



Green infrastructure provides important wild bee refuges in intensive agricultural landscapes: The case of Spanish drove roads

Paula Solascasas ^{a,b,c} , Francisco M. Azcárate ^{a,c} , Jose A. González ^{b,c}, Pablo Manzano ^{d,e} , Denis Michez ^f , Thomas J. Wood ^g , Violeta Hevia ^{b,c,*}

^a Terrestrial Ecology Group, Department of Ecology, Universidad Autónoma de Madrid, Darwin 2, Madrid 28049, Spain

^b Social-ecological Systems Laboratory, Department of Ecology, Universidad Autónoma de Madrid, Darwin 2, Madrid 28049, Spain

^c Centro de Investigación en Biodiversidad y Cambio Global (CIBG-UAM), Universidad Autónoma de Madrid, Spain

^d Basque Centre for Climate Change (BC3), Leioa 48940, Spain

^e Ikerbasque — Basque Foundation of Science, Bilbao 48011, Spain

^f Laboratory of Zoology, Research Institute of Biosciences, University of Mons, Place du parc 20, Mons 7000, Belgium

^g Naturalis Biodiversity Center, Darwinweg 2, Leiden 2333 CR, the Netherlands

ARTICLE INFO

Keywords:

Canada Real Conquense
Ecological corridor
Iberian Peninsula
Landscape heterogeneity
Livestock routes
Pan traps
Pollinators
Transhumance

ABSTRACT

Agricultural intensification and reduced proximity to natural habitats and their associated resources negatively impact wild bee diversity. The Spanish network of drove roads, a series of traditional routes which have been maintained through the practice of transhumant grazing and livestock movements, plays a fundamental role in mitigating some of these negative impacts. This network, functioning as a form of green infrastructure, provides permanent semi-natural grasslands that serve as refuges for pollinators in particularly intensively managed agricultural landscapes. To explore the effect of the *Conquense* drove road –over 400 km long and one of the most frequently used transhumant drove roads in Castilla-La Mancha (central Spain)– on the wild bee community, we sampled a 240 km section that extends across three distinct ecoregions (Campo de Calatrava, Llanura Manchega and Mancha Alta), which differ biogeographically in terms of geology and geomorphology, likely resulting in differences in bee communities. We collected wild bee specimens using pan traps across three land use types present within each ecoregion: drove road grasslands, patches of semi-natural vegetation and intensive crop fields. Wild bee community composition showed significant differences between the three ecoregions. Drove roads showed a significant positive effect on species richness and Shannon's diversity when the availability of semi-natural habitat was low. Functional richness of wild bees was significantly higher in drove road grasslands compared to the other two land use types (semi-natural vegetation and crops). Moreover, the interaction between semi-natural cover and drove roads revealed a significant positive effect of drove roads on both functional richness and dispersion, particularly under conditions of low semi-natural habitat cover. Our study highlights that drove road grasslands can offer suitable habitat resources that support bee taxonomic and functional diversity, particularly in landscapes heavily transformed by intensive agriculture and with reduced availability of semi-natural areas. The EU Pollinators Initiative emphasizes the need of restoring natural habitats in agricultural landscapes and creating a network of ecological corridors for pollinators. In this context, the preservation of the Spanish network of drove roads is highly relevant. Drove road grasslands, when maintained through traditional transhumant grazing, can provide feeding and nesting resources to wild bees and other pollinators, especially within a highly intensified agricultural matrix.

1. Introduction

The role of wild bees is critical for the health of terrestrial ecosystems worldwide, as they function as primary pollinators that ensure the

sexual reproduction of wild flowering plants (Klein et al., 2018; Potts et al., 2016; Wei et al., 2021). Furthermore, wild bees are essential for crop production and the maintenance of human well-being, as around 75 % of the most important crops depend on animal pollination, making

* Correspondence to: Departament of Ecology, Universidad Autónoma de Madrid, Darwin 2, Madrid 28049, Spain

E-mail address: violeta.hevia@uam.es (V. Hevia).

them essential for food production (Klein et al., 2007; IPBES et al., 2016). In the context of global decline that pollinators are facing (Potts et al., 2010), the dependence of wild bee species on the existence of a variety of floral and habitat resources makes them highly vulnerable to disturbance (Drossart and Gérard, 2020). Three of the main threats bee populations face are habitat loss and fragmentation and agricultural intensification (Astegiano et al., 2015; Duchenne et al., 2020; Winfree et al., 2009). Given the mobile nature of bees as central place foragers, there is considerable overlap between these three interacting threats; collectively, they reduce the access of wild bees to feeding and nesting resources, negatively impacting bee species richness, abundance, and community composition (Bommarco et al., 2010; Carré et al., 2009; Le Féon et al., 2010) and thus affecting the pollination services they provide (Kremen et al., 2002).

The presence of permanent grasslands, which constitute important habitats for wild bee species (Banaszak and Tward, 2018; Morandin et al., 2007; Nieto et al., 2014), increases the availability of nesting and floral resources at the landscape-scale, ensuring the maintenance of functionally diverse wild bee assemblages (Carrié et al., 2018). The meta-analysis of Garibaldi et al. (2011) showed that proximity to natural areas promotes crop pollination by wild bee species. In fragmented agroecosystems, remaining patches of native habitat and complementary low-input habitats, such as extensive pastures or meadows, act as biodiversity reservoirs for wild bee communities (Ekoos et al., 2020; Kwaiser and Hendrix, 2008; Pfiffner et al., 2018). Moreover, the diversity of semi-natural habitats (e.g. wooded and herbaceous) provides more pollen species and allows for a greater number of plant-bee interactions, ensuring food availability for wild bees in homogeneous and resource-poor agricultural landscapes (Maurer et al., 2022; Rivers-Moore et al., 2020).

Zones with a Mediterranean climate, most clearly the Old World Mediterranean basin, hold the greatest diversity of bees and are considered global hotspots for this group of insects (Orr et al., 2021; Winfree, 2010), with the Iberian Peninsula alone hosting more than 1000 wild bee species (Ortiz-Sánchez, 2020; Reverté et al., 2023). Mediterranean grasslands, and especially those embedded in a mosaic of vegetation at different successional stages, are key habitats for wild bee communities (Penado et al., 2022). The Spanish landscape stands out for the presence of an extensive network of drove roads (or livestock routes), which are the traditional paths used by transhumant shepherds to migrate between wintering and summering areas, in search of the most productive pastures (Manzano and Casas, 2010; Ruiz and Ruiz, 1986). These corridors are characterized by the presence of semi-natural grasslands, that are grazed by the herds during their seasonal movements. This traditional management of domestic livestock results in areas of high ecological value (Gómez-Sal, 2001; Oteros-Rozas et al., 2012), especially within intensive agricultural landscapes. Drove roads act as biodiversity reservoirs for both plants and animals, as well as a source of local landscape heterogeneity (Azcárate et al., 2013b, 2013a; Hevia et al., 2013). Although similar paths for livestock movement exist in other countries like France and Italy (Biber, 2010; Di Martino et al., 2006), the Spanish network is remarkable for its extent, occupying 421,000 ha (about 0.8 % of the national territory) and its legal protection since 1995 (Drove Roads Act). Drove roads can be classified into different categories according to their historical importance and width: Major Drove Roads (*Cañadas Reales*) are the broadest ones, with a legal width of 75 m, followed by smaller trails known as *cordeles* (approximately 37 m wide), *veredas* (about 20 m) and *coladas* (less than 20 m wide) (an image illustrating two examples of drove roads with different widths is provided in the Supplementary material, Figure S1). One of the main drove roads still in use is the *Conquense* Major Drove Road, a 75 m wide and 410 km long corridor that crosses the region of Castilla-La Mancha, connecting summering and wintering pasturelands.

Previous studies have shown that the presence of this particular drove road has a positive impact on wild bee richness and abundance when compared to adjacent crops, as well as promoting pollination

services (Hevia et al., 2016). Such facilitation also eases inbreeding in wild rangeland plant populations of the area, which highlights its role in providing ecological connectivity (García-Fernández et al., 2019). However, the importance of this drove road for the wild bee community across biogeographically diverse regions, compared not only to crops but to semi-natural uses, has never been assessed. The connection of patches of isolated natural habitats makes drove roads an example of green infrastructure that promotes connectivity at the landscape scale. Green Infrastructure, which has been defined by the European Commission as “a strategically planned network of natural and semi-natural areas with other environmental features, designed and managed to deliver a wide range of ecosystem services, while also enhancing biodiversity”, can therefore increase the availability of habitat and resources for wild bees in highly modified and resource-poor environments.

This study investigates the effect of three different land use types on wild bee communities across the *Conquense* drove road in Castilla-La Mancha: (a) permanent grasslands with seasonal transhumant grazing (referred to as drove road grasslands, DR), dominated by herbaceous plant species, (b) patches of semi-natural vegetation of different types (SN), including woody vegetation like hedgerows, trees and bushes, and (c) crops of different varieties (AG), which represent the predominant land use in the region. Beyond the demonstrated effect of uncultivated semi-natural habitats on wild pollinators, our hypothesis is that the drove road grasslands will act as a refuge for wild bees, with this effect being amplified in relative terms when the surrounding landscape is intensively cultivated. Therefore, we expect that the potential role of drove roads as biodiversity reservoirs for wild bees will become more evident under conditions of reduced semi-natural habitat availability.

2. Materials and methods

2.1. Study area

The research was conducted in Castilla-La Mancha (central Spain), along the *Conquense* drove road, one of the most used transhumant drove roads (Fig. 1a). Each year, around 9000 animals (mainly sheep and cattle) walk this drove road twice between the summering pasturelands in Montes Universales and Serranía de Cuenca, and the southern wintering *dehesas* of Sierra Morena (Oteros-Rozas et al., 2012). The study site extends across three ecoregions, from south to north: Campo de Calatrava, Llanura Manchega and Mancha Alta. The climate is continental Mediterranean, with significant thermal contrasts and pronounced summer drought, and the landscape is dominated by agriculture. However, each ecoregion has specific geological and geomorphological features that have led to substantial differences in the extent of remaining semi-natural uncultivated areas, as well as potentially in the composition of their bee communities.

