ARTICLE

Agricultural intensification indirectly reshapes bee–plant interaction networks through shifts in bee functional traits

Domingo Cano[1] | **Carlos Martínez-Núñez**[2] | **Antonio J. Pérez**[1] | **Julio M. Alcántara**[1,3] | **Marco Moretti**[4] | **Teresa Salido**[1] | **Pedro J. Rey**[1,3]

[1]Departamento de Biología Animal, Biología Vegetal y Ecología, Universidad de Jaén, Jaén, Spain

[2]Department of Ecology and Evolution, Estación Biológica de Doñana (EBD-CSIC), Seville, Spain

[3]Instituto Interuniversitario de Investigación del Sistema Tierra de Andalucía, Jaén, Spain

[4]Biodiversity and Conservation Biology, Swiss Federal Research Institute WSL, Birmensdorf, Switzerland

Correspondence
Domingo Cano
Email: dcano@ujaen.es

Abstract

High-intensity farming can lead to non-random local extinctions and functional filtering of pollinating insect assemblages, disproportionately harming species with certain traits. This process can ultimately reshape pollinator–plant interaction networks in predictable, consistent manners, although this pathway remains largely unexplored. Here, we investigate how agricultural intensification affects the structure of bee–plant interaction networks both directly and indirectly by influencing the functional composition and diversity (in terms of foraging and nesting traits) of the bee assemblages. We considered 24 paired olive farms with contrasting management over a gradient of landscape complexity. We characterized the network structure and functional composition of bee assemblages visiting floral patches in the olive fields by using both functional identity and diversity metrics. We then built Bayesian multilevel models to assess the direct and indirect (via functional filtering processes) effects of agricultural intensification on network properties. We found that most of the effects of agricultural intensification on bee–plant network properties in floral patches occur through the filtering of the bee functional traits. However, while the effects of farming practices occur fundamentally through the filtering of foraging traits, the landscape effects occur via the modification of the nesting guilds. High-intensity herb cover management negatively affected larger bees (also highly correlated with longer proboscis), resulting in a decrease in the overlap of bees' interaction niches. This filtering was mitigated in flowering patches with higher floral cover, which increased the functional diversity of bees, ultimately reducing the overlap of the plants' interaction niches. In turn, the loss of semi-natural habitats in the landscape disproportionately favored ground excavators, causing homogenization of nesting guild composition. This, coupled with decreased

floral abundance (patch scale), led to less diverse and structurally simpler networks. In conclusion, our study suggests that agricultural intensification reshapes bee–plant networks in olive landscapes through functional filtering of bee assemblages and provides cues to mitigate these effects. On a small scale, floral patches with abundant flowers buffer the filtering of bees' foraging traits, suggesting that well-managed flower patches help mitigate the functional depletion imposed by agricultural intensification. Meanwhile, favoring semi-natural remnants at a large scale attenuates the homogenization of nesting guild composition.

KEYWORDS
floral resources, foraging traits, functional filtering, land-use intensification, nesting traits, plant–pollinator interactions, trophic niches

INTRODUCTION

Agricultural intensification is a major driver of land-use change worldwide that exacerbates pollinator loss through habitat loss, landscape degradation, and pesticide application (Souza et al., 2015), which in turn diminishes the abundance and diversity of floral and nesting resources for pollinators (Habel et al., 2019). These changes pose ecological filters on pollinators, potentially disturbing the community composition and harming the pollination function through biotic homogenization (Gámez-Virués et al., 2015). The identity and diversity of functional traits in the pollinator community play a crucial role in determining the outcome of this filtering process (Leps et al., 2006). For example, smaller and low-mobile bees (i.e., with shorter foraging distances; Greenleaf et al., 2007) are more negatively affected in fragmented landscapes compared to larger bees, while larger bees appear to be more sensitive to pesticide exposure (Ward et al., 2022). Additionally, certain phenotypes, such as long proboscis that allow access to a wide variety of flower types, could confer an advantage in accessing floral resources in fields where flowers are scarce (Lara-Romero et al., 2019). Nesting mode, including nesting location and type, is also considered a crucial functional trait related to habitat disturbances (Fortuin & Gandhi, 2021; Williams et al., 2010). The response of species with different functional traits within a community may influence the processes shaping community assembly through functional filtering (Cornwell et al., 2006).

Functional traits influence how plants and pollinators interact (e.g., trait matching) while playing an important role in the structuring of interaction networks (e.g., Bartomeus et al., 2016; Maglianesi et al., 2015; Maruyama et al., 2018). Regarding pollinators, body size is a key trait, as larger individuals and species can access more floral resources (Greenleaf et al., 2007; Lara-Romero et al., 2019), potentially enhancing the interaction diversity and niche overlap of pollinators and plants, which is

related to the maintenance of network stability and resilience (Blüthgen & Klein, 2011). Similarly, a longer proboscis in pollinating insects is related to greater diet breadth (Johnson et al., 2017) through access to a higher diversity of floral resources (Lara-Romero et al., 2019), suggesting that proboscis length can also influence the properties of the interaction networks (Klumpers et al., 2019). At the community level, its species composition and the species' functional traits also shape the structural properties of interaction networks. The main mechanism behind these effects might be changes in the selection of interacting partners and the way trophic niches are partitioned among bees (Frund et al., 2013; Maglianesi et al., 2015). Pollinator assemblages with high functional diversity would shape interaction networks with greater partitioning in the use of floral resources, and consequently, this would lead to a higher degree of specialization in the interaction networks (Maglianesi et al., 2015). Moreover, nesting resource availability and diversity influence the composition of the bee assemblages (Fortuin & Gandhi, 2021), suggesting that shifts in the composition of nesting guilds would likely affect the structure of the interaction network. However, the underlying mechanisms remain largely unexplored. Despite the threat that agricultural intensification poses to species with certain traits and the functional diversity of pollinator assemblages, the indirect effects of agricultural intensification on interaction networks, mediated by functional filtering processes, remain largely elusive (but see Maruyama et al., 2018 in plant–hummingbird systems).

To contribute to filling this knowledge gap, here we characterized the functional traits and functional diversity of bees visiting floral patches in 24 paired olive farms in Andalusia (southern Spain) with contrasting ground herb cover management (high-intensity, which leaves soils persistently bare using different farming practices of herbaceous cover removal, vs. low-intensity, which leaves ground covers most part of the year) across a gradient of landscape complexity. Low-intensity herb cover management

constitutes the most common agri-environmental scheme (AES) in Europe in permanent croplands, aiming to recover biodiversity and prevent soil loss in olive farms, directly impacting pollinator communities by affecting floral resource availability. We then evaluated the structure of bee–plant interaction networks and examined both the direct and indirect effects of agricultural intensification on them, particularly focusing on the influence of functional filtering processes. We chose the olive grove as a suitable study system due to its great potential for the conservation of pollinating insects in the Mediterranean basin (e.g., Cano et al., 2022; Martínez-Núñez et al., 2020; Potts et al., 2006; Tscheulin et al., 2011) and for its socioeconomic and cultural importance for these regions. Previous research in olive groves has reported that the intensification of herb cover management disturbs floral visitor communities and how the surrounding landscape complexity moderates these effects (Cano et al., 2024; Martínez-Núñez et al., 2019). Yet, we still do not know how agricultural intensification shapes the pollinator–plant interaction networks through functional filtering and how this will influence the stability and resilience of such interaction networks in these key socio-economic and cultural agroecosystems.

