka index values, whereas solid lines and shaded areas represent fitted values from the beta regression models and their 95% confidence intervals. The Pianka index was transformed using the Smithson-Verkuilen transformation prior to model fitting.

pollen niche partitioning between managed honey bees and wild bees occurred.

Pollen use overlap with managed honey bees was here recorded in 58.7% of wild bee species interactions with a general medium-low level of niche overlap recorded. For the remaining 41.3% of wild bee species interactions, absence of pollen use overlap with managed honey bees was recorded. By comparing pollen gathered by honey bees and by wild bees, significant differences were detected for 26.67% of the interactions at genus level (i.e., *Bombus*, *Andrena*, *Seladonia*, *Colletes* and *Ceratina*), suggesting that honey bees and wild bees tend to exploit distinct floral resources even when co-occurring spatially and temporally. The strongest and most recurrent differentiation emerged between honey bees and *Bombus*, and between honey bees and *Andrena*. Such differences likely promote niche segregation and reduce direct trophic competition (Pardee et al. 2023) even in insular environments, where spatial constraints could theoretically intensify resource overlap (Lázaro et al. 2021). Despite the strong pollen resource partitioning between honey bees and bumblebees observed in this study, most of the existing literature reports competitive interactions between *A. mellifera* and *Bombus* spp. (Franco et al. 2009; Thomson 2016; Cappellari et al. 2022). In the literature, the high resource overlap between bumblebees and honey bees is attributed to the generalist diet characterizing both taxa, which consequently leads to an increased degree of trophic overlap (Franco et al. 2009; Goulson & Sparrow, 2009; Thomson 2016). Although both groups may exploit a broad range of floral resources, differences in the specific plant species selected, foraging behaviour and phenology may reduce the extent to which they actually share pollen resources when co-occurring. Alternatively, it may reflect methodological differences among studies, as many assessments of honey bee–bumblebee competition rely on flower visitation rates, rather than direct analyses of trophic resources, potentially overestimating competition by failing to discriminate among pollen types and resource quality. Finally, the disproportionate focus on bumblebees within competition studies may have introduced a taxonomic bias, limiting the generality of conclusions on the occurrence of trophic competition (Iwasaki & Hogendoorn, 2022).

When considering reliable Pianka estimates, pollen use overlap between managed honey bees and wild bee genera (*Andrena, Ceratina, Colletes, Bombus, Heriades, Megachile, Seladonia*) was consistently low. Reliable Pianka values ranged from 0.005 to 0.358, indicating minimal shared pollen use and no clear seasonal pattern or island-specific trend emerged. At species level, reliable Pianka indices were similarly low, ranging from 0.016 to 0.230, indicating limited pollen use sharing between managed honey bees and different wild bee species (*Andrena flavipes, Bombus terrestris, Bombus xanthopus x terrestris, Ceratina parvula, Heriades truncorum, Heriades crenulata, Megachile argentata, Seladonia orientana*). High degrees of niche overlap were recorded in only 12.2% and 16.7% of interactions analysed at the genus and species levels, respectively. As observed at genus level, no consistent seasonal or island-related

patterns were detected at species level, supporting the general conclusion of weak trophic overlap across scales. This may suggest that pollen niche partitioning could be a stable and pervasive feature of these pollinator communities, rather than a transient phenomenon.

A notable exception was *A. pusilla*, which showed a high and reliable Pianka index ($\alpha = 0.756$) in early spring on Elba Island. This high pollen overlap with managed honey bees was largely driven by the shared use of *Rhamnus* pollen. However, *Rhamnus* species are often highly abundant and widespread in Mediterranean habitats and in the Tuscan Archipelago (Foggi et al. 2006), and their pollen is unlikely a limiting resource. Thereby, since competition occurs when two species rely on limited resources (Park, 1962), the observed overlap does not necessarily imply trophic competition, but it may instead reflect an opportunistic exploitation of a highly abundant floral resource during early-season foraging, as already observed in continental protected areas (Boni et al. 2025). This case highlights the importance of interpreting high niche overlap values in relation to resource availability and ecological context, rather than assuming competitive interactions based solely on overlap metrics (Pike & Rittschoff, 2025).

Overall, obtained results support the evidence suggesting that coexistence between honey bees and wild bees is often facilitated by resource partitioning, rather than constrained by direct trophic competition (Rollin et al. 2013; Jeavons et al. 2020; Casanelles-Abella et al. 2021; Mohamadzade Namin et al. 2022; Boni et al. 2025). The differentiation in pollen use observed in this study may be related to differences in floral preferences, foraging behaviour and phenology between managed honey bees and wild bees. This pattern is consistent with the niche complementarity hypothesis, according to which co-occurring species tend to minimize competitive overlap through differentiation in one or more dimensions of their niche, including trophic and temporal dimensions (Schoener 1974). Functional diversity, phenological differences, and selective pollen use play a central role in maintaining pollinator community structure, even under conditions of honey bee management (Ollerton 2017). Such differences in resource use may promote niche segregation and reduce direct trophic competition (Pardee et al. 2023), even in insular environments, where spatial constraints could theoretically intensify resource overlap (Lázaro et al. 2021).

Nevertheless, the relationship between managed honey bee density and pollen overlap observed in this study suggests that pollen niche partitioning may also be influenced by the presence and abundance of managed honey bees. On Capraia Island, pollen overlap significantly decreased with increasing managed honey bee density, while a similar, although weaker, negative trend was observed on Elba Island. No relationship was detected on Giglio. These results indicate that increasing hive density was associated with a progressive reduction in pollen overlap between managed honey bees and wild bees, potentially suggesting a shift towards alternative pollen resources. An alternative, non-mutually exclusive mechanism underlying this pattern is that interspecific competition may promote differentiation in resource use. Many Apoidea species display flexible and generalist feeding habits (Hudewenz & Klein, 2015) and can shift their diet in the presence of other potentially competing Apoidea species (Page & Williams, 2023). Interestingly, this pattern may be compatible with the threshold saturation effect described in the review by Magrach et al. (2025), whereby ecological effects are strongest at relatively low honey bee densities and progressively level off as density increases. In this investigation, the observed decrease in pollen use overlap at higher honey bee densities may reflect a shift in the realized trophic niche of wild bees, potentially resulting from their behavioural flexibility and the exploitation of alternative floral resources unexploited by honey bees (Page & Williams, 2023). Thus, lower pollen use overlap should not necessarily be interpreted as evidence of reduced competition, as it may also reflect resource partitioning driven by competitive interactions. However, our observational data do not allow us to establish whether such niche displacement occurred or to identify a causal density threshold.

The absence of a significant relationship on Giglio, where relatively low colony densities were recorded during several sampling periods, further

highlights the context-dependent nature of these interactions. Steffan-Dewenter & Tscharntke (2000) inferred no negative effects on wild bee communities at honey bee densities of approximately 3.1 hives/km² in continental Germany. Although obtained in a different ecological context, this finding, together with our observations, suggests that maintaining relatively low colony densities may represent a precautionary approach in protected insular ecosystems. In this context, a density of approximately 3 hives/km² could be considered an illustrative conservation-oriented reference for low-intensity beekeeping management, rather than an empirically established ecological and a universally applicable threshold. For this reason, the suitability of a honey bee density threshold should be evaluated according to local ecological conditions and conservation priorities. Moreover, from a management perspective, these findings support the adoption of precautionary approaches differentiated according to the ecological characteristics, the conservation priorities and the zoning of the National Park.

Italian National Park are divided into zones based on bio-ecological, historical and socio-economic criteria and are characterized by different conservation objectives (Italian Law No. 394/1991, Art. 12). In areas subject to the highest levels of protection and where no human activity is allowed, such as Zone A, the exclusion of managed apiaries should be prioritized. In Zone B, *i.e.*, general-oriented reserves, where traditional agricultural activities are permitted only if the maintenance of ecosystem functionality is ensured, local studies assessing the potential effects of beekeeping on wild bee communities should be considered a priority. In areas where beekeeping is permitted, particularly in Zone C, low-intensity beekeeping could be regulated according to local ecological conditions, floral resource availability and wild bee conservation requirements.

The different patterns observed among islands further suggest that the relationship between managed honey bees and wild bees may depend on local ecological conditions, *e.g.* variation in the composition and availability of floral resources, wild bee communities and other ecological characteristics among islands. Therefore, the extent to which managed honey bees influence wild bee pollen use may not be uniform across insular systems but may depend on the local ecological context. However, because our study was observational, the observed negative relationship cannot be considered direct evidence that honey bees caused such a shift in wild bee resource use. This study focused on the three largest islands of the Tuscan Archipelago, and the results obtained cannot be directly transposed to the smaller islands of the archipelago. Giannutri is a small island (2.6 km²) entirely included within areas of integral protection and biodiversity conservation of the National Park (Type A zone). Using a manipulative experimental approach, Pasquali et al. (2025) reported negative effects of exploitative competition between managed honey bees and wild bees and recommended a substantial reduction or complete removal of managed honey bee hives from the island. The case of Giannutri, where negative effects of managed honey bees on wild bee communities have been reported (Pasquali et al. 2025), further emphasizes the need for island-specific management measures rather than uniform colony-density limits across the archipelago.

Although trophic niche overlap can provide useful information on the potential for interspecific interactions, it does not represent a direct measure of competition (Pike & Rittschoff, 2025). Similarly, pollen analysis provides an informative approach to assess potential trophic competition in bee communities (Pardee et al. 2023; Boni et al. 2025), but the observed degree of overlap cannot by itself demonstrate the occurrence or absence of competitive interactions.

A further limitation concerns the sample size of some wild bee taxa. In all cases in which no pollen use overlap was detected at species level, the sample size was represented by only one or two individuals. This could reflect undersampling rather than definitive niche separation. Few samples were also available for some niche overlap interaction analyses at genus and species levels, due to the difficulties in finding large numbers of individuals during field sampling of the same species or genera, especially for uncommon species. Therefore, it cannot be excluded that in some cases the results obtained may have been influenced by a low number of individuals in the sample size and they should be interpreted with

caution. Additional investigations with larger samples are necessary to confirm the patterns observed here. Nevertheless, the analysis at genus level and for wild bees as a group provided a complementary overview of pollen niche partitioning that was less dependent on the representation of individual species. In this investigation the municipality-level honey bee colony density was used as a proxy for local beekeeping pressure. Although this approach accounts for colonies distributed across a wider area than the sampling areas used here, it does not consider the spatial distribution and size of individual apiaries. Consequently, municipality-level density estimates may not accurately reflect the actual presence of managed honey bee colonies in the surroundings of the 0.5 km² sampling areas, requiring caution when interpreting the observed relationship between colony density and pollen resource overlap at the local scale. Future studies should therefore include a detailed survey of apiary locations and dimensions, allowing a more accurate characterization of managed honey bee colony distribution in relation to the sampling areas.

In conclusion, our results indicate a different composition of pollen gathered by managed honey bees and the wild bee genera analysed. Moreover, managed honey bees do not usually overlap with wild bees in pollen resource use within the studied insular systems. Strong pollen niche partitioning, mainly involving *Bombus* and *Andrena*, appears to be the dominant pattern, while high overlap values were rare, context-specific, and not necessarily indicative of trophic competition. The negative relationship between managed honey bee density and pollen overlap on Capraia and marginally on Elba further suggests that wild bees may modify their pollen resource use in relation to honey bee abundance. These findings highlight the importance of considering pollen resource use, colony density and local ecological context when assessing the compatibility of beekeeping with wild bee conservation in protected insular ecosystems. This study reflects the complexity of the ecological dynamics governing interspecific trophic competition and the extent to which it is strongly context-dependent. Further studies combining larger datasets and experimental approaches will be needed to clarify the mechanisms underlying these patterns and to refine management recommendations.

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AUTHOR CONTRIBUTION

Concept and Design AF, CBB, FC & SS, data collection CBB, FC, SP, ADR & LS, data analysis CBB, FC, SP, GDF, SS, SF, MQ, FG & ES, writing AF, CBB, FC & SS, edits and approval for publication AF, CBB, FC, SS, SP, ADR, GDA, SL, SF, MQ, ES & FG.

DISCLOSURE STATEMENT

The authors declare no conflict of interest. One of the authors, Francesca Giannini, is a biologist of the Tuscan Archipelago National Park; we planned and wrote the paper together.

GENERATIVE AI DISCLOSURE STATEMENT

No AI was used to write this article.

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are provided in the paper, in the Supplementary Materials and upon request to the corresponding author.

APPENDICES

Additional supporting information may be found in the online version of this article:

Supplementary Figure 1: Principal Coordinates Analysis (PCoA) of pollen composition gathered by *Apis mellifera* and wild bee genera.

Supplementary Table 1. List of wild bee species captured during the sampling period on Capraia, Elba and Giglio Islands of the Tuscan Archipelago National Park.

Supplementary Table 2. List of pollen types (n=122) detected through morphological or molecular analyses of pollen gathered by honey bees and wild bees on Capraia,

Elba and Giglio islands of the Tuscan Archipelago National Park.

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