Campo de Calatrava (CC), the southernmost region, exhibits the most heterogeneous landscape, with a moderately pronounced relief and, consequently, lower availability of cultivable surfaces. The Llanura Manchega region (LL), in the centre of the study area, predominantly features flat topography with minimal relief, which has facilitated intensive agricultural development, driven by the presence of several aquifers extensively exploited for irrigation. To the north, the Mancha Alta (MA) is characterized by undulating surfaces of cultivable materials alternating with rockier outcrops which provide some relief to the area and scattered natural and semi-natural fragments. Table 1 shows the main climatic variables for the three ecoregions, as well as the average percentage of semi-natural and agricultural cover for each land use type within each ecoregion. This cover was estimated using a 500 m buffer around each sampling point (which covers the mean foraging distance of most wild bee species, Gathmann and Tscharntke, 2002), based on the 2018 Corine Land Cover dataset (Figs. 1b, 1c and 1d).

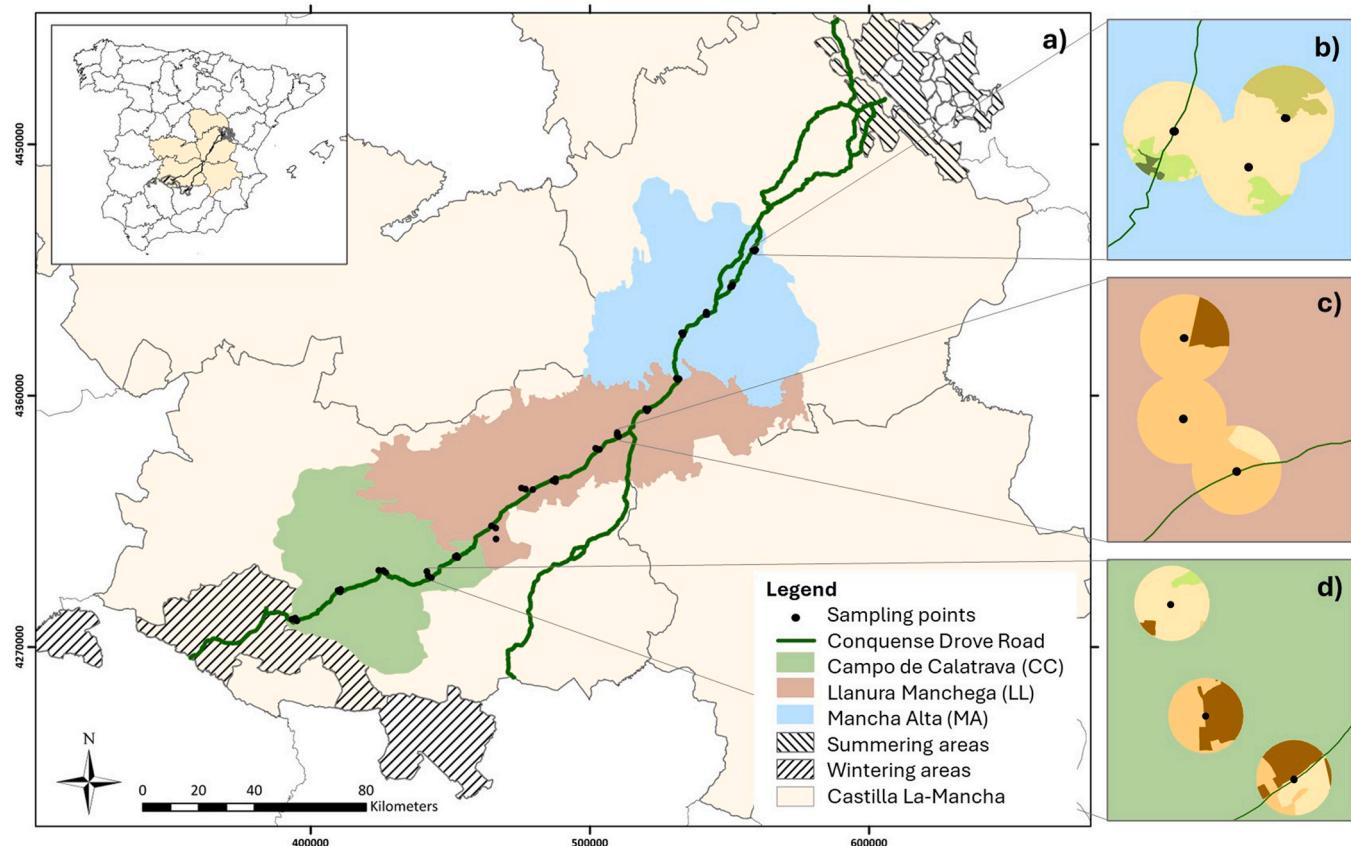


Fig. 1. a) Location of the sixteen sampling sites along the 240 km transect of the study area and examples of different land use intensity in the three ecoregions: b) Mancha Alta, c) Llanura Manchega and d) Campo de Calatrava. A 500 m buffer of the uses surrounding each point was created using the Corine Land Cover dataset (EEA, 2018), sand and brown tones represent agricultural uses while green tones represent semi-natural habitats.

Table 1

Climatic variables (average annual temperature and precipitation in the whole ecoregion), and average percentage of semi-natural and agricultural land cover for each land use type within each ecoregion. This cover was estimated using a 500 m buffer around each sampling point based on data from the Corine Land Cover dataset (2018).

Ecoregion	Temperature (°C)	Precipitation (mm)	Land use type	% semi-natural cover	% agricultural cover
Campo de Calatrava	13.5 – 16	400 – 550	DR	15.4	84.6
			SN	25.6	74.4
			AG	8.6	91.4
Llanura Manchega	15 – 16	400 – 450	DR	5.8	94.2
			SN	1	99
			AG	1.2	98.8
Mancha Alta	13.5 – 15.5	400 – 500	DR	16	84
			SN	18.2	81.8
			AG	8	92

2.2. Sampling design and data collection

We established sixteen sampling sites along a 240-km section of the *Conquense* drove road, five in the southern ecoregion (CC), six in the central ecoregion (LL), and five in the northern ecoregion (MA) (Fig. 1a), mean distance between sampling sites was 14.6 km. Field sampling was carried out between the 28th - 31st of May 2022, which is the optimal month for bee activity in this region. We used pan traps to capture bees at all sampling sites. Pan traps have been extensively used to sample bee communities and are efficient at standardising sampling effort (Westphal et al., 2008), despite having some limitations in terms of bee-flower interactions or underestimating bee richness (Popic et al., 2013).

At each of the sixteen sites, we established three sampling levels (Fig. 2), corresponding to the three land use types: (1) one within the

drove road grasslands (DR), dominated by xerophile, open short-grass perennial grasslands rich in therophytes (EU priority habitat type 6220, pseudo-steppe with grasses and annuals of the *Thero-Brachypodietea*) that turn into rupicolous calcareous or basophilic grasslands of the *Alyso-Sedion albi* (habitat type 6110) in rockier areas; (2) one in patches of semi-natural vegetation (SN), composed by a mixture of habitat types, including open grasslands (habitat type 6220) and also basophilous scrub (*Genista scorpius*, *Thymus vulgaris*, *Bupleurum fruticosum*) and other low-growing woody plants (habitat types 5210 and 5330); and (3) a further one inside crop fields (AG), mostly cereals (wheat, barley, and oats), vineyards, and sunflowers (*Helianthus annuus*). At each sampling level, we set up two pan trap clusters separated by 10 m. Each cluster consisted of three plastic bowls painted with blue, yellow, and white UV-reflective paint, and held at the same height as the surrounding vegetation. Samplings at each land use type were

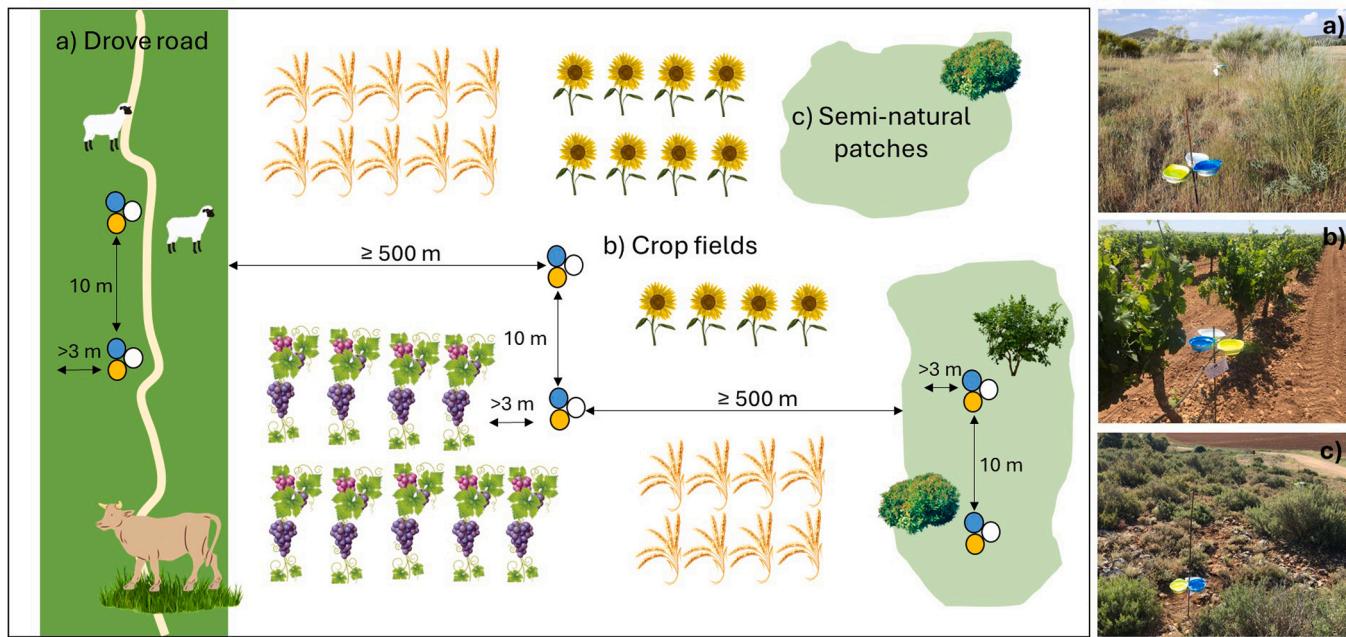


Fig. 2. Schematic representation of the three sampling levels corresponding to the three land use types: (a) drove road grasslands, (b) different types of crops and (c) semi-natural vegetation. This design was repeated throughout the 16 sampling sites.

separated from each other by at least 500 m, since this is the foraging range for most solitary bees (Gathmann and Tscharntke, 2002; Zurbuchen et al., 2010).

Each pan trap was filled up to $\frac{3}{4}$ with soapy water to reduce surface tension and laid out at each site for 48 consecutive hours on non-rainy weather days. The first eight sampling sites, from north to south, were set up the 28th of May, and after 24 h, the content was collected and the pan traps were re-filled and laid out for another 24 h. The remaining eight sampling points were set up the 29th of May and were managed following the same procedure. The specimens from the two immediately adjacent pan traps (within the same land use type) were pooled. Once specimens were retrieved, they were washed and stored in 70 % ethanol until they were dried and pinned for identification. We focused only on wild bee species, excluding *Apis mellifera* from our analyses. Captured bees were identified to the species level by professional entomologists. We followed the taxonomic framework of Ghisbain et al. (2023).

2.3. Data analyses

To explore the differences in wild bee communities, we compared species composition using Bray-Curtis dissimilarity as the distance matrix, based on species presence-absence data. The results of the comparisons were visualized using Classical (Metric) Multidimensional Scaling (MDS) ordination. The significance of the dissimilarities among the contrasted groups was tested with permutational multivariate analysis of variance (PERMANOVA) using the *vegan* package. Individual-based species accumulation curves of each ecoregion were created to compare total species richness between land uses with the *iNEXT* package (Hsieh et al., 2016).

Each sampling level was characterised by: (a) wild bee species richness, (b) Shannon's diversity, (c) functional richness (FRic), and (d) functional dispersion (FDis). FRic and FDis were obtained after measuring three quantitative functional traits (intertegular distance, wing length, and hair length at the mesonotum) in a random sample of 10 individuals per species, along with three categorical traits (diet, nesting site, and sociality), which were assigned based on literature sources. As the quantitative traits were correlated, residuals from linear models of wing length and hair length against intertegular distance were used (Hevia et al., 2021; Micó et al., 2020). Functional distances were

computed using the *Gawdis* package, weighting categorical traits so that they contributed equally to each quantitative trait. Functional richness (FRic) and functional dispersion (FDis) were then calculated using the *FD* package, based on *Gawdis* distances and log-transformed species abundance data.

We explored the effect of land use type (DR, SN and AG) on wild bee diversity and functional descriptors through generalized linear mixed models (GLMM). We also included the independent variable of semi-natural cover (estimated in a 500 m buffer around each sampling point using the 2018 Corine Land Cover dataset) and the interaction of land use type (DR, SN and AG) with the proportion of semi-natural cover, and added the three ecoregions (CC, LL and MA) and the sixteen sampling sites as random effect factors. We tested multiple family-link function combinations based on the data type (continuous or discrete) using *glmer* from the *lme4* package. Model selection was performed using AICc with *MuMin*, choosing the most parsimonious model. Residual diagnostics were assessed with *DHARMa* to ensure no major deviations from expected distributional assumptions. All statistical analyses were performed using R software (Version 4.2.2; R Development Core Team, 2022).

3. Results

Over the course of our study, we collected a total of 1439 individual wild bees from 127 species, including the extremely rare species *Dufourea longiglossa* that was previously known only from the province of Jaén in south-eastern Spain (Ebmer, 1993). *Lasioglossum* was the most abundant genus, accounting for 57 % of all specimens captured (see Supplementary material Table S1, for a complete list of species).

The ordination of bee species composition using MDS and the subsequent PERMANOVA revealed significant differences among the community composition of the three ecoregions with no influence of the land use type (PERMANOVA, $F = 7.7651$, $p\text{-value} < 0.05$) (Fig. 3), suggesting underlying biogeographic differences in species pools among them.

Accumulation curves show higher species richness of wild bees in drove road grasslands of the Llanura Manchega region, compared to semi-natural patches of vegetation and intensive crops (Fig. 4). Campo de Calatrava accumulation curves showed higher wild bee species richness in semi-natural vegetation patches, while the three land use

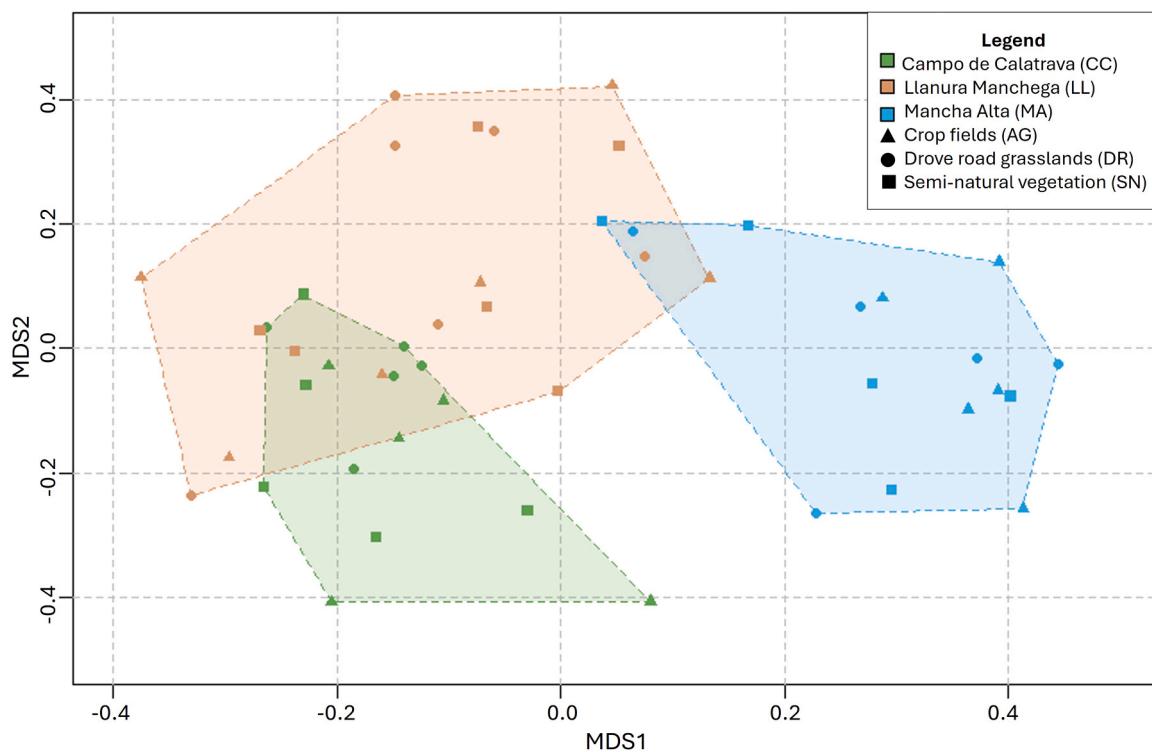


Fig. 3. MDS ordination plots showing the dissimilarities (Bray Curtis, presence-absence data) in the community composition of wild bees of the three Castilla-La Mancha regions (CC, LL and MA).

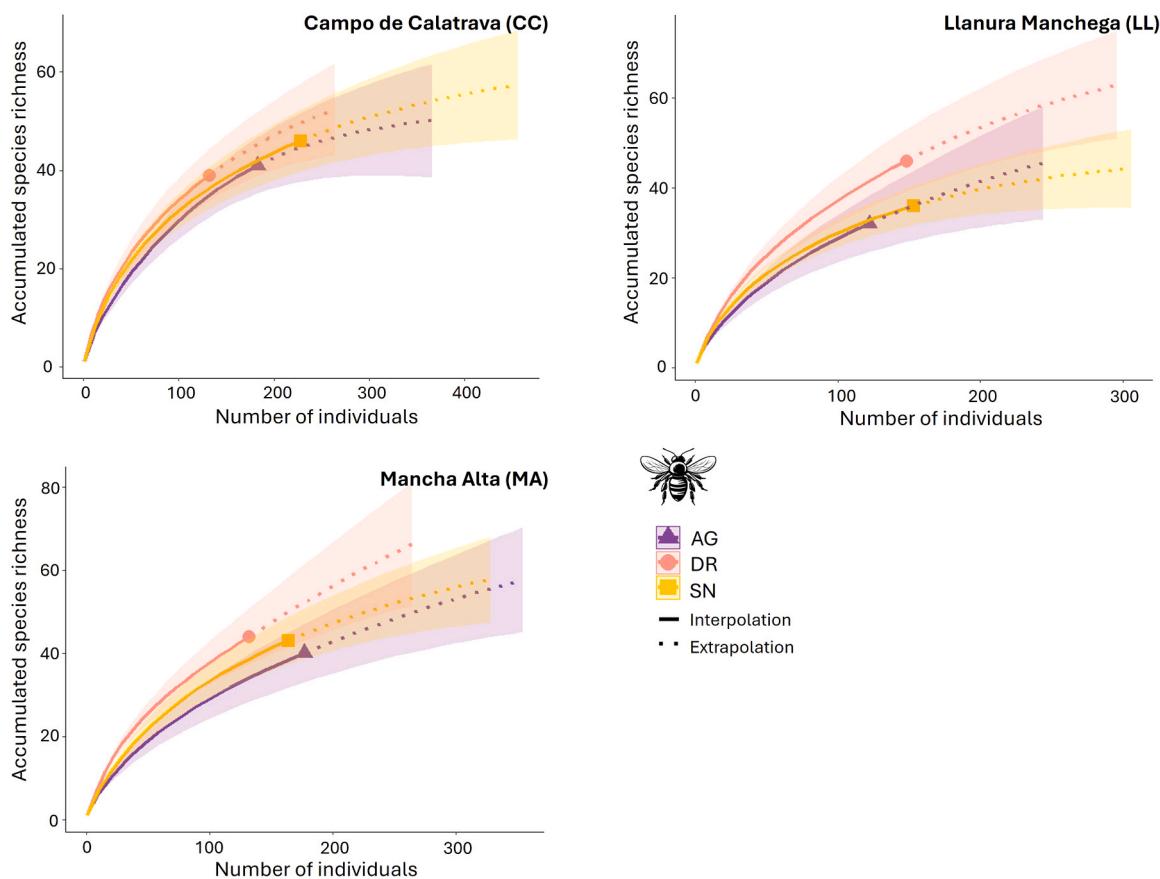


Fig. 4. Individual-based randomized species accumulation curves of each region comparing wild bee species richness between the three land use types (DR: drove road grasslands, SN: semi-natural vegetation, AG: crop fields). Shaded areas represent 95 % confidence intervals.

types in Mancha Alta region showed similar levels of accumulated species richness.

According to the models, both species richness and Shannon's diversity, as well as functional richness and functional dispersion, showed a significant and positive effect of semi-natural cover ($p < 0.05$), which was used as a proxy for land-use intensity across the three ecoregions (Fig. 5). Regarding land-use type, drove roads showed a marginally significant and positive effect on species richness but a clear significant positive effect on Shannon's diversity and functional richness (Fig. 6) (Table 2). However, the interaction between the drove road and semi-natural cover exhibited a marginally significant and negative effect—meaning that the positive influence of the drove road on species richness is stronger when semi-natural cover is low, and weaker (or even potentially reversed) when semi-natural cover is high (Fig. 7a). In the case of Shannon's diversity, the effect was more pronounced: both the drove road and semi-natural land-use types exhibited significantly higher Shannon's diversity compared to agricultural land (Table 2). Additionally, there was a significant negative effect of the interaction between each of these land-use types and semi-natural cover—indicating that the positive influence of both the drove road and semi-natural areas on Shannon diversity is stronger when semi-natural cover is low, and weaker (or even potentially reversed) when it is high (Fig. 7b). For functional richness, we found a significant and positive effect of the drove road compared to the other two land-use types, along with a significant and negative effect of its interaction with semi-natural cover (Table 2). This indicates that the positive influence of the drove road on functional richness is stronger when semi-natural cover is low, and weaker (or even potentially reversed) when it is high (Fig. 7c). The model results for functional dispersion were similar, showing a marginally significant effect of the drove road—functional dispersion was higher in drove roads compared to semi-natural and agricultural land (Table 2). Additionally, there was a significant and negative effect of the interaction between the drove road and semi-natural cover, indicating that the positive influence of the drove road on functional dispersion is stronger when semi-natural cover is low, and weaker when

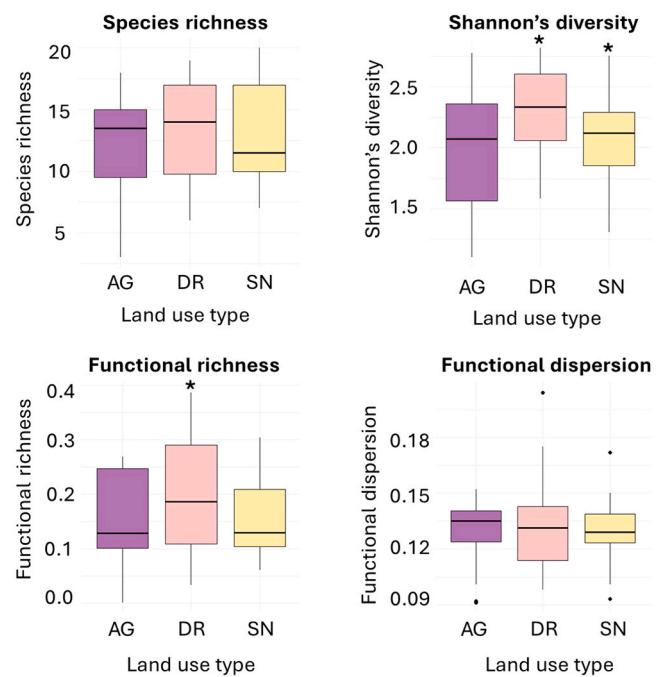


Fig. 6. Boxplots of the 4 descriptors of wild bee communities in relation to the three types of land use (AG: crops, DR: drove roads, SN: semi-natural vegetation). The asterisks indicate the land use categories for which a specific descriptor of wild bee communities showed a significant effect in the conducted GLMMs. (*) $P < 0.05$.

it is high (Fig. 7d).

4. Discussion

Our results support the hypothesis that drove road grasslands can

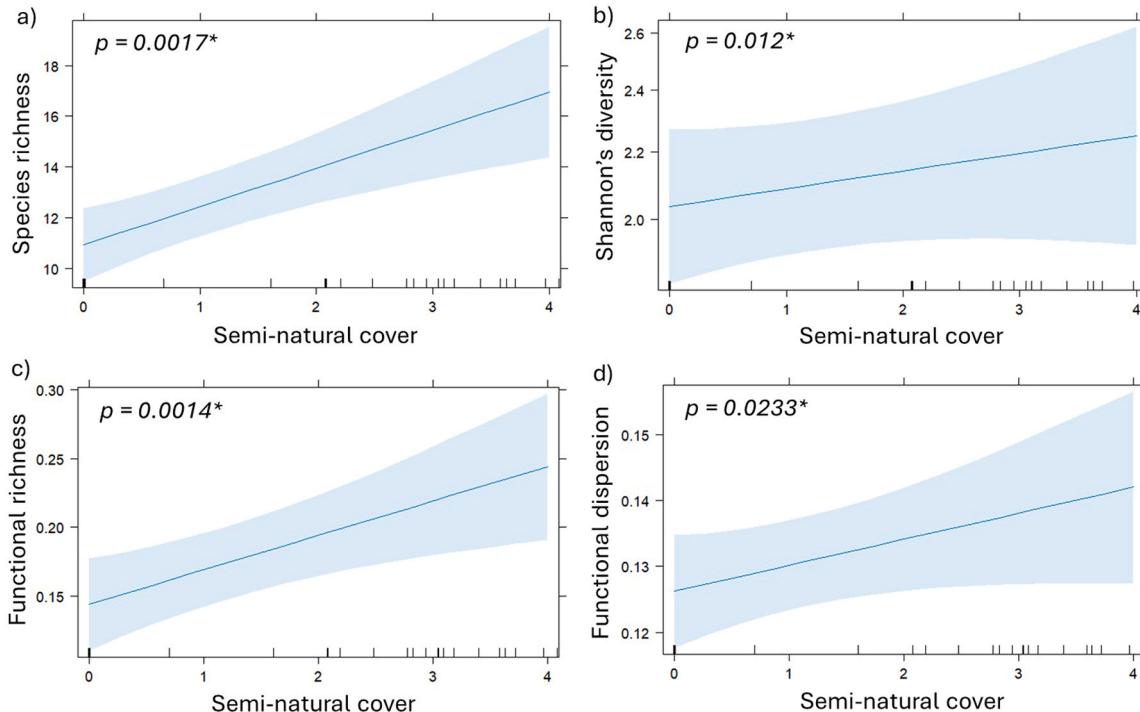


Fig. 5. Predicted responses to the quantitative variables and 95 % confidence intervals of (a) wild bee species richness, (b) Shannon's diversity; (c) functional richness and (d) functional dispersion. WL and HL are the residuals of their regressions with ITD. Effects plots are based on the GLMMs shown in Table 2. Quantitative predictors were introduced into the models after normalization. At the top of each plot, the P-value obtained for each predictor is displayed. (*) $P < 0.05$.

Table 2

Coefficients and standard errors for each of the predictors included in the generalised linear mixed models (GLMM) estimated for a) species richness, b) Shannon's diversity, c) functional richness and d) functional dispersion. For the factor 'land use type' the model estimated coefficients for 'DR' and 'SN' while 'AG' was integrated into the intercept. For the interaction between 'semi-natural cover' and 'land use type', the model estimated coefficients for 'semi-natural cover:DR' and 'semi-natural cover:SN' while 'semi-natural cover:AG' was integrated into the intercept.

Model	Distribution	Fixed effects	Estimate	Std. Error	p-value
a) Species richness	Poisson (link = "identity")	Semi-natural cover	2.4266	0.7739	0.00171 *
		Land use DR	2.7371	1.5713	0.08152 .
		Land use SN	1.8006	1.5075	0.23232
		Semi-natural cover:Land use DR	-1.7114	0.9523	0.07232 .
		Semi-natural cover:Land use SN	-1.0498	0.9539	0.27109
b) Shannon's diversity	Gaussian (link = "log")	Semi-natural cover	0.09292	0.03700	0.012038 *
		Land use DR	0.25279	0.07374	0.000608 *
		Land use SN	0.18454	0.07574	0.014833 *
		Semi-natural cover:Land use DR	-0.10371	0.03850	0.007058 *
		Semi-natural cover:Land use SN	-0.10015	0.03877	0.009780 *
c) Functional richness	Gaussian (link = "identity")	Semi-natural cover	0.05366	0.01577	0.00135 *
		Land use DR	0.10694	0.03584	0.00522 *
		Land use SN	0.03467	0.03516	0.33110
		Semi-natural cover:Land use DR	-0.05667	0.01931	0.00565 *
		Semi-natural cover:Land use SN	-0.02912	0.01912	0.13609
d) Functional dispersion	Gamma (link = "identity")	Semi-natural cover	0.009698	0.004274	0.0233 *
		Land use DR	0.016415	0.009396	0.0806 .
		Land use SN	0.008212	0.008912	0.3568
		Semi-natural cover:Land use DR	-0.010628	0.005300	0.0449 *
		Semi-natural cover:Land use SN	-0.006663	0.005270	0.2061

function as reservoirs of diversity and functional richness for wild bee populations in intensively managed agricultural landscapes, with this effect being particularly significant when the availability of semi-natural habitats is limited and landscape heterogeneity is reduced. In addition, we found that the community composition of wild bee assemblages was significantly influenced by land use intensity, with effects on bee diversity that were consistent across ecoregions. Different intensities of land use result in different landscape configurations, which in turn may impact the availability of feeding and nesting resources (Roulston and Goodell, 2011), reinforcing the idea that landscape-scale management plays a crucial role in sustaining wild bee communities.

In addition to the demonstrated role of drove roads as reservoirs of bee diversity compared to intensive crops such as sunflower (Hevia et al., 2016), their contribution to wild bee communities at the landscape level can be particularly important, especially in areas where the proportion of land occupied by semi-natural habitats is notably small. In line with expectations, wild bee species richness and Shannon's diversity differed between land use types, with both diversity measures exhibiting higher levels in drove road grasslands, although the effect was only marginally significant in the case of species richness. In addition, the interaction between semi-natural habitat cover (used as a proxy for land use intensity) and the drove road use was significant and negative, emphasizing that the positive effect of drove roads on wild bee diversity is stronger under lower levels of semi-natural habitat cover. Similarly, Rundlöf et al. (2008) found that the positive effect of organic farms vs. conventional farms in bumble bee species richness was only significant in homogeneous landscapes but couldn't be observed in more heterogeneous contexts, suggesting that organic farms might be acting as a source of heterogeneity, comparably to the effect of the interaction between drove road grasslands and semi-natural habitat cover in our study. A meta-analysis on bee responses to anthropogenic disturbances also showed that bee richness was negatively impacted by habitat loss and fragmentation, but this was only significant when the proportion of natural habitats was low (Winfree et al., 2009). This is coherent with the results we obtained in this research, where the lack of semi-natural habitats and landscape homogenisation make the role of drove road grasslands more relevant for wild bee populations.

The positive impact of an increased proportion of semi-natural habitats on wild bees in agricultural landscapes has been widely researched (Clough et al., 2014; Le Féon et al., 2010; Maurer et al., 2022) and this was also supported by the effects of the semi-natural

habitat cover model on the variables analysed in our study. The absence of statistically significant differences in wild bee diversity between drove roads and semi-natural vegetation patches could be related to the fact that bees are highly mobile organisms during their lifetime, which can persist in small habitat fragments and easily move between them, but also to the provision of similar resources (food and nesting sites) in both land use types. In this regard, Rivers-Moore et al. (2020) highlighted the complementarity of herbaceous and wooded habitats in supporting bee diversity, with both types providing essential resources for different bee species, although the specific interactions between plants and bees can also affect community composition.

Additionally, our study presents a limitation that should be considered regarding the number of sampling events conducted. According to Banaszak et al. (2014), a single sampling event may be insufficient to fully represent the bee species diversity within a study area. The study highlights that bee species richness significantly varies with sampling frequency. Given the phenological variability of bee species, which depends on factors like flowering and seasonal patterns, a one-time sample is likely to miss species, particularly those with short or irregular activity periods. This lack of sampling across different times of the season may lead to the exclusion of important species, thereby affecting the representativeness of the data. Therefore, our results should be interpreted cautiously, as a single sampling event does not ensure adequate species coverage, especially when considering the seasonal and interannual variability in species emergence. To obtain more reliable results, multiple sampling occasions throughout the bee activity season are recommended, preferably at higher frequencies than a single sampling event.

On the other hand, in our study, the use of pan traps for sampling bees may have introduced biases that affect the representativeness of the results. Previous research has shown that pan traps tend to under-represent certain species, particularly floral specialists and larger-bodied bees such as *Bombus* and *Apis* species. Cane et al. (2000) found that pan traps fail to capture many common native bee species, especially those associated with specific floral resources. Similarly, Hudson et al. (2020) observed that only 19 % of bees attracted to pan traps were captured, with smaller-bodied bees like *Lasioglossum* spp. being overrepresented compared to larger bees. This bias may have influenced the composition of our sampled bee community, especially if larger bees were abundant in the study area but less likely to be captured in pan traps.

Furthermore, the effectiveness of pan traps can vary depending on

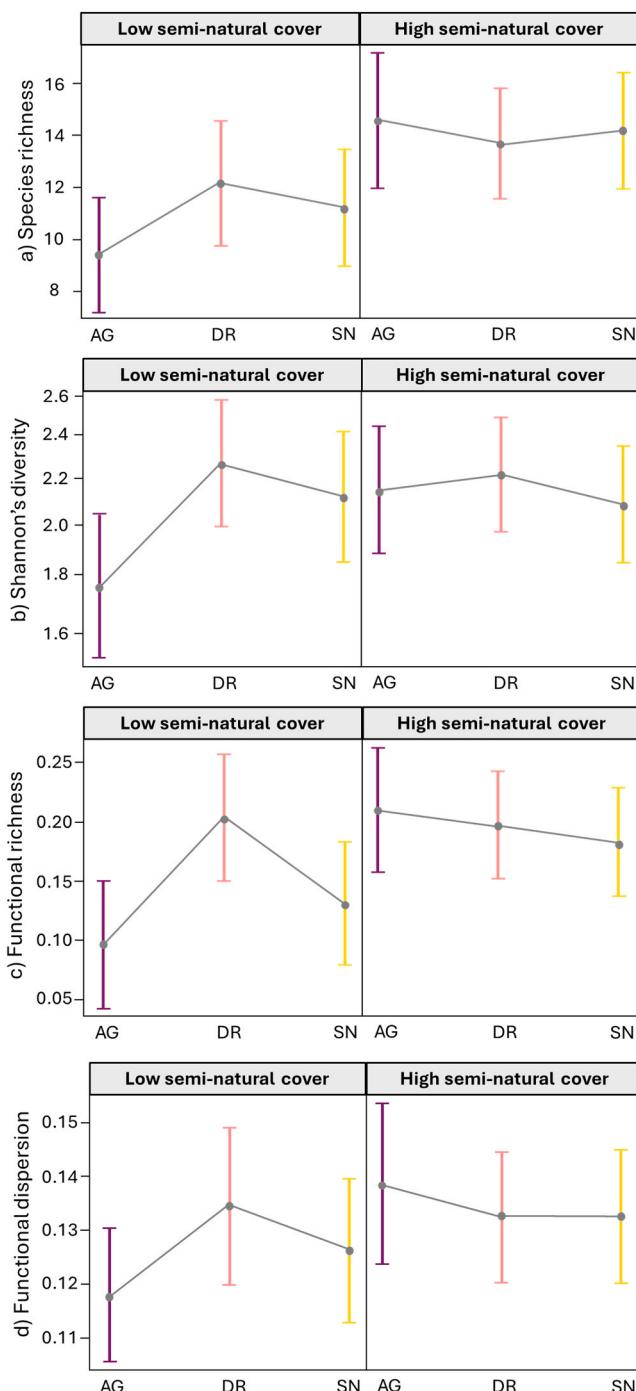


Fig. 7. Effects of the interaction between land use type (AG, DR or SN) and semi-natural cover (obtained from Corine Land Cover 2018) on wild bee a) species richness, b) Shannon's diversity, c) functional richness and d) functional dispersion. Two scenarios are shown to illustrate how the effect changes: on the left, the effect of the interaction between land use type and semi-natural cover when the semi-natural cover is low, on the right, the effect of the interaction between land use type and semi-natural cover when the semi-natural cover is high. Effects plots are based on the GLMMs shown in Table 2.

the habitat and floral resources available. Wilson et al. (2008) found that pan traps may not capture the full diversity of bee species, especially when specific species avoid the trap colours or when floral resources are abundant, which can reduce trap effectiveness. Given these limitations, it is clear that pan traps alone may not provide a complete assessment of bee diversity. As suggested by multiple studies, including those by Cane

et al. (2000) and Wilson et al. (2008), combining pan trapping with additional sampling methods, such as net sampling, would likely provide a more comprehensive and unbiased representation of the bee community.

Functional richness in our study was significantly higher in transhumant drove roads compared to the other land use types (agriculture and semi-natural vegetation). Similar to what was observed for diversity, the interaction between semi-natural habitat cover and drove road land use was significant and negative, highlighting that the positive effect of drove roads on wild bee functional richness is stronger in areas with reduced semi-natural habitat cover. This was also the case for functional dispersion. Functional diversity has been found to be critical for pollinator responses to agricultural intensification, contributing to the sustainability of the pollination function (Roquer-Beni et al., 2021). Our results provide important insights into the relevant role of transhumant drove roads in homogeneous agricultural landscapes as green infrastructure that supports the stability of pollination services, on which adjacent crops depend. This is the case of sunflower and almond crops, which have shown to greatly rely on a variety of pollinators to ensure seed production (Bogusch et al., 2023; Klein et al., 2012; Perrot et al., 2018). While the pollination of the majority of entomophilous crop species meaningfully benefit from wild pollinators in addition to honeybees (Goulson et al., 2015; MacInnis and Forrest, 2019; Winfree et al., 2018, 2008), in the past decades the use of managed bees to sustain the pollination of pollinator-dependent crops has increased (Aizen and Harder, 2009), despite the potentially negative effects this may have on wild bees (Agüero et al., 2018; Aslan et al., 2016; Mallinger et al., 2017; Weekers et al., 2022). Overall, the dependence of these crops on honeybees for pollination services and seed production threatens the resilience of the system, increasing instability.

Our results support the idea that, in landscapes heavily transformed by intensive agriculture and with reduced availability of semi-natural areas, drove road grasslands can act as a reservoir of bee taxonomic and functional diversity. The mobile and intermittent grazing that drove road grasslands experience during the biannual transhumant movements could also be beneficial to wild bee communities, changes in the diversity of the floral community as a result of moderate grazing have been shown to affect bee abundance and richness, as well as other pollinators (Lázaro et al., 2016; Vulliamy et al., 2006), while the increase in the availability of nesting areas in grazed sites can also favour bee abundance (Vulliamy et al., 2006). Further research is needed to uncover the potential benefits of transhumant livestock, as opposed to continuous grazing, for other pollinator groups. In addition, our study highlights the relevance of human-managed green infrastructures, such as drove roads, which constitute another type of semi-natural habitat with the potential to increase ecological connectivity within fragmented agricultural landscapes.

5. Conclusion

Considering the extent of the *Conquense* drove road, and the fact that it crosses such diverse territories, we suggest future research into the potential effect of drove roads on connectivity between wild bee populations. In this sense, the revised EU Pollinators Initiative - which aims to reverse the decline of pollinators by 2030 - emphasizes the need of restoring natural habitats in agricultural landscapes and promoting the development of a network of ecological corridors for pollinators ('Buzz Lines'). These corridors, such as the Spanish network of drove roads, when used by mobile livestock, can provide feeding and nesting resources to wild bees and other pollinators and connect otherwise fragmented habitats. This is also coherent with the EU Green Infrastructure Strategy, which aims to preserve, restore and enhance green infrastructure to mitigate biodiversity loss. In addition, the recent EU Nature Restoration Law which requires 30 % of land to be restored, provides a good scenario for the restoration of other drove roads. Although many are less well-preserved than the *Conquense*, they retain potential as

ecological corridors. These restoration efforts could enhance territorial connectivity and provide essential habitats and resources for wild bee communities.

Funding

This work was financially supported by the European Union Life Program (project LIFE CANADAS, LIFE 18 NAT/ES/000930). Pablo Manzano is funded by the Spanish Ministry of Science, Innovation and Universities through a María de Maeztu excellence accreditation 2023–2026 (Ref. CEX2021–001201-M, funded by MCIN/AEI/1013039/501100011033); by the Basque Government through the BERC 2022–2024 programme and through a Fellowship of Ikerbasque—Basque Foundation for Science; and by IUBS through the project “Pastoralism as a global herbivory socio-ecosystem”.

CRediT authorship contribution statement

Denis Michez: Writing – review & editing, Resources. **Pablo Manzano:** Writing – review & editing, Methodology, Investigation. **González José A.:** Writing – review & editing, Methodology, Conceptualization. **Francisco M. Azcárate:** Writing – review & editing, Methodology, Investigation, Funding acquisition, Conceptualization. **Paula Solascasas:** Writing – original draft, Methodology, Investigation, Formal analysis. **Violeta Hevia:** Writing – review & editing, Methodology, Investigation, Funding acquisition, Conceptualization. **Thomas J. Wood:** Writing – review & editing, Resources.

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.

Acknowledgments

The authors thank the *Dirección General de Medio Natural y Biodiversidad (Consejería de Desarrollo Sostenible, Junta de Comunidades de Castilla-La Mancha)* for providing permission to work in the drove road network. Special thanks to Juan Castro for helping measure traits, and to Tom Wood, Sara Reverté, Paolo Rosa and Romain Le Divelec, for their help with bee taxonomy.

Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at [doi:10.1016/j.agee.2025.109777](https://doi.org/10.1016/j.agee.2025.109777).

Data availability

Data will be made available on request.

References

- Agüero, J.I., Rollin, O., Torretta, J.P., Aizen, M.A., Requier, F., Garibaldi, L.A., 2018. Impactos de la abeja melífera sobre plantas y abejas silvestres. *Ecosistemas* 27, 60–69. <https://doi.org/10.7818/ECOS.1365>.
- Aizen, M.A., Harder, L.D., 2009. The global stock of domesticated honey bees is growing slower than agricultural demand for pollination. *Curr. Biol.* 19, 915–918. <https://doi.org/10.1016/j.cub.2009.03.071>.
- Aslan, C.E., Liang, C.T., Galindo, B., Hill, K., Topete, W., 2016. The role of honey bees as pollinators in natural areas. *Nat. Areas J.* 36, 478–488. <https://doi.org/10.3375/043.036.0414>.
- Astegiano, J., Guimaraes, P.R., Cheptou, P.O., Vidal, M.M., Mandai, C.Y., Ashworth, L., Massol, F., 2015. Persistence of plants and pollinators in the face of habitat loss: Insights from trait-based metacommunity models, 1st ed. *Advances in Ecological Research*. Elsevier Ltd. <https://doi.org/10.1016/bs.aecr.2015.09.005>.
- Azcárate, F.M., Robleño, I., Seoane, J., Manzano, P., Peco, B., 2013a. Drove roads as local biodiversity reservoirs: effects on landscape pattern and plant communities in a Mediterranean region. *Appl. Veg. Sci.* 16, 480–490. <https://doi.org/10.1111/avsc.12003>.
- Azcárate, F.M., Seoane, J., Castro, S., Peco, B., 2013b. Drove roads: keystone structures that promote ant diversity in Mediterranean forest landscapes. *Acta Oecologica* 49, 107–115. <https://doi.org/10.1016/j.actao.2013.03.011>.
- Banaszak, J., Banaszak-Cibicka, W., Szefer, P., 2014. Guidelines on sampling intensity of bees (Hymenoptera: Apoidea: Apiformes). *J. Insect Conserv* 18, 651–656. <https://doi.org/10.1007/s10841-014-9671-3>.
- Banaszak, J., Tward, L., 2018. Importance of thermophilous habitats for protection of wild bees (Apiformes). *Community Ecol.* 19, 239–247. <https://doi.org/10.1556/168.2018.19.3.5>.
- Biber, J.-P., 2010. Transhumance in France. *Pastoralism* 1, 91–98. <https://doi.org/10.3362/2041-7136.2010.006>.
- Bogusch, P., Hostinská, L., Heneberg, P., 2023. Towards integrated pollination management in Spanish almond orchards. *Apidologie* 54. <https://doi.org/10.1007/s13592-023-01033-9>.
- Bommarco, R., Biesmeijer, J.C., Meyer, B., Potts, S.G., Pöyry, J., Roberts, S.P.M., Steffan-Dewenter, I., Ockinger, E., 2010. Dispersal capacity and diet breadth modify the response of wild bees to habitat loss. *Proc. R. Soc. B Biol. Sci.* 277, 2075–2082. <https://doi.org/10.1098/rspb.2009.2221>.
- Cane, J.H., Minckley, L., Kervin, L.J., 2000. Sampling Bees (Hymenoptera: Apiformes) for pollinator community studies: pitfalls of pan-trapping. *J. Kans. Entomol. Soc.* 73, 225–231.
- Carré, G., Roche, P., Chifflet, R., Morison, N., Bommarco, R., Harrison-Cripps, J., Krewenka, K., Potts, S.G., Roberts, S.P.M., Rodet, G., Settele, J., Steffan-Dewenter, I., Szentgyörgyi, H., Tscheulin, T., Westphal, C., Woyciechowski, M., Vaissière, B.E., 2009. Landscape context and habitat type as drivers of bee diversity in European annual crops. *Agric. Ecosyst. Environ.* 133, 40–47. <https://doi.org/10.1016/j.agee.2009.05.001>.
- Carrié, R., Lopes, M., Ouin, A., Andrieu, E., 2018. Bee diversity in crop fields is influenced by remotely-sensed nesting resources in surrounding permanent grasslands. *Ecol. Indic.* 90, 606–614. <https://doi.org/10.1016/j.ecolind.2018.03.054>.
- Clough, Y., Ekroos, J., Báldi, A., Batáry, P., Bommarco, R., Gross, N., Holzschuh, A., Hopfenmüller, S., Knop, E., Kuussaari, M., Lindborg, R., Marini, L., Öckinger, E., Potts, S.G., Pöyry, J., Roberts, S.P., Steffan-Dewenter, I., Smith, H.G., 2014. Density of insect-pollinated grassland plants decreases with increasing surrounding land-use intensity. *Ecol. Lett.* 17, 1168–1177. <https://doi.org/10.1111/ele.12325>.
- Di Martino, P., Di Marzio, P., Giancola, C., Ottaviano, M., 2006. The forest landscape of transhumance in Molise, Italy. In: Parrotta, J., Agnolotti, M., Johann, E. (Eds.), *Cultural Heritage and Sustainable Forest Management: The Role of Traditional Knowledge. Proceedings of the Conference 8–11 June 2006. Florence, Italy*. MCPFE Liaison Unit, Warsaw, Florence, Italy, pp. 196–208.
- Drossart, M., Gérard, M., 2020. Beyond the decline of wild bees: optimizing conservation measures and bringing together the actors. *Insects* 11, 1–23. <https://doi.org/10.3390/insects11090649>.
- Duchenne, F., Thébault, E., Michez, D., Gérard, M., Devaux, C., Rasmont, P., Vereecken, N.J., Fontaine, C., 2020. Long-term effects of global change on occupancy and flight period of wild bees in Belgium. *Glob. Chang. Biol.* 26, 6753–6766. <https://doi.org/10.1111/gcb.15379>.
- Ebmer, A.W., 1993. Die westpaläarktischen Arten der Gattung *Dufourea Lepeletier 1841* mit illustrierten Bestimmungstabellen (Insecta: Hymenoptera: Apoidea: Halictidae: Rophitinae). *Dritte Nachtrag. Linz. Biol. Beitr.* äge 25, 15–42.
- Ekroos, J., Kleijn, D., Batáry, P., Albrecht, M., Báldi, A., Blüthgen, N., Knop, E., Kovács-Hostyánszki, A., Smith, H.G., 2020. High land-use intensity in grasslands constrains wild bee species richness in Europe. *Biol. Conserv* 241. <https://doi.org/10.1016/j.biocon.2019.108255>.
- European Environment Agency. (2018). CORINE Land Cover (CLC) 2018, Version 20. Copernicus Land Monitoring Service. <https://land.copernicus.eu/pan-european/corine-land-cover>.
- García-Fernández, A., Manzano, P., Seoane, J., Azcárate, F.M., Iriondo, J.M., Peco, B., 2019. Herbivore corridors sustain genetic footprint in plant populations: a case for Spanish drove roads. *PeerJ* 7. <https://doi.org/10.7717/peerj.7311>.
- Garibaldi, L.A., Steffan-Dewenter, I., Kremen, C., Morales, J.M., Bommarco, R., Cunningham, S.A., Carvalheiro, L.G., Chacoff, N.P., Dudenhöffer, J.H., Greenleaf, S.S., Holzschuh, A., Isaacs, R., Krewenka, K., Mandelik, Y., Mayfield, M.M., Morandin, L.A., Potts, S.G., Ricketts, T.H., Szentgyörgyi, H., Viana, B.F., Westphal, C., Winfree, R., Klein, A.M., 2011. Stability of pollination services decreases with isolation from natural areas despite honey bee visits. *Ecol. Lett.* 14, 1062–1072. <https://doi.org/10.1111/j.1461-0248.2011.01669.x>.
- Gathmann, A., Tscharntke, T., 2002. Foraging ranges of solitary bees. *J. Anim. Ecol.* 71, 757–764. <https://doi.org/10.1046/j.1365-2656.2002.00641.x>.
- Ghisbain, G., Rosa, P., Bogusch, P., Flaminio, S., Le Divelec, R., Dorchin, A., Kasparek, M., Kuhlmann, M., Litman, J., Mignot, M., Müller, A., Praz, C., Radchenko, V.G., Rasmont, P., Risch, S., Roberts, S.P.M., Smit, J., Wood, T.J., Michez, D., Reverté, S., 2023. The new annotated checklist of the wild bees of Europe (Hymenoptera: Anthophila). *Zootaxa*. <https://doi.org/10.11646/zootaxa.5327.1.1>.
- Gómez-Sal, A., 2001. The ecological rationale and nature conservation value of extensive livestock systems in the Iberian Peninsula. In: Bunce, R., Pérez-Soba, M., Elbersen, B., Prados, M., Andersen, E., Bell, M., Smeets, P. (Eds.), *Examples of European Agri-Environment Schemes and Livestock Systems and Their Influence on Spanish Cultural Landscapes. Green World Research Proceedings*. Wageningen, Netherlands., Wageningen, Netherlands, pp. 103–123.

- Goulson, D., Nicholls, E., Botías, C., Rotheray, E.L., 2015. Bee declines driven by combined Stress from parasites, pesticides, and lack of flowers (80-). *Science* 347, 1–16. <https://doi.org/10.1126/science.1255957>.
- Hevia, V., Azcárate, F.M., Oteros-Rozas, E., González, J.A., 2013. Exploring the role of transhumance drove roads on the conservation of ant diversity in Mediterranean agroecosystems. *Biodivers. Conserv* 22, 2567–2581. <https://doi.org/10.1007/s10531-013-0539-8>.
- Hevia, V., Bosch, J., Azcárate, F.M., Fernández, E., Rodrigo, A., Barril-Graells, H., González, J.A., 2016. Bee diversity and abundance in a livestock drove road and its impact on pollination and seed set in adjacent sunflower fields. *Agric. Ecosyst. Environ.* 232, 336–344. <https://doi.org/10.1016/j.agee.2016.08.021>.
- Hevia, V., Carmona, C.P., Azcárate, F.M., Heredia, R., González, J.A., 2021. Role of floral strips and semi-natural habitats as enhancers of wild bee functional diversity in intensive agricultural landscapes. *Agric. Ecosyst. Environ.* 319, 1–9. <https://doi.org/10.1016/j.agee.2021.107544>.
- Hsieh, T.C., Ma, K.H., Chao, A., 2016. iNEXT: an R package for rarefaction and extrapolation of species diversity (Hill numbers). *Methods Ecol. Evol.* 7, 1451–1456. <https://doi.org/10.1111/2041-210X.12613>.
- Hudson, J., Horn, S., Hanula, J.L., 2020. Assessing the efficiency of pan traps for collecting bees (Hymenoptera: Apoidea). *J. Entomol. Sci.* 55, 321–328. <https://doi.org/10.18472/0749-8004-55.3.321>.
- IPBES, 2016. The assessment report of the Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services on pollinators, pollination, and food production. In: Potts, S.G., Imperatriz-Fonseca, V.L., Ngo, H.T. (Eds.), Secretariat of the Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services. Bonn, Germany, p. 552 pages. <https://doi.org/10.5281/zenodo.3402856>.
- Klein, A.M., Boreux, V., Fornoff, F., Mupepele, A.C., Pufal, G., 2018. Relevance of wild and managed bees for human well-being. *Curr. Opin. Insect Sci.* 26, 82–88. <https://doi.org/10.1016/j.cois.2018.02.011>.
- Klein, A.M., Brittain, C., Hendrix, S.D., Thorp, R., Williams, N., Kremen, C., 2012. Wild pollination services to California almond rely on semi-natural habitat. *J. Appl. Ecol.* 49, 723–732. <https://doi.org/10.1111/j.1365-2664.2012.02144.x>.
- Klein, A.M., Vaissière, B.E., Cane, J.H., Steffan-Dewenter, I., Cunningham, S.A., Kremen, C., Tscharntke, T., 2007. Importance of pollinators in changing landscapes for world crops. *Proc. R. Soc. B Biol. Sci.* 274, 303–313. <https://doi.org/10.1098/rspb.2006.3721>.
- Kremen, C., Williams, N.M., Thorp, R.W., 2002. Crop pollination from native bees at risk from agricultural intensification. *Proc. Natl. Acad. Sci. U. S. A.* 99, 16812–16816. <https://doi.org/10.1073/pnas.262413599>.
- Kwaisher, K.S., Hendrix, S.D., 2008. Diversity and abundance of bees (Hymenoptera: Apiformes) in native and ruderal grasslands of agriculturally dominated landscapes. *Agric. Ecosyst. Environ.* 124, 200–204. <https://doi.org/10.1016/j.agee.2007.09.012>.
- Lázaro, A., Tscheulin, T., Devalez, J., Nakas, G., Petanidou, T., 2016. Effects of grazing intensity on pollinator abundance and diversity, and on pollination services. *Ecol. Entomol.* 41, 400–412. <https://doi.org/10.1111/een.12310>.
- Le Féon, V., Schermann-Legionnet, A., Delettre, Y., Aviron, S., Billeter, R., Bugter, R., Hendrickx, F., Burel, F., 2010. Intensification of agriculture, landscape composition and wild bee communities: a large scale study in four European countries. *Agric. Ecosyst. Environ.* 137, 143–150. <https://doi.org/10.1016/j.agee.2010.01.015>.
- MacInnis, G., Forrest, J.R.K., 2019. Pollination by wild bees yields larger strawberries than pollination by honey bees. *J. Appl. Ecol.* 56, 824–832. <https://doi.org/10.1111/1365-2664.13344>.
- Mallinger, R.E., Gaines-Day, H.R., Gratton, C., 2017. Do managed bees have negative effects on wild bees? a systematic review of the literature. *PLoS ONE*. <https://doi.org/10.1371/journal.pone.0189268>.
- Manzano, P., Casas, R., 2010. Past, present and future of Trashumancia in Spain: nomadism in a developed country. *Pastor. Res. Policy Pr.* 1, 72–90. <https://doi.org/10.3362/2041-7136.2010.005>.
- Maurer, C., Sutter, L., Martínez-Núñez, C., Pellissier, L., Albrecht, M., 2022. Different types of semi-natural habitat are required to sustain diverse wild bee communities across agricultural landscapes. *J. Appl. Ecol.* 59, 2604–2615. <https://doi.org/10.1111/1365-2664.14260>.
- Micó, E., Ramilo, P., Thorn, S., Müller, J., Galante, E., Carmona, C.P., 2020. Contrasting functional structure of saproxyllic beetle assemblages associated to different microhabitats. *Sci. Rep.* 10, 1–11. <https://doi.org/10.1038/s41598-020-58408-6>.
- Morandini, L.A., Winston, M.L., Abbott, V.A., Franklin, M.T., 2007. Can pastureland increase wild bee abundance in agriculturally intense areas? *Basic Appl. Ecol.* 8, 117–124. <https://doi.org/10.1016/j.jbae.2006.06.003>.
- Nieto, A., Roberts, S.P.M., Kemp, J., Rasmont, P., Kuhlmann, M., García Criado, M., Biesmeijer, J.C., Bogusch, P., Dathe, H.H., De la Rúa, P., De Meulemeester, T., Dehon, M., Dewulf, A., Ortiz-Sánchez, F.J., Lhomme, P., Pauly, A., Potts, S.G., Praz, C., Quaranta, M., Radchenko, V.G., Scheuchl, E., Smit, J., Straka, J., Terzo, M., Tomozzi, B., Window, J., Michez, D., 2014. European red list of bees. Luxemb.: Publ. Off. Eur. Union. <https://doi.org/10.2779/77003>.
- Orr, M.C., Hughes, A.C., Chesters, D., Pickering, J., Zhu, C.D., Ascher, J.S., 2021. Global patterns and drivers of bee distribution. *Curr. Biol.* 31, 451–458. <https://doi.org/10.1016/j.cub.2020.10.053>.
- Ortiz-Sánchez, F.J., 2020. Checklist de Fauna Ibérica. Serie Anthophila (Insecta: Hymenoptera: Apoidea) en la península ibérica e islas Baleares (edición 2020). En Doc. Fauna Ibérica, 14. In: Ramos, M.A., Sánchez Ruiz, M. (Eds.), Mus. Nac. Ciencias Nat. CSIC, Madrid.
- Oteros-Rozas, E., González, J.A., Martín-López, B., López, C.A., Zorrilla-Miras, P., Montes, C., 2012. Evaluating ecosystem services in transhumance cultural landscapes. An interdisciplinary and participatory framework. *GAIA - Ecol. Perspect. Sci. Soc.* 21, 185–193. <https://doi.org/10.14512/gaia.21.3.9>.
- Penado, A., Rebelo, H., Goulson, D., Wood, T.J., Porto, M., Rotheray, E.L., Beja, P., 2022. From pastures to forests: changes in Mediterranean wild bee communities after rural land abandonment. *Insect Conserv. Divers* 15, 325–336. <https://doi.org/10.1111/icad.12562>.
- Perrot, T., Gaba, S., Roncoroni, M., Gautier, J.L., Saintilan, A., Bretagnolle, V., 2018. Experimental quantification of insect pollination on sunflower yield, reconciling plant and field scale estimates. *Basic Appl. Ecol.* 34, 75–84. <https://doi.org/10.1016/j.baae.2018.09.005>.
- Pfiffner, L., Ostermaier, M., Stoeckli, S., Müller, A., 2018. Wild bees respond complementarily to 'high-quality' perennial and annual habitats of organic farms in a complex landscape. *J. Insect Conserv.* 22, 551–562. <https://doi.org/10.1007/s10841-018-0084-6>.
- Popic, T.J., Davila, Y.C., Wardle, G.M., 2013. Evaluation of common methods for sampling invertebrate pollinator assemblages: net sampling out-perform pan traps. *PLoS One* 8. <https://doi.org/10.1371/journal.pone.0066665>.
- Potts, S.G., Biesmeijer, J.C., Kremen, C., Neumann, P., Schweiger, O., Kunin, W.E., 2010. Global pollinator declines: trends, impacts and drivers. *Trends Ecol. Evol.* 25, 345–353. <https://doi.org/10.1016/j.tree.2010.01.007>.
- Potts, S.G., Imperatriz-Fonseca, V., Ngo, H.T., Aizen, M.A., Biesmeijer, J.C., Breeze, T.D., Dicks, L.V., Garibaldi, L.A., Hill, R., Settele, J., Vanbergen, A.J., 2016. Safeguarding pollinators and their values to human well-being. *Nature* 540, 220–229. <https://doi.org/10.1038/nature20588>.
- R Development Core Team, 2022. R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria.
- Reverté, S., Milićić, M., Čaćanski, J., Andrić, A., Aracil, A., Aubert, M., Balzan, M.V., Bartomeus, I., Bogusch, P., Bosch, J., Budrys, E., Cantú-Salazar, L., Castro, S., Cornalba, M., Demeter, I., Devalez, J., Dorchin, A., Dufrêne, E., Dordević, A., Fisler, L., Fitzpatrick, Ú., Flaminio, S., Földesi, R., Gaspar, H., Genoud, D., Geslin, B., Ghisbain, G., Gilbert, F., Gogala, A., Grković, A., Heimburg, H., Herrera-Mesías, F., Jacobs, M., Janković Milosavljević, M., Janssen, K., Jensen, J.K., Ješovnik, A., Józán, Z., Karlis, G., Kasparek, M., Kovács-Hostyánszki, A., Kuhlmann, M., Le Divelec, R., Leclercq, N., Likov, L., Litman, J., Ljubomirov, T., Madsen, H.B., Marshall, L., Mazánek, L., Milić, D., Mignot, M., Mudri-Stojnić, S., Müller, A., Nedeljković, Z., Nikolić, P., Ødegaard, F., Patiny, S., Paukkunen, J., Pennards, G., Pérez-Bañón, C., Perrard, A., Petanidou, T., Pettersson, L.B., Popov, G., Popov, S., Praz, C., Prokhorov, A., Quaranta, M., Radchenko, V.G., Radenković, S., Rasmont, P., Rasmussen, C., Reemer, M., Ricarte, A., Risch, S., Roberts, S.P.M., Rojo, S., Ropars, L., Rosa, P., Ruiz, C., Sentil, A., Shapryk, V., Smit, J., Sommaggiò, D., Soon, V., Ssymank, A., Ståhl, G., Stavrinides, M., Straka, J., Tarlap, P., Terzo, M., Tomozzi, B., Tot, T., van der Ent, L.J., van Steenis, J., van Steenis, W., Varnava, A.I., Vereecken, N.J., Veselić, S., Vesnić, A., Weigand, A., Wisniowski, B., Wood, T.J., Zimmermann, D., Michez, D., Vujčić, A., 2023. National records of 3000 European bee and hoverfly species: a contribution to pollinator conservation. *Insect Conserv. Divers* 16, 758–775. <https://doi.org/10.1111/icad.12680>.
- Rivers-Moore, J., Andrieu, E., Vialatte, A., Ouin, A., 2020. Wooded semi-natural habitats complement permanent grasslands in supporting wild bee diversity in agricultural landscapes. *Insects* 11, 1–21. <https://doi.org/10.3390/insects11110812>.
- Roquer-Beni, L., Alins, G., Arnan, X., Boreux, V., García, D., Hambäck, P.A., Happé, A.K., Klein, A.M., Miñarro, M., Mody, K., Porcel, M., Rodrigo, A., Samnegård, U., Tasin, M., Bosch, J., 2021. Management-dependent effects of pollinator functional diversity on apple pollination services: a response–effect trait approach. *J. Appl. Ecol.* 58, 2843–2853. <https://doi.org/10.1111/1365-2664.14022>.
- Roulston, T.H., Goodell, K., 2011. The role of resources and risks in regulating wild bee populations. *Annu. Rev. Entomol.* 56, 293–312. <https://doi.org/10.1146/annurev-ento-120709-144802>.
- Ruiz, M., Ruiz, J.P., 1986. Ecological history of transhumance in Spain. *Biol. Conserv* 37, 73–86. [https://doi.org/10.1016/0006-3207\(86\)90035-2](https://doi.org/10.1016/0006-3207(86)90035-2).
- Rundlöf, M., Nilsson, H., Smith, H.G., 2008. Interacting effects of farming practice and landscape context on bumble bees. *Biol. Conserv* 141, 417–426. <https://doi.org/10.1016/j.biocon.2007.10.011>.
- Vulliamy, B., Potts, S.G., Willmer, P.G., 2006. The effects of cattle grazing on plant-pollinator communities in a fragmented Mediterranean landscape. *Oikos* 114, 529–543. <https://doi.org/10.1111/j.2006.0030-1299.14004.x>.
- Weekers, T., Marshall, L., Leclercq, N., Wood, T.J., Cejas, D., Drepper, B., Hutchinson, L., Michez, D., Molenberg, J.M., Smaghe, G., Vandamme, P., Vereecken, N.J., 2022. Dominance of honey bees is negatively associated with wild bee diversity in commercial apple orchards regardless of management practices. *Agric. Ecosyst. Environ.* 323, 107697. <https://doi.org/10.1016/j.agee.2021.107697>.
- Wei, N., Kaczorowski, R.L., Arceo-Gómez, G., O'Neill, E.M., Hayes, R.A., Ashman, T.L., 2021. Pollinators contribute to the maintenance of flowering plant diversity. *Nature* 597, 688–692. <https://doi.org/10.1038/s41586-021-03890-9>.
- Westphal, C., Bommarco, R., Carré, G., Lamborn, E., Morison, N., Petanidou, T., Potts, S. G., Roberts, S.P.M., Szentgyörgyi, H., Tscheulin, T., Vaissière, B.E., Woyciechowski, M., Biesmeuer, J.C., Kunin, W.E., Settele, J., Steffan-Dewenter, I., 2008. Measuring bee diversity in different European habitats and biogeographical regions. *Ecol. Monogr.* 78, 653–671. <https://doi.org/10.1890/07-1292.1>.
- Wilson, J.S., Griswold, T., Messinger, O.J., 2008. Sampling bee communities (Hymenoptera: Apiformes) in a desert landscape: are pan traps sufficient? *J. Kans. Entomol. Soc.* 81, 288–300. <https://doi.org/10.2317/JKES-802.06.1>.
- Winfree, R., 2010. The conservation and restoration of wild bees. *Ann. N. Y. Acad. Sci.* 1195, 169–197. <https://doi.org/10.1111/j.1749-6632.2010.05449.x>.
- Winfree, R., Aguilar, R., Vázquez, D.P., LeBuhn, G., Aizen, M.A., 2009. A meta-analysis of bees' responses to anthropogenic disturbance. *Ecology* 90, 2068–2076.
- Winfree, R., Reilly, J.R., Bartomeus, I., Cariveau, D.P., Williams, N.M., Gibbs, J., 2018. Species turnover promotes the importance of bee diversity for crop pollination at

- regional scales (80-). Science 359, 791–793. <https://doi.org/10.1126/science.aoa2117>.
- Winfrey, R., Williams, N.M., Gaines, H., Ascher, J.S., Kremen, C., 2008. Wild bee pollinators provide the majority of crop visitation across land-use gradients in New Jersey and Pennsylvania, USA. *J. Appl. Ecol.* 45, 793–802. <https://doi.org/10.1111/j.1365-2664.2007.01418.x>.
- Zurbuchen, A., Landert, L., Klaiber, J., Müller, A., Hein, S., Dorn, S., 2010. Maximum foraging ranges in solitary bees: only few individuals have the capability to cover long foraging distances. *Biol. Conserv.* 143, 669–676. <https://doi.org/10.1016/j.biocon.2009.12.003>.