Our major aim is to disentangle the direct and indirect effects of agricultural intensification on bee pollination network properties by assessing the role of functional trait filtering in bee assemblages. To this end, we address the following specific objectives: (1) assessing to what extent agricultural intensification in olive groves at both farm (management intensity) and landscape (landscape complexity) scales imposes functional filtering on bee assemblages; (2) determining to what extent the pollination network structure is driven by functional trait identity and functional diversity of the bee assemblages; and (3) assessing which changes in the pollination network structure are directly affected by agricultural intensification. Furthermore, by combining (1) and (2) we will be able to evaluate (4) which changes in interaction networks arise indirectly from the functional filtering of bee assemblages caused by agricultural intensification.

Gaining a comprehensive mechanistic understanding of how functional filtering, driven by agricultural intensification, restructures pollination interaction networks should provide fundamental insights for the management of bee diversity and pollination function in farming landscapes.

MATERIALS AND METHODS

Study sites and experimental design

We selected a total of 24 paired olive farms located in 12 localities spread out across the main cultivation area of olive groves in Andalusia, Spain (Appendix S1: Figure S1). Each pair of farms was located in the same locality and shared a common landscape (i.e., they were both within a circular area of 2-km radius). The mean distance between localities was 80.90 km (ranging from 9.9 to 293.2 km), and the mean farm size was 92.89 ha (ranging from 4.84 to 742.14 ha). Each pair of farms consisted of a farm with high-intensity herb cover management and a farm with low-intensity herb cover management (Appendix S1: Figure S1a,b, respectively). Low-intensity management involves maintaining herb cover for most of the year, only being removed by mechanical mowing or cattle after April–May, and the use of few or no pesticides. In contrast, high-intensity herb cover management consists of the removal of the herb cover almost permanently by using herbicides or inversion plowing several times a year and the use of high levels of insecticides. To corroborate that both managements entail substantial differences in herb cover, we estimated herb cover visually from 10 m^2 quadrats randomly distributed in each farm, which were monitored monthly from April to June, during the same study year of pollinator surveys. We corroborated that these two types of herb cover management resulted in differences in the herb cover, with 40.5% $\pm$ 4% (mean $\pm$ SE) of cover in the low-intensity-managed olive farms and 17.7% $\pm$ 3.9% (mean $\pm$ SE) in high-intensity-managed ones. Detailed information about herb cover management and pesticide application is provided in Appendix S1: Table S1.

Within each olive farm, we surveyed two multi-floral patches located within the cultivated area of the olive farms, avoiding edges and semi-natural patches within the olive farms. We chose large and flower-diverse patches to cover as many bee species and unique interactions as possible. We considered 10 m^2 (usually 2 m × 5 m) as the sampling area in each multi-floral patch. On each farm, the minimum distance between each pair of patches was 150 m when possible (note that in some high-intensity farms floral patches were extremely rare).

We considered several predictors to characterize both the landscape complexity around olive farms and the quality of patches within olive farms since scale-dependent factors determine how landscape and surrounding complexity affects biodiversity (Cano et al., 2022, 2024; Dainese et al., 2015). At the landscape level, we measured the proportion of semi-natural habitats (including field edges, woodlands, shrublands, permanent grasslands, hedgerows, and road verges) in a 1 km radius buffer around the centroid of each olive farm as a descriptor of landscape complexity. We used recent land-use cartography (data from SIOSE 2016 available at http://www.juntadeandalucia.es/medioambiente/site/rediam/) using the GIS platform (QGIS v.2.14). Within patches, we measured via visual

inspection the herb richness and the total floral cover inside each 10 m² sampling area as descriptors of the quality of patches.

Surveys

The surveys were carried out in 48 multi-floral patches (two patches per olive farm) from March to June in three sampling rounds, 5 to 6 weeks apart. We sampled each patch for 15 min in the morning (until 13 h) and for 15 min in the afternoon (until 17 h) in each sampling round, totalling 90 min of sampling time per multi-floral patch. We always chose sunny and rain-free days with temperatures above 18°C and wind speeds below 5 km/h to ensure maximum bee activity. We measured the temperature with a thermometer in the field and estimated the wind speed based on the Beaufort scale.

During each sampling round, we recorded simultaneously the plant-bee interactions and the abundance of each bee species. We considered an interaction event as the contact of an individual bee with the reproductive part of a flower. Sampling was conducted by experienced researchers skilled in observing interactions and identifying pollinator species within olive farms. Most bee taxa were visually identified at the genus level in the field, but after each survey, we collected at least one individual of each morphotype using a sweep net for its posterior identification at the species or morphospecies level in the laboratory.

Bee traits

Functional traits were selected according to their potential response to agricultural intensification and their potential relationship with network metrics based on previous studies (e.g., Bartomeus et al., 2016; Fortuin & Gandhi, 2021; Maglianesi et al., 2015; Maruyama et al., 2018). We used the inter-tegular distance (ITD, in millimeters) and the relative proboscis length (in millimeters) as quantitative traits. The ITD refers to the distance in a straight line between the inner edges of tegulae, and it is used as a proxy of body size and related to the foraging range (Greenleaf et al., 2007). Measurements of ITD were performed using a Dino-Lite Edge Digital Microscope with the Dino Capture 2.0 software to obtain dorsal images of the thorax and ImageJ software to accurately measure the distance from ITD. We used pinned samples from our surveys to obtain the measurements of the ITD from a minimum of three females (whenever possible) similarly to other studies (Cappellari et al., 2022). Males and/or fewer

than three specimens were used when it was not possible to collect more females. The length of the proboscis was estimated using the R package "BeeIT" from family identity and ITD data for each taxon (Cariveau et al., 2016). Then, we used this estimate to obtain the relative length of the proboscis as the ratio between the estimated length of the proboscis and the ITD. We used this relative measure to assess proboscis length independently of body size. Furthermore, it provides additional insights beyond a simple proboscis measurement, allowing us to understand how long- and short-tongued bees (i.e., with higher and lower relation proboscis length/ITD respectively) respond to agricultural intensification and its impact on interaction network structure.

Additionally, we selected the nesting guild as a qualitative trait so that each taxon was classified according to its nesting site (i.e., dead stem excavators, ground excavators, above-ground cavity renters, below-ground cavity renters, snail shell renters, and kleptoparasites) similarly to other studies (e.g., Williams et al., 2010). This great variety in nesting biology makes this trait a good indicator of sensitivity to landscape complexity and habitat quality. The assignment of nesting guilds was based on literature (e.g., Michener, 2000; Müller, 2022). See Appendix S1: Table S2 for the mean values of ITD and the relative proboscis length, along with the respective nesting guild assignments of the species.

Functional characterization of bee assemblages

To functionally characterize the bee community in each olive farm, we used three complementary metrics:

1. Nesting guild composition, which characterizes the composition of nesting guilds in bee assemblages within each farm. We used a principal coordinate analysis (PCoA) based on a matrix of Bray–Curtis dissimilarities of abundance data for each nesting guild between olive farms. The composition of the assemblages for each olive farm was defined by the first two PCoA axes (scores of PCoA-1 and PCoA-2, respectively), which were subsequently used as composition variables in the models. This analysis was conducted using the "vegan" package in R (Oksanen et al., 2020).
2. Community weighted mean (CWM), which represents the mean trait value in a bee community, weighted by species abundance. We calculated CWM for two functional traits in this case: ITD and relative proboscis length using the "FD" package in R (Laliberté & Legendre, 2010).
3. RaoQ index, a multi-trait functional diversity metric measuring the pairwise functional divergence

between species considering their relative abundances (Botta-Dukát, 2005). Given our small sample size, we used RaoQ index instead of individual metrics for each component of functional diversity (richness, evenness, and divergence). Here, we used the ITD, the relative proboscis length, and the nesting bee guilds to obtain the RaoQ index by using the "FD" package in R (Laliberté & Legendre, 2010).

These metrics together provide complementary information about bee assemblages functional components (Ricotta & Moretti, 2011).

Network metrics

We built one bee–plant interaction network for each olive farm, pooling all the interactions observed across patches and sampling rounds. For each network, we computed the following set of network metrics: bee richness, diversity of interactions (Shannon index), interaction specialization (H_2'), and niche overlap of both bees and plants separately. H_2' measures the specificity of the interaction network across interacting species (Blüthgen et al., 2008), with values ranging from 0, indicating complete generalization, to 1, indicating maximum specialization degree. Niche overlap was determined using the Horn index, focusing on similarities in interaction patterns between species, so that values close to 0 indicate minimal niche overlap between species, while values close to 1 suggest a significant degree of niche overlap (Horn, 1966). We chose these network metrics for their proven effectiveness in assessing the complexity, stability and resilience of networks against agricultural intensification (e.g., Blüthgen & Klein, 2011; Martínez-Núñez et al., 2019; Olsson et al., 2021). Additionally, the selected bee functional traits offer a mechanistic understanding of how these network metrics respond to the environmental changes, according to the literature (e.g., Devictor et al., 2010).

Interaction networks and estimation of network metrics were conducted using the "bipartite" package in R (Dormann & Strauss, 2014).

Statistical analyses

Our main objective was to assess how agricultural intensification in olive crops impacts bee–plant interaction networks directly and indirectly through functional trait filtering (Appendix S1: Figure S2). We fitted three sets of models to assess (1) the direct effects of agricultural intensification on the functional diversity of bee communities, (2) how the functional diversity of bee communities affects the bee–plant network topology, and (3) the direct effects of agricultural intensification on network topology. Through the detection of significant effects in these three sets of models, we seek to infer the existence of indirect effects of agricultural intensification on network properties mediated by its incidence on the functional traits of bee assemblages. Multi-level mixed Bayesian models were fitted through Markov Chain Monte Carlo (MCMC) with 50,000 iterations (with the first 10,000 burned). We used an uninformative diffuse prior. The locality was always used as a random factor in all these models. To avoid multicollinearity, we checked correlations between variables and together with the variance inflation factor (VIF) for each predictor in the models (Appendix S1: Table S3). VIF values informed multicollinearity problems (VIF > 5) between the CWM-ITD and the CWM-relative proboscis length (Appendix S1: Table S3), which were further highly correlated ($r = 0.92$), advising the elimination of one of them. However, they provide ecologically complementary information since both are distinct functional traits of bees with different implications for structuring interaction networks and might be influenced differently by agricultural intensification (as stated in the Introduction section). Consequently, we opted to keep just one (CWM-ITD) when analyzing the indirect effects of agricultural intensification on network metrics mediated by bee functional traits but discuss how both traits are affected by agricultural intensification and the implications for variation in network metrics.

The first set of models was built considering each functional descriptor of bee assemblages as response variable (CWM-ITD, RaoQ index, PCoA-1 and PCoA-2) and the effect of herb cover management type (categorical variable with two levels (i.e., high intensity and low intensity) considering the herb management across the entire farm) as predictor. One subset of these models also incorporated floral cover and herb richness at the patch scale as explanatory variables, while a second subset incorporated the proportion of semi-natural habitats at the landscape scale (Appendix S1: Table S4). Given the limited number of olive farms of this study, these two subsets were analyzed separately since their split in separate models better explored the effects of agricultural intensification at the landscape and patch scales. More complex models, combining both scales and with different predictors appropriated to each scale, could produce unreliable estimates given our limited sample size. Additionally, this approach ensures consistency with other studies on pollinators within the same study system (Cano et al., 2022, 2024), facilitating a better understanding of the entire set of concatenated results on factors influencing bee–plant interactions and pollination service in olive landscapes. Recent agroecological theory suggests

landscape context can influence the effects of agricultural practices on biodiversity (Rey et al., 2019; Tscharntke et al., 2005). Therefore, in each subset of models, we fitted a series of competing models that included the simple main effects of each descriptor, their additive combinations, and the interaction between herb cover management type and each of the other explanatory variables. In summary, it amounts a total of four competing models for the landscape scale subset and 8 competing models for the patch scale subset for each response variable (Appendix S1: Table S4).

For the second set of models, we used the interaction network metrics as response variables (bee richness, H'_2, niche overlap of bees, niche overlap of plants and diversity of interactions), with the functional descriptors of bee assemblages as explanatory variables. We fitted two subsets of models for each response variable (Appendix S1: Table S5); one of them consisted of models considering the simple and additive effects of the functional diversity metrics (i.e., CWM-ITD and Rao index), and the other subset considered models with the simple and additive effects of the descriptors of the composition of nesting bee guilds (i.e., the coordinates of PCoA axes 1 and 2).

Finally, in the third set (Appendix S1: Table S6), we fitted the same models as in the first set, but this time using the network metrics as response variables.

Model performance was assessed using the approximate leave-one-out (LOO) cross-validation method in the "loo" R package (Vehtari et al., 2017). This method allows ranking the models for each response variable according to their LOO information criterion (LOOIC). Lower LOO means better model fit and parsimony. The LOO approach provides an estimate of the predictive ability of a model (ELPD-LOO: Bayesian LOO estimate of the theoretically expected log-pointwise predictive density). Then, we followed two criteria to select the best models. First, if the difference ± SE in ELPD between a given model and the model with the lowest LOOIC includes zero, its predictive performance cannot be differentiated from the one with the lowest LOOIC (Bürkner, 2017), and thus they are considered equivalent. Second, when multiple models were equivalent to the one with the lowest LOOIC, we selected the model with the highest R^2 and containing a variable with strong effects (i.e., estimates and their 95% credible interval excluding 0). No effect can be attributed to a predictor variable if the null model is one of the equivalent models; in this case, there is no better model than the null model.

RESULTS

We recorded 4,869 individuals of bees belonging to 5 families, 36 genera, and 166 species/ morphospecies (Appendix S1: Table S2). In terms of abundance, short proboscis bees (i.e., Andrenidae, Colletidae, and Halictidae) were more representative (66.18%) than long-proboscis bees (i.e., Apidae and Megachilidae; 33.82%). Regarding the nesting guilds, the most abundant groups were the ground excavator and renters of above-ground cavities (80.63% and 15.52% respectively) and the minority groups were the dead stem renters, the kleptoparasites, and the renters of below-ground cavities and snail shells (1.77%, 0.98%, 0.74% and 0.33% respectively). They performed a total of 599 unique interactions with 108 flowering herb species (Appendix S1: List S1).

Direct effects of agricultural intensification on functional metrics of the bee community

We detected an interaction effect between farm-scale herb cover management and floral cover at the patch scale on CWM-ITD (Table 1a; see also Appendix S1: Table S4 for competing models). The CWM-ITD was higher in low-intensity managed olive farms (Figure 1a). However, this effect was mitigated when high-quality floral patches were present, such that in patches with high floral cover, the trait filtering effect of high-intensity management was canceled (Figure 1b). The models fitted with the RaoQ index showed a positive relationship between the functional diversity of the bee assemblages and the floral cover on the patch scale (Table 1b; Figure 1c; see also Appendix S1: Table S4). The proportion of semi-natural habitats at the landscape scale and the low-intensity herb cover management negatively impacted the occurrence of ground excavator bees, which were positively related to PCoA-1. However, the evidence for this effect was weak, as indicated by credible intervals (Table 1c; see also Appendix S1: Table S4 and Figure S3). Finally, the proportion of semi-natural habitats had a positive effect on PCoA-2, which was associated with a higher proportion of bees nesting in dead stems and cavities both above and below ground (Table 1d; Figure 1d; see also Appendix S1: Table S4 and Figure S3).

Relationships between the topology of the pollination network and the functional metrics of the bee community

We found a positive relationship between the proportion of bees nesting in dead stems and in cavities both above and below ground (i.e., PCoA-2 in Appendix S1: Figure S3; Table 2a; Figure 2a; see Appendix S1: Table S5 for competing models) and the bee richness in the interaction

TABLE 1 Estimates for the selected best Bayesian mixed model of the relationship between the agricultural intensification variables and the functional diversity metrics.

Model code	Fixed factor	Estimate	SE	95% LCI	95% UCI
(a) CWM-ITD ~ Agricultural intensification (patch scale)					
mITD-6	**Intercept**	**1.29**	**0.28**	**0.66**	**1.79**
	Low intensity	**1.14**	**0.36**	**0.45**	**1.88**
	Floral cover	0.01	0.01	−0.01	0.02
	Low intensity: Floral cover	**−0.02**	**0.01**	**−0.03**	**−0.01**
(b) RaoQ ~ Agricultural intensification (patch scale)					
mRao-4	**Intercept**	**0.07**	**0.10**	**−0.13**	**0.27**
	Floral cover	**0.00**	**0.00**	**0.00**	**0.01**
(c) PCoA1 ~ Agricultural intensification (landscape scale)					
mPCOA1 − 2	Intercept	0.06 (0.05[a])	0.07 (0.06[a])	−0.07 (0.01[a])	0.19 (0.00[a])
	Low intensity	−0.06 (−0.06[a])	0.06 (0.05[a])	−0.17 (−0.09[a])	0.05 (−0.00[a])
	SNH	−0.01 (−0.00[a])	0.00 (0.00[a])	−0.01 (−0.00[a])	0.00 (−0.00[a])
(d) PCoA2 ~ Agricultural intensification (landscape scale)					
mPCOA2-1	Intercept	−0.06	0.03	−0.12	0.00
	SNH	**0.00**	**0.00**	**0.01**	**0.01**

Note: The table displays the posterior estimate, SE, and 95% credible intervals of estimates with the lower (LCI) and the upper extremes (UCI). In bold, estimates with credible intervals not including 0. The first column identifies the code of the best model for each response variable. CWM-ITD = community weighted mean of inter-tegular distance; PCoA1 and PCoA2 = coordinates of axis 1 and axis 2 respectively of the principal coordinate analysis. SNH = proportion of semi-natural habitat at 1 km radius buffer. All alternative candidate models tested and their codes are shown in Appendix S1: Table S4.
[a]Coefficient values for the 75% credible intervals.

networks (i.e., number of nodes representing bee species visiting flowers). The CWM-ITD showed a positive relationship with the niche overlap of bees in networks (Table 2b; Figure 2b). The bee niche overlap also augmented as the proportion of bees nesting in dead stems and cavities both above and below ground (PCoA-2) increased (Table 2c; Figure 2c; see Appendix S1: Table S5). In contrast, the plant niche overlap decreased with increasing values of the RaoQ index of the bee assemblages (Table 2d; Figure 2d; see Appendix S1: Table S5). Interaction diversity and specialization (H_2') were not affected by any of the functional metrics assessed.
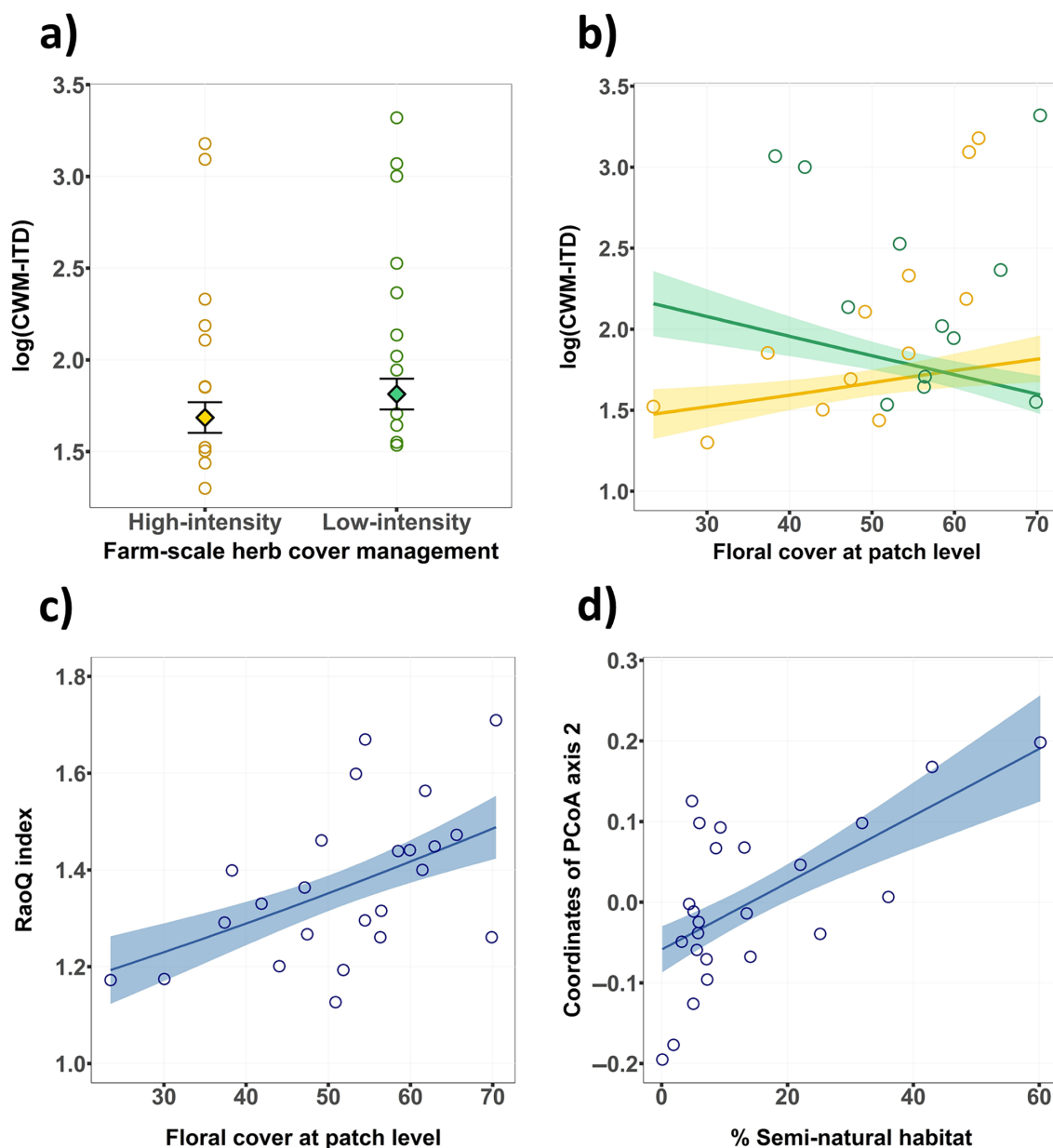
Direct effects of agricultural intensification on network topology

Bee species richness showed a positive relationship with the increase in the floral cover in the patches (Table 3a; Figure 3a; see also Appendix S1: Table S6 for competing models). Bee niche overlap was positively affected by the proportion of semi-natural habitats at the large scale (Table 3b; Figure 3b; see also Appendix S1: Table S6). The best fitted models for the diversity of interactions and H_2' were equivalent to the null models, while the best models for plant niche overlap were the null models, so we

cannot attribute any effect of the agricultural intensification variables on these network metrics (Appendix S1: Table S6).

Indirect effects of agricultural intensification on network topology through functional filtering of bee assemblages

We found four indirect paths of effects from agricultural intensification in olive orchards to interaction network properties (Figure 4). First, the farm-scale intensity of herb cover management indirectly decreased the niche overlap of the bees by decreasing the CWM-ITD of the assemblages (yellow arrow in Figure 4). Second, we found a negative indirect effect of floral cover at the patch scale on the niche overlap of plants mediated by the functional diversity of bee assemblages (i.e., increasing of the RaoQ index). Finally, the increase in the proportion of semi-natural habitats indirectly and positively impacted both bee richness (third indirect path) and bee niche overlap (fourth indirect path) in the interaction networks through changes in the nesting guild composition of bee assemblages, specifically toward a higher representation of bee guilds that require additional resources beyond bare soil for nesting.

FIGURE 1 Effects for the best Bayesian mixed model of agricultural intensification variables on each diversity functional metric. Plots showing the relationship between (a) community weighted mean of inter-tegular distance (CWM-ITD) and farm-scale herb management; (b) the interaction of farm-scale herb management with the floral cover at patch level and CWM-ITD; (c) RaoQ index and the floral cover at the patch level; (d) the composition of bee nesting guilds (coordinates of PCoA-2) with the proportion of semi-natural habitats at 1 km radius buffer. Boxplot represents the predicted mean with the SE, lines represent the posterior estimates, circles represent the original raw data and the shaded areas represent the SE. Green and yellow colors refer to the response of bee assemblages within low-intensity and high-intensity managed olive farms respectively. Blue color refers to the response of the whole bee assemblage. PCoA, principal coordinate analysis.

DISCUSSION

Our results provide some of the first empirical evidence of how agricultural intensification indirectly influences the properties of bee–plant interaction networks through functional filtering processes. Furthermore, our results revealed that part of this functional filtering of bee communities in high-intensity managed farms, especially in

relation to foraging traits, could be mitigated by maintaining high-quality floral patches with abundant and diverse floral resources. Additionally, preserving higher proportions of semi-natural habitats could also help to prevent the expected reduction in the functional heterogeneity of nesting guild composition caused by landscape simplification. Although there were direct effects of agricultural intensification on network

TABLE 2 Estimates for the selected best Bayesian mixed model between the different functional diversity metrics and the network metrics.

Model code	Fixed factor	Estimate	SE	95% LCI	95% UCI
(a) Bee richness ~ Composition of nesting guilds					
mBr-1.5	**Intercept**	**2.93**	**0.05**	**2.83**	**3.03**
	PCoA2	**1.90**	**0.51**	**0.90**	**2.90**
(b) Niche overlap of bees ~ Functional diversity metrics					
mNOV_Bee-1.1	**Intercept**	**−2.64**	**0.47**	**−3.57**	**−1.73**
	CWM-ITD	**0.58**	**0.20**	**0.19**	**0.98**
(c) Niche overlap of bees ~ Composition of nesting guilds					
mNOV_Bee-1.5	**Intercept**	**−1.39**	**0.14**	**−1.67**	**−1.12**
	PCoA2	**3.10**	**1.29**	**0.50**	**5.58**
(d) Niche overlap of plants ~ Functional diversity metrics					
mNOV_Pla-1.3	Intercept	1.12	0.94	−0.71	2.99
	CWM-ITD	0.83	0.21	−0.42	1.23
	RaoQ index	**−3.65**	**0.89**	**−5.42**	**−1.89**

Note: The table shows the posterior estimate, SE, and 95% credible intervals of the estimate with the lower (LCI) and the upper extremes (UCI). In bold, estimates with credible intervals not including 0. The first column identifies the code of the best model for each response variable. CWM-ITD = community weighted mean of inter-tegular distance; PCoA1 and PCoA2 = coordinates of axis 1 and axis 2 respectively, of the principal coordinate analysis. The alternative candidate models and their codes are shown in Appendix S1: Table S5.

properties, they were less pervasive than those mediated by changes in the functional properties of bee communities, as indicated by the higher number of indirect pathways compared to the direct ones.

Indirect effects of agricultural intensification on bee–plant interaction networks mediated by functional filtering of bee traits

We found four indirect pathways through which agricultural intensification influences bee–plant interaction networks at different spatial scales by shifting the functional properties of bee floral visitor assemblages.

First, the high-intensity herb cover management indirectly decreases the niche overlap of bees by reducing the proportion of bees with larger ITDs (typically related to larger body size), suggesting that larger bees tend to avoid high-intensity managed olive orchards. This pattern may be explained by the fact that larger bees have higher pollen and energy demands (Cresswell et al., 2000) and can track floral resources through longer distances (Greenleaf et al., 2007). The buffering effect of patches with higher availability of floral resources in high-intensity managed olive farms, increasing the ITD of the bee assemblages, could be explained by their strong attractiveness to pollinating insects (e.g., Cole et al., 2017), which is even more evident in high-intensity managed farms due to the

crowding effect (Vallejos et al., 2020). Accordingly, Maas et al. (2021) also found that the proportion of larger bees increased in newly established grasslands with higher floral resources compared to cereal fields where floral resources are scarce. The greater niche overlap observed in networks composed of bee assemblages with higher ITD is supported by the positive relationship between the body size of bees and their diet breadth (Lara-Romero et al., 2019). Therefore, this general tendency of larger bees to be more generalist would contribute to the increase in the degree of niche overlap in places where they are predominant, as observed in the low-intensity managed olive farms. CWM-ITD and CWM-proboscis length were strongly correlated; in fact, all the effects observed for CWM-ITD are also found for CWM-proboscis length if we swap one for the other in the analyses (data not shown), so the ecological meaning of the effects on CWM-proboscis length deserves additional consideration. Thus, the high-intensity herb cover management also indirectly led to a reduction in bee niche overlap by reducing the CWM-proboscis length. This suggests that bees with longer proboscis found more optimal conditions for foraging in low-intensity olive fields. The high-intensity herb cover management on olive farms makes herb assemblages more functionally homogeneous, disfavoring insect-pollinated herb species (Tarifa et al., 2021). Therefore, this homogenization likely results in a plant community less suited for foraging by larger bees with long proboscis, which are more efficient on flowers of deep corollas containing
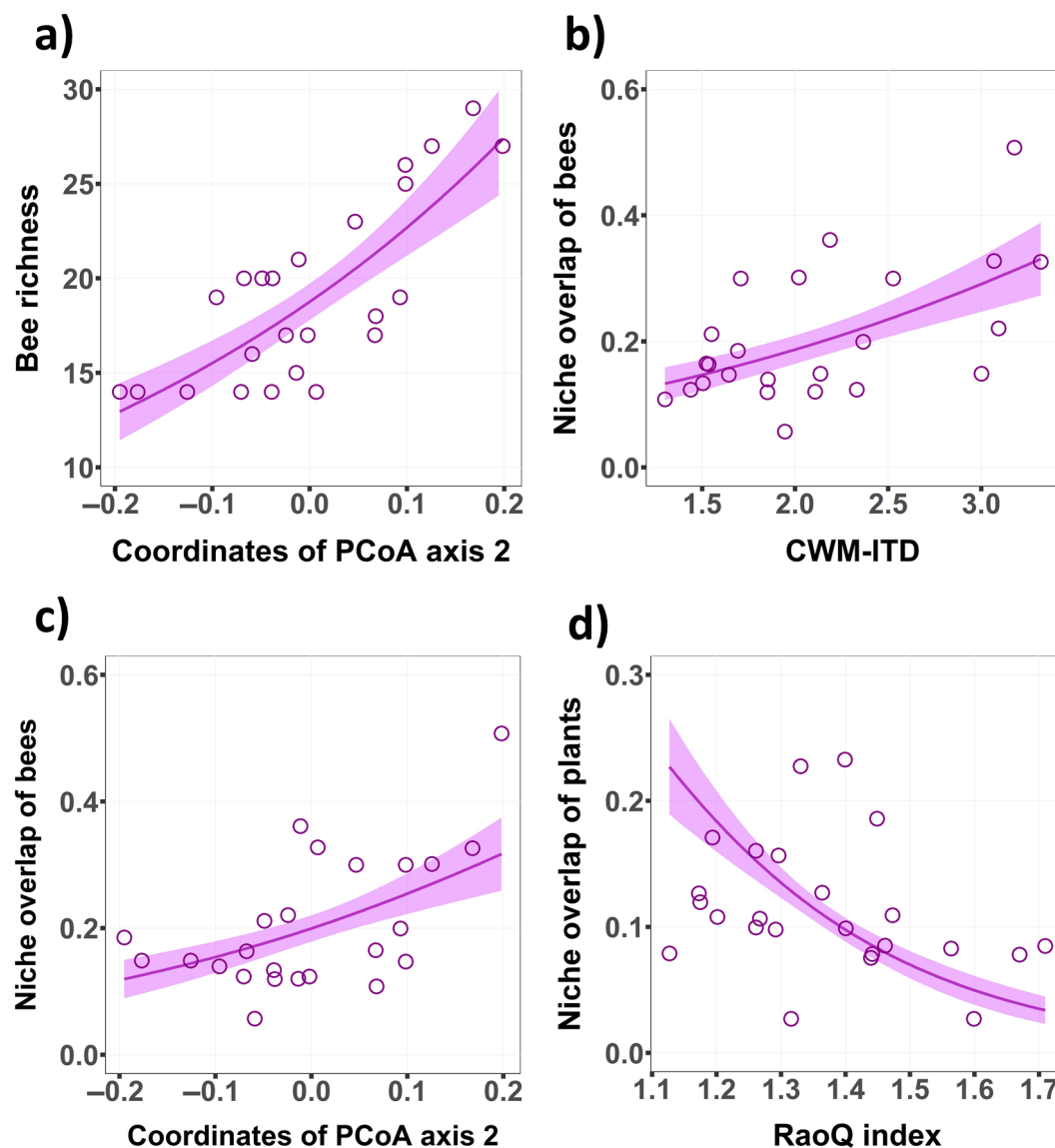
FIGURE 2 Effects for the best Bayesian mixed model of functional characterization of bee assemblages (i.e., diversity functional metrics) on interaction network metrics. Plots showing the relationship between (a) the bee richness in networks with the composition of bee nesting guilds (coordinates of PCoA-2); the niche overlap of bees in the networks and (b) the community weighted mean (CWM) of the inter-tegula distance (ITD) and (c) the composition of bee nesting guilds (coordinates of PCoA-2); (d) the niche overlap of plants in networks and the RaoQ index. Lines represent the posterior estimates, circles represent the original raw data, and the shaded areas represent the SE. PCoA, principal coordinate analysis.

larger nectar volumes (as *Echium*, Peat et al., 2005). Increasing floral availability in the remnant flowering patches in high-intensity managed farms can mitigate this effect. Likewise, the establishment of bee assemblages with longer relative proboscis also led to an increase in the niche overlap of bees because it favors a higher degree (i.e., the number of plant species with which they interact) and generalization in interaction networks (Lara-Romero et al., 2019). The increased niche overlap of bees should thus lead to an increase in generalization and functional redundancy in these interaction networks, which is associated with increased resilience

against disturbances when functional redundancy occurs (Blüthgen & Klein, 2011; Elmqvist et al., 2003). Thus, these findings have important implications because they provide information on how conditions promoted by low-intensity management support more stable and resilient bee communities.

Second, floral cover at the patch level decreased plant niche overlap through an increase in bee functional diversity (i.e., RaoQ index), which might be primarily driven by the strong attraction displayed by locally abundant floral resources (Hegland & Boeke, 2006). This indicates that bee assemblages become more functionally heterogeneous as

TABLE 3 Estimates for the selected best Bayesian mixed model of the relationship between the agricultural intensification variables and the interaction network metrics.

Model code	Fixed factor	Estimate	SE	95% LCI	95% UCI
(a) Bee richness ~ Agricultural intensification (patch scale)					
mBr-2.4	Intercept	2.32	0.26	1.80	2.82
	Floral cover	0.01	0.00	0.00	0.02
(b) Niche overlap of bees ~ Agricultural intensification (landscape scale)					
mNOV_Bee-2.1	Intercept	−1.81	0.22	−2.28	−1.40
	SNH	0.03	0.01	0.01	0.05

Note: The table displays the posterior estimate, SE, and 95% credible intervals. In bold, estimates with credible intervals not including 0. The first column identifies the code of the best model for each response variable. SNH = proportion of semi-natural habitat at 1 km radius buffer. All alternative models and their codes are shown in Appendix S1: Table S6.
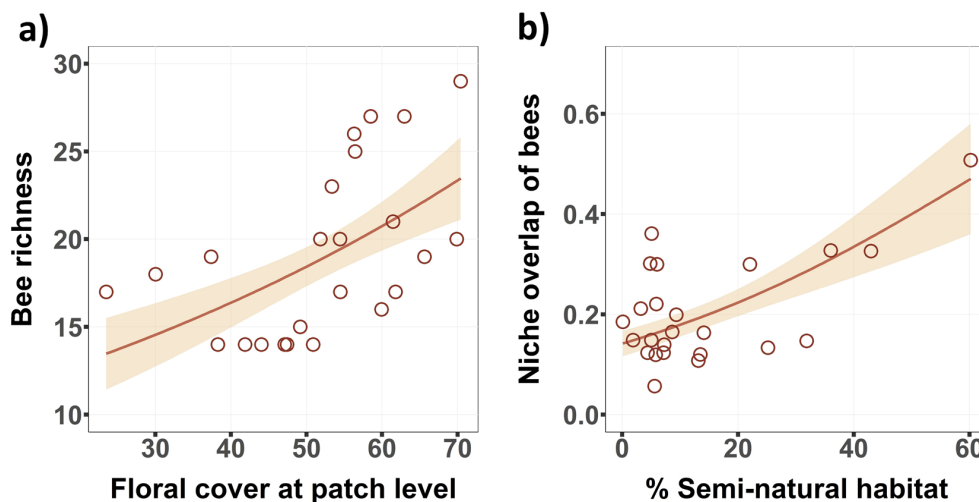
FIGURE 3 Effects for the best Bayesian mixed model of agricultural intensification variables on interaction network metrics. Plots showing the relationship between (a) bee richness in networks and the floral cover at the patch level; (b) niche overlap of bees in networks and the proportion of semi-natural habitats at a 1 km radius buffer. Lines represent the posterior estimates, circles represent the original raw data, and the shaded areas represent the SE.

the patch attractiveness increases. Moreover, it suggests that each bee species greatly contributes to the functional diversity within the assemblages, as evidenced by other studies (Odanaka & Rehan, 2019). The positive relationship between floral cover and bee functional diversity ultimately resulted in a decrease in the degree of niche overlap of the plant assemblages. Segregation in plant interactions constitutes a reasonable consequence of increased bee functional diversity since it allows floral resource partitioning by enhancing the degree of matching between flower and bee traits (Goulnik et al., 2021). From the herbaceous plant assemblage's perspective, decreasing their niche overlap may be beneficial because it increases plant niche complementarity, which could potentially enhance the pollination service of their flowering herb species (Magrach et al., 2021).

Finally, landscape areas with a higher proportion of semi-natural habitats were associated with increased bee richness and niche overlap of bees in interaction networks in olive fields' floral patches, mainly by modifying the bee nesting guild composition. This increased bee richness and niche overlap suggest more stable and resilient interaction networks (Blüthgen & Klein, 2011). The influence of semi-natural areas surrounding olive farms on the nesting guild composition of bees visiting olive fields' floral patches aligns with our expectations, as higher proportions of semi-natural remnants offer a broader range of specific nesting resources and nesting sites crucial for certain bee guilds (Murray et al., 2012; Williams et al., 2010). Consequently, the increased variability in resource availability and nesting sites within more complex agricultural landscapes creates new ecological niches for bees (in a broad sense), bolstering
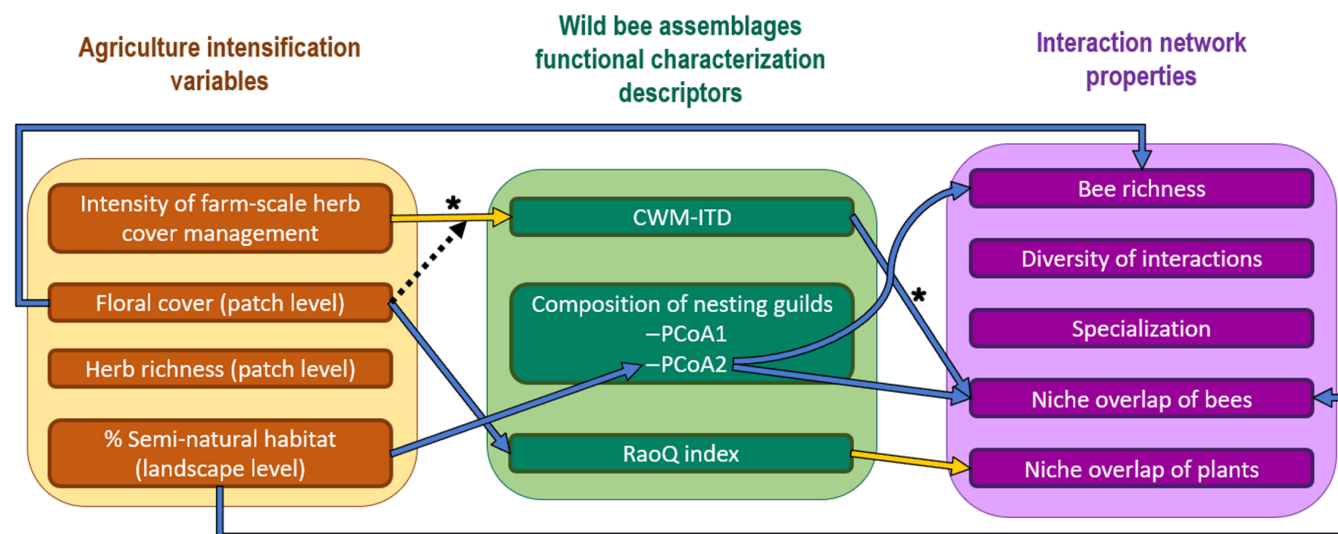
FIGURE 4 Diagram showing direct and indirect effects (through functional filtering processes) of agricultural intensification of olive crops on bee–plant interaction network properties. Positive and negative effects are indicated with blue and yellow arrows respectively. Dark dashed arrows show the interaction between the floral cover at patch level buffering the negative effect of farm-scale herb cover management intensification on community weighted mean of inter-tegular distance (CWM-ITD). The paths marked with an asterisk appear regardless of whether CWM-ITD or CWM-relative proboscis length is used. PCoA, principal coordinate analysis.

species richness within bee communities and their trophic niche overlap. More specifically, our results inform that the higher diversity of nesting guilds in farms within complex landscapes probably happens because of a decrease in the over-dominance of ground excavators (the main group contributing to PCoA-1). Thus, we further found a negative (although weak) relationship between ground excavators and the semi-natural habitat cover, while its relationship was positive with the intensity of herb cover management. Therefore, it suggests that more intensified agricultural landscapes and olive farms could favor the over-dominance of ground excavators and the homogenization of the bee assemblages visiting the floral patches in the olive fields.

Direct effects of agricultural intensification on bee–plant interaction networks

Agricultural intensification also directly influenced bee–plant interaction networks. Consistent with other studies, we observed that greater floral abundance at patch scale enriched bee assemblages (Hegland & Boeke, 2006). Furthermore, the niche overlap of bees augmented with the increase in the proportion of semi-natural habitats at the landscape scale. This could be mediated by the dilution effect of bees in patches when the proportion of semi-natural habitats increases, which leads to an expansion of the trophic niches of bee species, thus increasing

their niche overlap (Blüthgen & Klein, 2011). Unlike studies focused on specific guilds of bees or complete communities of pollinators (e.g., Martínez-Núñez et al., 2019; Olsson et al., 2021; respectively), we found no direct effects of herb cover management on either interaction diversity or H_2', presumably due to the flexible and generalist foraging behavior displayed by bees (Frund et al., 2013).

CONCLUSIONS

Our results revealed that both the intensity of ground herb cover management (persistent removal of ground cover conducing to bare soils vs. leaving ground covers) and the landscape simplification around olive farms (as estimated by semi-natural habitat cover) negatively impact the properties of the bee–plant interaction network in floral patches. This happened mainly indirectly, mediated by the filtering of functional traits of bee assemblages related to foraging and nesting behavior, respectively. Promoting dense floral patches and higher proportions of semi-natural habitats at the landscape scale contributes to shaping bee–plant interaction networks with greater bee richness and bee niche overlap while decreasing the niche overlap of plants. This supports healthy and resilient plant communities favoring bees, potentially ensuring pollination service for plant species of the herb cover of olive farms. In particular, it is worth noting the key role of maintaining some high-quality dense floral

patches in the olive groves for buffering the negative effects of farming practice intensification on bees with larger body sizes and longer proboscis lengths. Meanwhile, promoting semi-natural habitats at the larger landscape scale attenuates the homogenization of bee nesting guild composition.

AUTHOR CONTRIBUTIONS

ACKNOWLEDGMENTS

CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

Data (Cano, 2025) are available in Figshare at https://doi.org/10.6084/m9.figshare.29655062.

ORCID

Domingo Cano https://orcid.org/0000-0003-3933-0456
Carlos Martínez-Núñez https://orcid.org/0000-0001-7814-4985
Julio M. Alcántara https://orcid.org/0000-0002-8003-7844
Marco Moretti https://orcid.org/0000-0002-5845-3198
Pedro J. Rey https://orcid.org/0000-0001-5550-0393

REFERENCES

Bartomeus, I., D. Gravel, J. M. Tylianakis, M. A. Aizen, I. A. Dickie, and M. Bernard-Verdier. 2016. "A Common Framework for Identifying Linkage Rules across Different Types of Interactions." *Functional Ecology* 30(12): 1894–1903. https://doi.org/10.1111/1365-2435.12666.

Blüthgen, N., J. Fründ, D. P. V'azquez, and F. Menzel. 2008. "What Do Interaction Network Metrics Tell Us about Specialization and Biological Traits?" *Ecology* 89(12): 1–24. https://doi.org/10.1890/07-2121.1.

Blüthgen, N., and A. M. Klein. 2011. "Functional Complementarity and Specialisation: The Role of Biodiversity in Plant-Pollinator Interactions." *Basic and Applied Ecology* 12(4): 282–291. https://doi.org/10.1016/j.baae.2010.11.001.

Botta-Dukát, Z. 2005. "Rao's Quadratic Entropy as a Measure of Functional Diversity Based on Multiple Traits." *Journal of Vegetation Science* 16(5): 533–540. https://doi.org/10.1111/j.1654-1103.2005.tb02393.x.

Bürkner, P. C. 2017. "Brms: An R Package for Bayesian Multilevel Models Using Stan." *Journal of Statistical Software* 80(1): 1–28. https://doi.org/10.18637/jss.v080.i01.

Cano, D. 2025. "Completed_Data_Base_Ecol_Appl.Xlsx." Figshare. Dataset. https://doi.org/10.6084/m9.figshare.29655062.v1.

Cano, D., C. Martínez-Núñez, A. J. Pérez, J. M. Alcántara, T. Salido, and P. J. Rey. 2024. "Intensive Ground Cover Management and Landscape Simplification Affect Community-Wide Floral Visitor-Plant Interactions in Olive Groves." *Agriculture, Ecosystems & Environment* 373: 109124. https://doi.org/10.1016/j.agee.2024.109124.

Cano, D., C. Martínez-Núñez, A. J. Pérez, T. Salido, and P. J. Rey. 2022. "Small Floral Patches Are Resistant Reservoirs of Wild Floral Visitor Insects and the Pollination Service in Agricultural Landscapes." *Biological Conservation* 276: 109789. https://doi.org/10.1016/j.biocon.2022.109789.

Cappellari, A., G. Bonaldi, M. Mei, D. Paniccia, P. Cerretti, and L. Marini. 2022. "Functional Traits of Plants and Pollinators Explain Resource Overlap between Honeybees and Wild Pollinators." *Oecologia* 198(4): 1019–29.

Cariveau, D. P., G. K. Nayak, I. Bartomeus, J. Zientek, J. S. Ascher, J. Gibbs, and R. Winfree. 2016. "The Allometry of Bee Proboscis Length and Its Uses in Ecology." *PLoS One* 11(3): e0151482. https://doi.org/10.1371/journal.pone.0151482.

Cole, L. J., S. Brocklehurst, D. Robertson, W. Harrison, and D. I. McCracken. 2017. "Exploring the Interactions between Resource Availability and the Utilisation of Semi-Natural Habitats by Insect Pollinators in an Intensive Agricultural Landscape." *Agriculture, Ecosystems and Environment* 246: 157–167. https://doi.org/10.1016/j.agee.2017.05.007.

Cornwell, W. K., D. W. Schwilk, and D. D. Ackerly. 2006. "A Trait-Based Test for Habitat Filtering: Convex Hull Volume." *Ecology* 87(6): 1465–71. https://doi.org/10.1890/0012-9658(2006)87[1465:ATTFHF]2.0.CO;2.

Cresswell, J. E., J. L. Osborne, and D. Goulson. 2000. "An Economic Model of the Limits to Foraging Range in Central Place Foragers with Numerical Solutions for Bumblebees." *Ecological Entomology* 25(3): 249–255. https://doi.org/10.1046/j.1365-2311.2000.00264.x.

Dainese, M., D. I. Luna, T. Sitzia, and L. Marini. 2015. "Testing Scale-Dependent Effects of Seminatural Habitats on Farmland

Biodiversity." *Ecological Applications* 25(6): 1681–90. https://doi.org/10.1890/14-1321.1.

Devictor, V., J. Clavel, R. Julliard, S. Lavergne, D. Mouillot, W. Thuiller, P. Venail, S. Villéger, and N. Mouquet. 2010. "Defining and Measuring Ecological Specialization." *Journal of Applied Ecology* 47(1): 15–25. https://doi.org/10.1111/j.1365-2664.2009.01744.x.

Dormann, C. F., and R. Strauss. 2014. "A Method for Detecting Modules in Quantitative Bipartite Networks." *Methods in Ecology and Evolution* 5: 90–98. https://doi.org/10.1111/2041-210X.12139.

Elmqvist, T., C. Folke, M. Nyström, G. Peterson, J. Bengtsson, B. Walker, and J. Norberg. 2003. "Response Diversity, Ecosystem Change, and Resilience." *Frontiers in Ecology and the Environment* 1(9): 488–494.

Fortuin, C. C., and K. J. K. Gandhi. 2021. "Functional Traits and Nesting Habitats Distinguish the Structure of Bee Communities in Clearcut and Managed Hardwood and Pine Forests in Southeastern USA." *Forest Ecology and Management* 496: 119351. https://doi.org/10.1016/j.foreco.2021.119351.

Frund, J., C. F. Dormann, A. Holzschuh, and T. Tscharntke. 2013. "Bee Diversity Effects on Pollination Depend on Functional Complementarity and Niche Shifts." *Ecology* 94(9): 2042–54. https://doi.org/10.1890/12-1620.1.

Gámez-Virués, S., D. J. Perović, M. M. Gossner, C. Börschig, N. Blüthgen, H. De Jong, N. K. Simons, et al. 2015. "Landscape Simplification Filters Species Traits and Drives Biotic Homogenization." *Nature Communications* 6(1): 8568. https://doi.org/10.1038/ncomms9568.

Goulnik, J., S. Plantureux, I. Dajoz, and A. Michelot-Antalik. 2021. "Using Matching Traits to Study the Impacts of Land-Use Intensification on Plant–Pollinator Interactions in European Grasslands: A Review." *Insects* 12(8): 1–16. https://doi.org/10.3390/insects12080680.

Greenleaf, S. S., N. M. Williams, R. Winfree, and C. Kremen. 2007. "Bee Foraging Ranges and Their Relationship to Body Size." *Oecologia* 153(3): 589–596. https://doi.org/10.1007/s00442-007-0752-9.

Habel, J. C., M. J. Samways, and T. Schmitt. 2019. "Mitigating the Precipitous Decline of Terrestrial European Insects: Requirements for a New Strategy." *Biodiversity and Conservation* 28(6): 1343–60. https://doi.org/10.1007/s10531-019-01741-8.

Hegland, S. J., and L. Boeke. 2006. "Relationships between the Density and Diversity of Floral Resources and Flower Visitor Activity in a Temperate Grassland Community." *Ecological Entomology* 31(5): 532–38. https://doi.org/10.1111/j.1365-2311.2006.00812.x.

Horn, H. 1966. "Measurement of "Overlap" in Comparative Ecological Studies." *The American Naturalist* 100(914): 419–424.

Johnson, S. D., M. Moré, F. W. Amorim, W. A. Haber, G. W. Frankie, D. A. Stanley, A. A. Cocucci, and R. A. Raguso. 2017. "The Long and the Short of It: A Global Analysis of Hawkmoth Pollination Niches and Interaction Networks." *Functional Ecology* 31(1): 101–115. https://doi.org/10.1111/1365-2435.12753.

Klumpers, S. G. T., M. Stang, and P. G. L. Klinkhamer. 2019. "Foraging Efficiency and Size Matching in a Plant–Pollinator Community: The Importance of Sugar Content and Tongue Length." *Ecology Letters* 22(3): 469–479. https://doi.org/10.1111/ele.13204.

Laliberté, E., and P. Legendre. 2010. "A Distance-Based Framework for Measuring Functional Diversity from Multiple Traits." *Ecology* 91(1): 299–305. http://www.ecolag.univ-montp2.fr/softwarei.

Lara-Romero, C., J. