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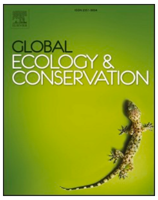

Original research article

Drivers of wild bee abundance and diversity in social-ecological landscapes

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ABSTRACT

Concern over pollinator loss has driven conservation efforts globally, yet significant gaps remain in understanding the combined effects of local and landscape factors on pollinator communities, and their status and trends in social-ecological landscapes. Using four years of data, covering 204 sites, from a national monitoring dataset on plant-wild bee interactions in the Maltese Islands, this study examines the links between local and landscape habitat factors, wild bee abundance, species richness, and functional diversity. Functional diversity was assessed using multiple traits to calculate functional divergence, richness, evenness, and dispersion. Both local and landscape factors influenced wild bee communities. At the local scale, plant species richness was positively associated with wild bee abundance, species richness, and functional divergence and dispersion. Agricultural habitats supported higher abundance, and functional richness and dispersion of wild bees than other habitats. Honeybee abundance negatively impacted functional richness and dispersion, particularly in road verge and steppe habitats. At the landscape scale, urban areas and the Shannon Landscape Diversity Index negatively affected wild bee species richness and functional diversity. A combined negative impact of the urban heat island effect and honeybee hive density on wild bee functional diversity was observed across scales, suggesting that urban-driven fragmentation favours generalist, social species with greater foraging ranges. Effective wild bee conservation requires actions across scales, focusing on maintaining plant species richness and preserving agricultural habitats, while promoting land use planning that reduces further expansion of urban development into predominantly agricultural landscapes and integrating wild bee habitats within urban areas to mitigate fragmentation effects.

1. Introduction

Human disturbances, particularly changes in land use and management, have been linked to the decline in pollinator diversity and abundance (Dicks et al., 2021; Millard et al., 2021) and have attracted public and policy attention. Substantial efforts are underway to respond, through action at global (Convention on Biological Diversity, 2018), regional and national scales, with countries adopting pollinator strategies and action plans (European Commission, 2023a, 2023b). The recently adopted European Union (EU) Nature Restoration Law requires the EU Member States to take appropriate measures to improve pollinator diversity and reverse the decline of

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pollinator populations by 2030 and thereafter achieve an increasing trend in pollinator populations. Nonetheless, several challenges are anticipated in its implementation, including the need for well-defined and practical strategies, reliable data, resource and finance mobilisation and effective community engagement, are anticipated, and may compromise the success of the Nature Restoration Law (Hering et al., 2023; Stoffers et al., 2024).

Habitat modification, at both at local micro-habitat and landscape scales, affects the abundance and diversity of pollinators (Duchenne et al., 2020; Gaspar et al., 2022; Kleijn et al., 2018; Scheper et al., 2015). The persistence of pollinator species at local scale is a consequence of the interplay between the local micro-habitat conditions and landscape management practices (Cohen et al., 2022; Coutinho et al., 2021; Gaspar et al., 2022; Marcacci et al., 2022; Rodríguez et al., 2021). Increased availability and diversity of food resources and nesting sites at the local scale are positively related with pollinator richness and abundance. Similarly, proximity to semi-/natural habitats is associated with diverse and abundant pollinator communities (Gaspar et al., 2022; Marcacci et al., 2022).

Landscape-scale variables may exert stronger influence on pollinator abundance and diversity than local variables, as positive landscape-level effects can offset smaller negative impacts at the local level (Perović et al., 2015; Steckel et al., 2014). For example, wild bee abundance, richness and functional diversity increased with vegetation diversity in road verges, but these results were influenced by landscape diversity, distance from the city and pollinator traits (Dietzel et al., 2024). There is a growing body of research addressing the impact of local and landscape variables on wild bee communities but most of the studies focus on agricultural and natural systems, and we know less about the impact of environmental variables on bee communities in urban systems (Buchholz and Egerer, 2020; Cohen et al., 2022; Fauviau et al., 2024; Liang et al., 2023; Wenzel et al., 2020), and even less on the variation in wild bee communities across landscapes having different habitats combined with gradients of environmental conditions in social-ecological landscapes (Biella et al., 2022; Gillespie et al., 2024; Neokosmidis et al., 2016).

Social-ecological factors impacting wild bee communities include abiotic factors, such as soil structure, slope, aspect and temperature (Antoine and Forrest, 2021; Kammerer et al., 2021; Maher et al., 2019), but also biotic factors, like interspecific interactions with managed bees (Baldock, 2020; Iwasaki and Hogendoorn, 2022). These social-ecological filters often interact, resulting in filtered functional trait combinations at the local scale, and therefore impacting on ecosystem functions and services (Grilo et al., 2022). For example, urbanisation causes drastic and often irreversible habitat changes leading to overall negative impacts on pollinator richness and abundance (Liang et al., 2023) but can also have neutral or positive effects on pollinators depending on the availability of specific urban features such as botanical gardens, allotments, residential gardens, and vacant lots which may serve as important habitats and improve habitat connectivity for pollinator communities (Baldock, 2020; Biella et al., 2022; Theodorou et al., 2020). Such refuges often support high wild bee richness, particularly in landscapes with well-connected urban green areas (Baldock et al., 2019; Biella et al., 2022; Wenzel et al., 2020). The abundance and diversity of bee communities has also been shown to be correlated with socio-economic drivers, with income inequality affecting bee abundance and richness (Baldock et al., 2019; Reynolds et al., 2025). Since the responses of pollinators often are trait-specific (Buchholz and Egerer, 2020; Liang et al., 2023), these complex and interacting social-ecological variables can also affect the functional traits of bee communities through filtering, hence affecting fitness and survival. For example, ground nesting and solitary bees are more strongly negatively affected by urbanisation (Liang et al., 2023) while those with polylectic diets (i.e. generalist), cavity-nesting behaviour and later emergence are also expected to be more favoured compared to other groups by urban development (Ayers and Rehan, 2021). More dense urban areas, with highly fragmented green spaces and characterised by and urban heat island effect favour large, social, polylectic and/or above-ground nesting species (Ferrari and Polidori, 2022).

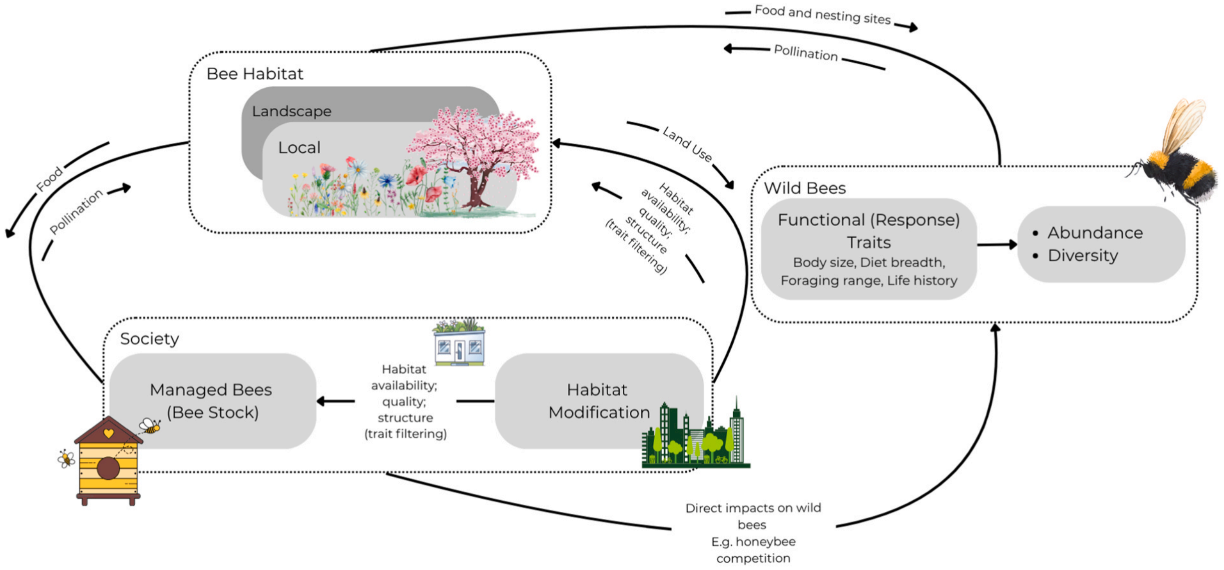

Fig. 1. Conceptual framework to analyse the impact of local and landscape habitat variables on wild bee communities.

The interactions within these social-ecological systems impact on wild bee abundance and functional diversity are developed here into a conceptual framework that has been used to identify the following research questions (Fig. 1):

a) How do local habitat factors (i.e. local habitat type and plant species richness) impact wild bee abundance, species richness and functional diversity?
b) How do landscape scale factors (i.e. altitude, slope, aspect, proximity to urban areas, Normalised Difference Vegetation Index (NDVI) and Landscape Shannon Diversity Index (LSDI)) impact wild bee abundance, species richness and functional diversity?
c) Does honeybee abundance modify the impact of local and landscape factors on wild bee abundance, species richness and functional diversity?

2. Methodology

2.1. Study area and sampling design

The study was conducted in the archipelago of Malta, characterised by Mediterranean climatic conditions, and namely dry and hot summers and mild and wet winters. The islands consist of heterogeneous landscapes shaped by both natural processes and centuries of human activity, and including steppe, garrigue, shrubland and woodland habitats within an agricultural and urban and built-up area matrix. The archipelago predominantly consists of limestone, influencing soil composition and structure, and the topography which consists of low-lying hills and plateaus with valleys supporting riparian vegetation (Balzan et al., 2018). Centuries of human activities have altered soil and vegetation cover, converted land for cultivation, led to the construction of terraces, and driven intensive urban sprawl. Current drivers are related to rapid urban development leading to increased densification and urban sprawl across the main islands, Malta and Gozo, with an observed rural-urban gradient in the reduction of green space availability and ecosystem service capacities, together with the contemporary agricultural abandonment of less productive land and agricultural intensification in other areas (Balzan et al., 2022).

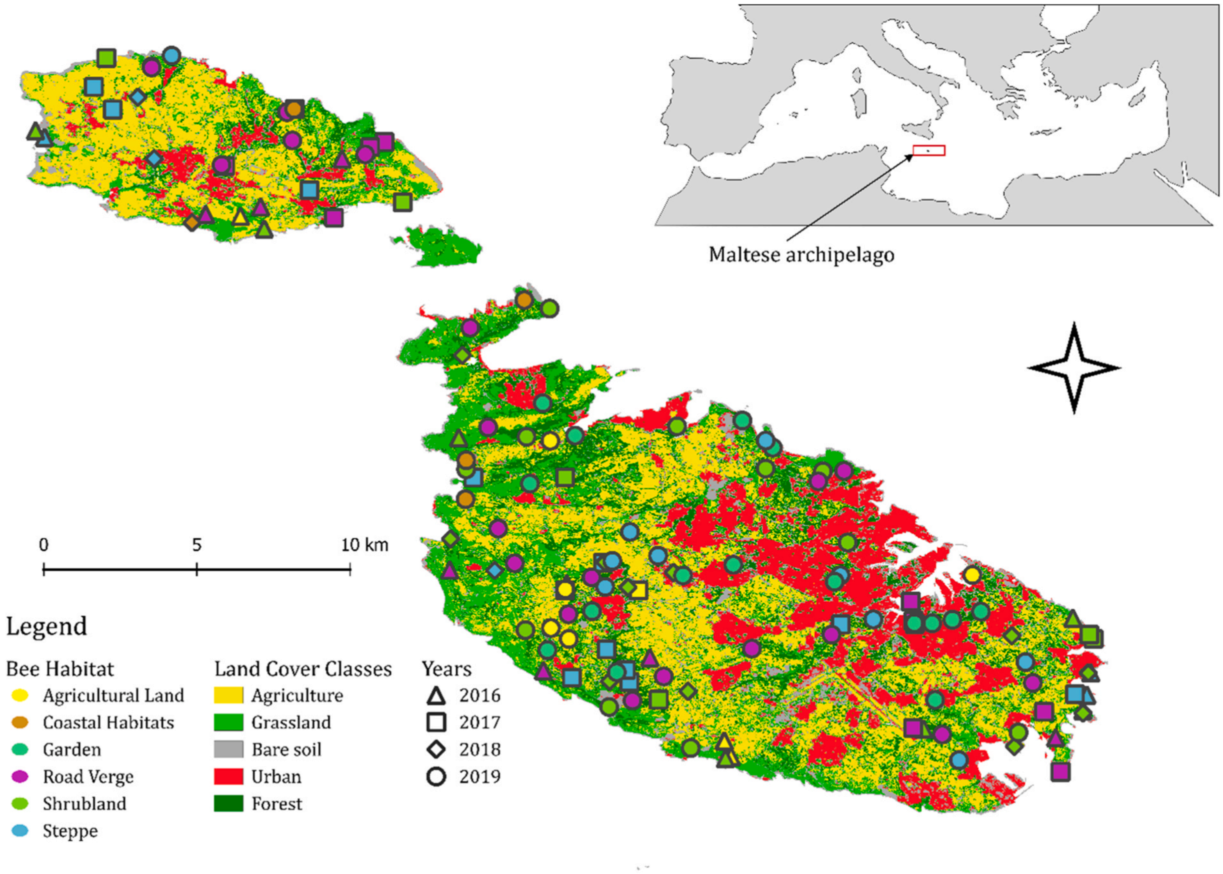

Fig. 2. Sampling points location within the study region (LULC map: Copernicus Coastal Zones Land Cover/Land Use 2018).

2.2. Bee transects and functional traits

The data analysed in this study were derived from a national monitoring dataset of plant-bee interactions in the Maltese Islands (Balzan et al., 2023, 2017, 2016) with data collection conducted annually using standardised transects across six habitat types: agricultural, coastal, garden, road verge, steppe, and shrubland habitats (Table A.1, Supplementary Information). A total of 204 sites were visited between April and May from 2016 to 2019, with each site visited once each year. The transects were carried out under dry, cloudless, and low-wind conditions to minimise weather-related variability. At each site, standardised, geolocated belt transects measuring 2 × 25 m were surveyed through timed walks of 20 min by a single observer. While some transects were revisited in multiple years, others were sampled once to maximise spatial and habitat representativeness across the Maltese Islands. Given the objective of this study to assess the wild bee functional diversity, we only considered the transects with wild bee abundance (Fig. 2; Table A.1). During these transects, flower-visiting bees were captured using a hand net, with both the plant and bee species identities recorded for each interaction. Bees that were identified in the transect were released immediately, while collected bees were identified in the laboratory to genus level (Michez et al., 2019) and then sent to a specialist for determination at species level (see Acknowledgment section). Bees that were not possible to identify to species level were identified to the genus level.

Functional traits of wild bees, presented in Supplementary Information Table C.1, were considered as they determine how species respond to habitat change. For example, body size, diet breadth, sociality, and nesting behaviour influence the species response to urbanisation (Brasil et al., 2024). Body size was measured quantitatively using a digital calliper for the intertegular distance (ITD) and body length (in mm), while the dry weight was measured by dehydrating the specimens at 70°C for 24 h to remove any residual moisture, then weighing them using an analytical balance (detection limit: 0.001 g). Additional traits data were extracted from the European Pollinator Traits Database (Miličić and Vujić, 2023).

Using the functional trait data, Functional Diversity (FD) indices were calculated using the FD-package (version 1.0–12.1; (Laliberté and Legendre, 2010). Functional Richness (FRic) measures the extent of multi-dimensional functional space occupied by a community. The FRic increases with the addition of functionally unique species but remains the same with the addition of a redundant species. Functional Evenness (FEve) assesses how species traits are distributed across trait space and are weighted by the relative abundance of each species. Functional Divergence (FDiv) captures the extent to which species differ in their functional traits relative to the centre of the functional space while considering the abundance of these species. If a newly added species is functionally similar, then an increase in its abundance will lead to a decrease in FDiv. Functional Dispersion (FDis) is the mean distance in multidimensional trait spaces of individuals species from its abundance-weighted community centroid. FDis is used to identify environmental filtering processes that shape communities (Laliberté and Legendre, 2010; Mason et al., 2005; Villeger et al., 2008). A low dispersion is recorded when bee species with similar traits accumulate at sites and high dispersion is recorded with higher trait diversity and niche partitioning (Buchholz et al., 2020; Coutinho et al., 2021; Dietzel et al., 2024).

2.3. Local and landscape drivers

We considered the “local level” to be the sampling plot as a representative of the habitat in which it is found. For the local scale metrics, we considered the local habitat type category (described in Table A.1, Supplementary Information) and flowering plant

Table 1
Measured habitat variables at local and landscape scales.

Variable	Scale	Info/Source
Plant species richness	Local	Number of plant species recorded within each transect
Local Habitat Type	Local	Categorical variable with habitat type at transect level (agricultural, coastal, garden, road verge, steppe, shrubland and woodland)
Number of honeybees recorded	Local	Abundance of honeybees within each transect.
Altitude	Landscape	Elevation, measured in metres, and extracted from a 2012 Digital Terrain Model (DTM) of the Maltese Islands, sourced from an airborne LiDAR survey at a 1-metre resolution. Median values calculated for each landscape buffer (Source: msdi.data.gov.mt).
Slope	Landscape	Derived from the DTM using ArcGIS Pro’s terrain analysis tools. Slope values, representing terrain steepness, were calculated by measuring the rate of elevation change across horizontal distances. Median values were calculated for each landscape buffer (Source: own interpretation).
Aspect	Landscape	To derive aspect, we used ArcGIS Pro’s terrain analysis tools. The aspect was calculated with the Spatial Analyst toolbox. Aspect represents the direction of the steepest descent from each cell (Source: own interpretation).
Distance to urban areas	Landscape	Euclidean distance of the plot to the edge of different land cover classes, measured in meters (Source: Balzan et al., 2018).
Shannon Diversity Index	Landscape	Shannon Diversity Index using the land use land cover map for the study area (Source: Balzan et al., 2018).
NDVI	Landscape	Calculated from Sentinel−2 imagery (Copernicus programme) using the Near-Infrared (NIR) and Red spectral bands (NDVI = (NIR - Red) / (NIR + Red)). Values range from −1 to + 1, with higher values indicating greater vegetation density and health. Sentinel−2 images were collected during both the dry and wet seasons to capture seasonal variation in vegetation cover. For each site, the median NDVI was calculated per season across multiple years, providing a robust indicator of vegetation condition and enabling consistent comparison of seasonal and interannual trends in habitat quality.
Honeybee density	Landscape	Hive density in 1 Km^2 cells covering the Maltese Islands (Source: agriculture.gov.mt)

species richness in each transect. When including wild bee abundance and diversity, or the functional diversity indices as a response variable, we also considered honeybee abundance as an independent variable. For the landscape scale metrics, we used national datasets and remotely sensed data, which is presented and described in Table 1, to characterise the habitat conditions surrounding the transects within circular buffers with varying radii (r = 100, 200, 500, 1000, 2000 m). Terrain data was obtained from a Digital Terrain Model (DTM) acquired in 2012 for the Maltese Islands from airborne LIDAR survey carried out in 2012 at a resolution of 1 m. Land use land cover data was obtained from (Balzan et al., 2018), who had developed a land use land cover (LULC) map using Sentinel 2 satellite images provided by Copernicus. Within the context of increasing impact of urbanisation on biodiversity and ecosystem services (Balzan et al., 2018; Balzan and Santis, 2023), we considered distance of each transect from the nearest urban land cover and Shannon Diversity Index. Sentinel-2 imagery from the dry and wet seasons between 2018 and 2023 was used to assess vegetation coverage while we obtained Level-2 Land Surface Temperature (LST) data from the Sentinel-3 satellite images spanning multiple dates and covering both the dry and wet seasons during the years 2019–2023, to ensure comprehensive temporal coverage. To reduce the bias arising from using only one satellite image/product, we used the median during the sampling year while cloudy images were discarded. Honeybee hive density data at 1Km2 resolution was digitised using anonymised records of hive density as provided by the Ministry for Agriculture, Fisheries and Animal Rights (MAFA), Malta in 2020.

2.4. Data analysis

To analyse the influence of local and landscape factors (Table 1) on wild bee diversity we applied Generalized Linear Mixed Models (GLMM) using the R package glmmADMB (Fournier et al., 2012; Skaug et al., 2016). We used a negative binomial and Poisson distribution formula to model bee abundance and species richness respectively, and Gaussian distribution formula for functional diversity. All predictor values included in the model selection were scaled and centred to zero due to the range of absolute values that varied naturally. We clustered sites with overlapping landscapes at each considered scale using Density-Based Spatial Clustering of Applications with Noise (DBSCAN) (Hahsler et al., 2019). The cluster was then included as a random factor to control for possible spatial autocorrelation. Two GLMMs were fitted on each response variable, with Model 1 assessing the influence of local habitat type, plant species richness and honeybee abundance on each response variable, with year and the spatial cluster considered as random variables. Model 2 considered the variables at the landscape scale. For the landscape models, random effects were incorporated to

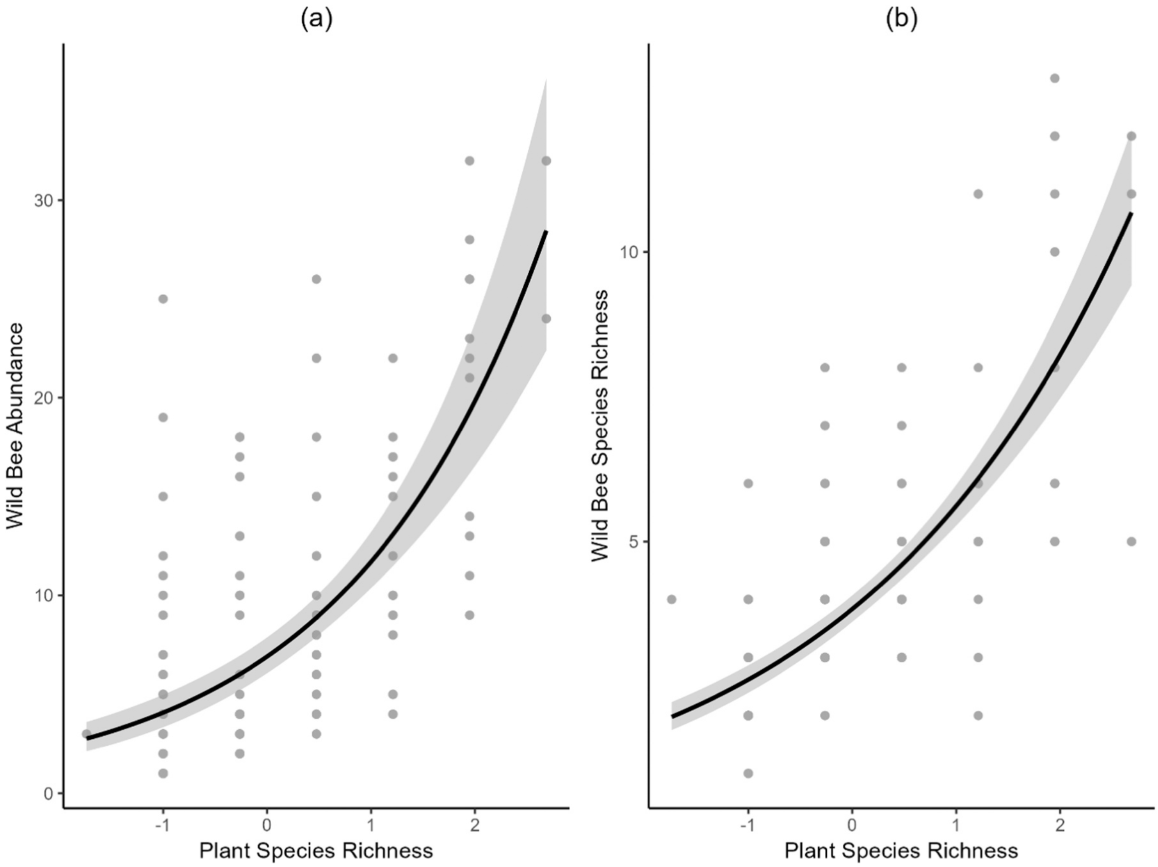

Fig. 3. Relationship between plant species richness (centred and scaled) and wild bee (a) abundance and (b) species richness. Fitted lines and 95 % confidence intervals (shaded areas) are based on a quasipoisson Generalised Linear Models. Grey points represent individual observations.

account for potential variations due to year, spatial cluster, local habitat type and plant species richness. Four model formulations with different random effect structures were considered: $\sim (1|\text{Year} + 1|\text{Cluster} + 1|\text{Local Habitat})$; $\sim(1|\text{Year}/\text{Cluster} + 1|\text{Local Habitat})$; $\sim (1|\text{Year} + 1|\text{Cluster} + S_{\text{plant}}|\text{Local Habitat})$, and $\sim(1|\text{Year}/\text{Cluster} + S_{\text{plant}}|\text{Local Habitat})$, and models were selected based on the Akaike Information Criterion corrected for small sample sizes (AICc), ranking them using the AICc differences (ΔAICc) from the best model and Akaike weights (ω). The *dredge* function of the MuMIn package in R was applied to determine the best models built with all possible combinations of explanatory variables (Barton, 2009). Models with $\Delta\text{AICc} < 2$ were considered equally supported by the data. Variance inflation factors (VIF), implemented with the vif function of the R package car (Fox and Weisberg, 2019), were used to test for multicollinearity in the predictors (Zuur et al., 2010). Thus, models containing collinear variables ($\text{VIF} > 3$) were excluded from the model selection.

3. Results

In total, 4487 individuals from a total 67 bee species were sampled in the study area. Honeybees made most of the records with a total of 3214 individuals recorded. The mean wild bee abundance and species richness per site were 8.07 ± 7.49 and 4.14 ± 2.39 respectively, while mean honeybee abundance was 18.46 ± 24.41. 39.8 % of the recorded species were only recorded less than 5 times across all sites. The mean plant species richness recorded within the transects was 2.36 ± 1.36. A GLM with a quasipoisson error distribution and using local habitat type as a predictor of plant species richness showed that local habitat type was not a statistically significant predictor of plant richness ($p > .05$), and the model explained only a small proportion of the variation in plant species richness (residual deviance = 102.17 on 148 df; null deviance = 116.22 on 153 df).

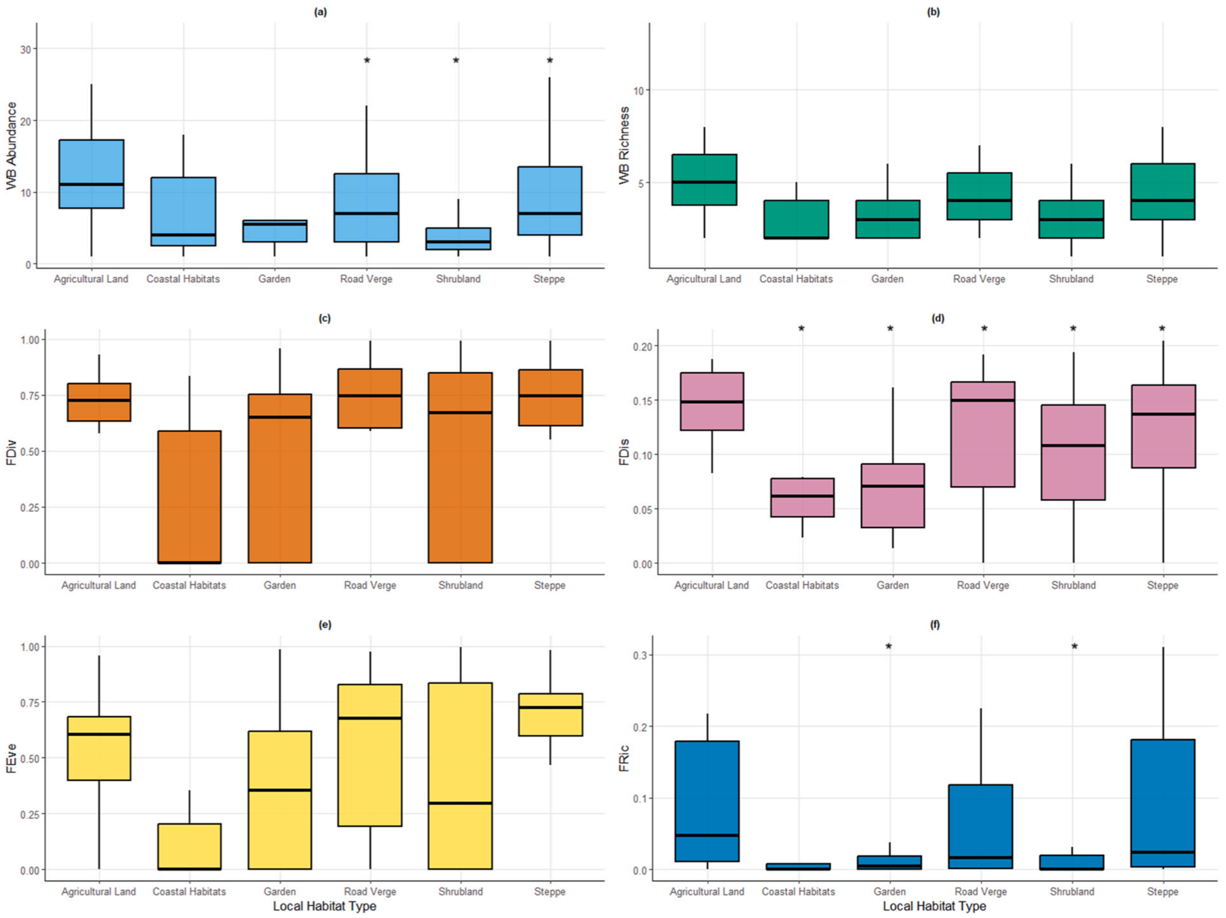

Fig. 4. Variation in wild bee community metrics and functional diversity indices across local habitat types. Boxplots show distributions of: (a) wild bee abundance, (b) wild bee species richness, (c) functional divergence (FDiv), (d) functional dispersion (FDis), (e) functional evenness (FEve), and (f) functional richness (FRic) per local habitat type. Boxes represent the interquartile range, horizontal lines indicate medians, and whiskers extend to 1.5 x interquartile range. Asterisks indicate habitat types significantly different from agricultural habitats based on GLMMs on local habitat data (presented in Appendix D).

3.1. Bee abundance, richness and functional diversity at the local scale

Wild bee abundance and species richness increased with plant species richness within the transect independently of the local habitat (Fig. 3). Similarly, FDiv and FDis were positively associated with plant species richness. Agricultural habitats had a significantly higher wild bee abundance then road verge, shrubland and steppe habitats and significantly higher FRic when compared to garden and shrubland habitats (Fig. 4; Appendix C). FEve was not significantly associated with any of the variables at the local scale. Agricultural habitats had significantly higher FDis when compared to all other habitats. FDis was negatively correlated with honeybee abundance, with significant negative interactions recorded between honeybee abundance and road verge and steppe habitats, while a negative association between honeybee abundance and FRic was also recorded (Fig. 5).

3.2. Bee abundance, richness and functional diversity at the landscape scale

The considered landscape habitat variables affected both wild bees and honeybees, as shown by the GLMM results (Appendix D). Wild bee abundance was negatively influenced by NDVI at 100 m scale (est = −0.14 ± 0.07, z = 2.06, p = 0.04) but positively associated with NDVI at 2000 m (est = 0.17 ± 0.08, z = 2.01, p = 0.04; Table 3). No significant association of landscape variables with wild bee species richness was recorded but several significant relationships between the landscape-scale predictors and functional diversity indices were recorded across landscape scales. FDiv was positively associated with distance to urban areas, with significant effects observed at the 200 m scale (est = 0.07 ± 0.03, z = 2.47, p = 0.01), 1000 m scale (est = 0.07 ± 0.03, z = 2.54, p = 0.01), and 2000 m scale (est = 0.06599 ± 0.02672, z = 2.73, p = 0.006), indicating that urban proximity decreases divergence in functional traits among wild bee species, and potentially reflecting lower niche differentiation in urban-associated environments. Similarly, FRic at the 500 m scale was positively associated with distance to urban areas (est = 0.02 ± 0.01, z = 1.98, p = 0.047) and, supporting results obtained at the local scale, increased hive density was associated with increased FRic at this scale (est = 0.02 ± 0.01, z = 2.43, p = 0.02) but were significantly influenced by the negative interaction between land surface temperature and honeybee hive density (est = −0.02 ± 0.01, z = 2.32, p = 0.02). FEve was significantly negatively influenced by the interaction between land surface temperature and honeybee hive density at the 100 m scale (est = −0.08 ± 0.03, z = 2.41, p = 0.01), 200 m (est = −0.07 ± 0.03, z = 2.17, p = 0.03) and 1000 m scales (est = −0.11 ± 0.03, z = 3.31, p = <0.001), indicating combined negative impact of abiotic heat stress and competition from managed honeybees reduces the evenness of trait distributions within the bee community. FEve was positively associated with NDVI (est = 0.08 ± 0.04, z = 2.33, p = 0.02) and negatively associated with the landscape Shannon Diversity Index (est = −0.08 ± 0.04, z = 2.33, p = 0.02) at r = 500 m. FDis was similarly positively associated with NDVI (r = 500 m, est = 0.02 ± 0.01, z = 3.06, p = 0.002; r = 1000 m, est = 0.01 ± 0.01, z = 2.26, p = 0.02) and negatively associated with SDI (r = 500 m; est = −0.02 ± 0.01, z = 3.19, p = 0.001; r = 1000 m; est = −0.01 ± 0.01, z = 2.15, p = 0.03;), and negatively influenced by the interaction between land surface temperature and honeybee hive density at r = 200 m (est = −0.06 ± 0.03, z = 2.17, p = 0.03) and 1000 m (est = −0.01 ± 0.00, z = 2.86, p = 0.004).

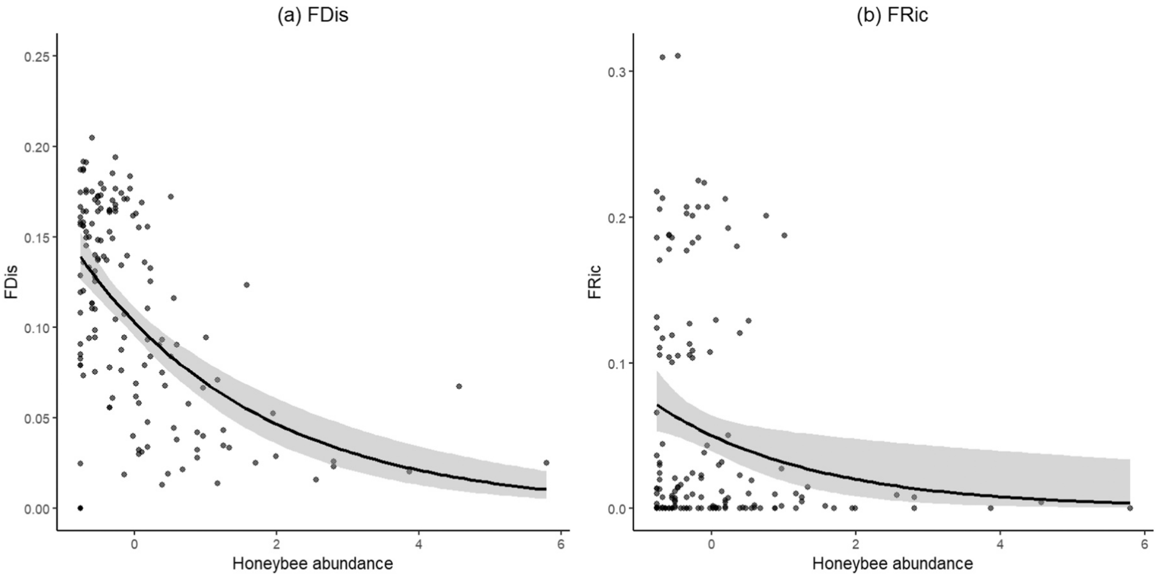

Fig. 5. Relationship between honeybee abundance (Apis mellifera) and wild bee functional diversity indices across sampling sites: (a) functional dispersion (FDis) and (b) functional richness (FRic). Lines and shaded areas represent fitted values and 95 % confidence intervals from quasipoisson Generalised Linear Models.

4. Discussion

In this study, we have assessed the impact of local and landscape habitat variables on wild bee abundance, species richness and functional diversity, and evaluated how these interactions are altered by honeybee abundance.

4.1. Impact of local scale variables on bee communities

Our findings show a positive association between plant species richness and wild bee abundance, richness and functional diversity indices. Bee richness was only sensitive to plant richness and was not sensitive to the other local variables (i.e. local habitat type and honey bee abundance), emphasising the importance of plant diversity in maintaining wild bee diversity. Floral richness plays a critical role in sustaining diverse pollinator communities across time and space (Marcacci et al., 2022; Neumüller et al., 2020), as it supports pollinator species with different floral preferences and levels of specialisation and is important to sustain crop pollination services from unmanaged pollinators (Isbell et al., 2017; Orford et al., 2016; Rodríguez et al., 2021).

Wild bee abundance, FDis and FRic were generally higher in agricultural habitats compared to other local habitats. With agriculture being generally fragmented, and consisting of small field parcels under extensive management, these results may be linked to the role of agricultural habitats under traditional Mediterranean land management in providing nesting and floral resources to wild bees (Nielsen et al., 2011; Potts et al., 2006), and is in line with previous research, for instance, indicating greater bee FRic and FDis in agroforestry compared to arable land uses (Staton et al., 2022) and in low-intensity land uses (Forrest et al., 2015; Roquer-Beni et al., 2021).

4.2. Impact of landscape scale variables on bee communities

Urban proximity was associated with a reduction in FDiv and FRic, but no significant impact on wild bee abundance or richness was observed. This result, therefore, does not support previous observations suggesting that urbanisation impacts negatively on pollinator abundance and richness (Ayers and Rehan, 2021; Biella et al., 2022; Liang et al., 2023), but indicates a reduction in functional diversity. Landscapes characterised by high compositional heterogeneity may offer additional foraging and nesting resources (Martin et al., 2019), reduce foraging distances (Danner et al., 2017), and supporting a higher number of species (Bottero et al., 2023; Kirsch et al., 2024; Zanini et al., 2024). However, urban-driven fragmentation has been shown to be associated with the loss of wild bee diversity and a higher abundance of social species, the latter having a broader pollen diet spectrum, larger foraging distances and displaying a higher degree of tolerance to transformations of the environment (Banaszak-Cibicka et al., 2018; Ferrari and Polidori, 2022). Results obtained here indicate a positive association of FEve and FDis (within 500 m and 1000 m scales) and wild bee abundance (2000 m) with the NDVI, and a negative association between the Landscape Shannon Diversity Index and both FEve and FDis within the 500 and 1000 m radii. These results support previous observations of a differentiation between habitat use by wild bees compared to honeybees, indicating that wild bees appear to benefit from increased distance to urban areas, with wild bee functional diversity being positively associated with reduced fragmentation caused by urban development.

Table 2

Significant ($p < 0.05$) model averaged coefficients of the best supported ($\Delta AIC < 2$) GLMM explaining wild bee (WB) abundance and functional diversity indices of the bee assemblages in the transects. Predictors correspond to landscape habitat variables which were included together with their interactions with honeybee hive density (HB Density). The full list of coefficients and GLMMs is provided in Appendix D.

Response Variables	Scale (m)	Predictors								
		Aspect	Slope	Distance to Urban	SDI	LST	NDVI	HB Density	LST:HB Density	NDVI:HB Density
HB Abundance	1000								(0.25)*	
WB Abundance	100						(−0.14)*			
WB Abundance	2000						(0.2)*			
FDiv	200			(0.07)*						
FDiv	1000			(0.07)*						
FDiv	2000			(0.07)**						
FEve	100								(−0.08)*	
FEve	200								(−0.06)*	(−0.05)*
FEve	500				(−0.08)*		(0.08)*			
FEve	1000								(−0.11)***	
FDis	100								(−0.01)*	
FDis	200								(−0.01)*	
FDis	500				(−0.02)*		(0.02)*			
FDis	1000				(−0.01)*		(0.01)*		(−0.01)**	
FRic	500			(0.02)*				(0.02)*	(−0.02)*	

4.3. Impact of honeybees on bee communities

Honeybees were the most abundant species and dominated the plant-bee interaction networks. At the local scale, and when considering different habitats, honeybee abundance did not significantly influence wild bee abundance or richness, contrasting with previous observations from the study area (Balzan and De Santis, 2023) and other Mediterranean regions (Lázaro et al., 2021; Ropars et al., 2022; Shavit et al., 2009; but see Sentil et al., 2024). However, interspecific competition varies across time and with species and functional groups and is mediated by the availability of floral resources (Rodríguez et al., 2021; Ropars et al., 2022; Sentil et al., 2024). Ropars et al. (2022) found that competition with different wild bee groups changed across the season, with more intense competition recorded at the start of the season but lower competition late in the season, potentially caused by transhumance or the increased availability of floral resources. Iwasaki and Hogendoorn (2022) indicate that competition of honeybees is mainly with larger and social bees, and Gillespie et al. (2024) record a positive association between honeybee abundance and the bee FDis and richness indices, with small, solitary bees benefiting from the high honeybee abundance. In our study, honeybee abundance was negatively associated with FDis and FRic. The FDis captures the average distance between species based both on their functional attributes and relative abundance in a multidimensional space, indicating a reduction in the breadth of functional roles with increasing honeybee abundance. At the landscape scale, honeybee hive density was associated with increased FRic, which may be caused by the high relative abundance of honeybees compared to wild bees, therefore increasing the volume in a multi-functional space occupied by a bee community with low diversity.

A combined negative effect of honeybee hive density and land surface temperature on FEve, FDis and FRic was recorded in this study. Conversely, a positive interaction between honeybee hive density and land surface temperature was recorded for honeybee abundance, indicating an opposite effect on honeybees. Higher land surface temperature is normally associated with the urban heat island effect in cities, with literature indicating that the UHI can influence different taxa variably (Burdine and McCluney, 2019; Ferrari and Polidori, 2022; Graf et al., 2022), in warmer locations, higher temperatures may push species closer to their thermal tolerances, impact their abundance and filter communities according to functional traits (Brant et al., 2022; Kammerer et al., 2021; Polidori et al., 2023). These results support previous observations that more compact urban areas, with highly fragmented bee habitats, favours polylectic and social species with greater foraging ranges.

4.4. Caveats and research needs

Our analysis highlights the influence of local and landscape habitat characteristics on wild bee communities and functional diversity, drawing from multi-year data across diverse habitat categories. The results show how the combined effect of different local and landscape habitat variables impact the bee abundance and functional diversity across different habitats in coupled social-ecological systems. While previous research has demonstrated the importance of greenspace management, such as wildflower seeding in urban areas (Anderson et al., 2023; Banaszak-Cibicka et al., 2018), and improved ground cover and floral resources in agroecosystems (Cano et al., 2024; Kratschmer et al., 2019), the integration of these findings across multiple land-use categories and their cumulative impact remain underexplored. Similarly, the influence of the temporal availability of floral resources, driven by seasonal weather patterns, may be particularly relevant for Mediterranean conditions with higher temperatures, reduced annual precipitation, and increased interannual variability of rainfall leading to frequent drought occurrence (Balzan et al., 2020; Cherif et al., 2020), as these are known to influence interspecific competition and bee diversity (Ropars et al., 2022). Nonetheless, there is limited understanding of how these spatial and temporal variations interact with species-specific functional traits to shape pollinator communities across landscapes.

5. Conclusions

First, we conclude that plant species richness and agricultural habitats at the local scale positively affected wild bee abundance and species richness, and functional diversity. Secondly, we conclude that, at the landscape scale, wild bee species richness and functional diversity were negatively affected by urban development and landscape diversity, which appears to be reversed for honeybees. These findings were found across the different spatial scales considered in this study. We argue that the reduction in bee functional diversity with landscape diversity may be a consequence of urban driven fragmentation, which reduces the availability of floral and nesting resources, and favouring polylectic, social species with greater foraging ranges.

Third, while honeybee abundance did not affect wild bee abundance or richness in this study, it did influence bee functional diversity at both local and landscape scales. Honeybee abundance was associated with a reduction in FDiv and FRic at the local scale. A combined negative effect of honeybee hive density and land surface temperature on FEve, FDis and FRic was recorded supporting previous observations that more compact urban areas, with highly fragmented bee habitats, favours polylectic and social species with greater foraging ranges.

Together, these results provide valuable insights into the combined effects of local and landscape habitat structures on flower-visiting bee communities across habitats. In addressing pollinator declines and the loss of ecosystem services, these findings emphasise the importance of assessing both pollinator abundance and functional diversity. Measures to promote honeybee conservation and beekeeping can help maintain pollination ecosystem services but also reduce functional trait diversity, potentially impairing the pollination of more specialised plant species. While further research is needed to evaluate how habitat management across different land uses within cultural landscapes can support managed and wild pollinator communities, this study shows that landscape-scale responses of honeybees and wild bee functional diversity were primarily driven by urban processes. These findings highlight the important role of urban and land use planning in cultural landscapes for the conservation of wild pollinator communities.

Ethics statement

If this manuscript involves research on animals or humans, it is imperative to disclose all approval details.

If Yes, please provide your text here:

This manuscript investigates the impact of social-ecological variables on wild bee communities. Transects were carried out across Malta with measures taken to reduce impact on the environment, including by, wherever possible, identifying species on the wing and releasing collected specimens following identification. This is explained in more detail in the Methodology section of the manuscript.

CRediT authorship contribution statement

Balzan Mario V.: Writing – review & editing, Writing – original draft, Visualization, Validation, Supervision, Resources, Project administration, Methodology, Investigation, Funding acquisition, Formal analysis, Data curation, Conceptualization. **Leticia De Santis:** Writing – review & editing, Data curation. **Ahlam Sentil:** Writing – review & editing, Data curation. **Denis Michez:** Writing – review & editing, Validation, Supervision, Data curation, Conceptualization.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.gecco.2025.e03765.

Data availability

Data will be made available on request.

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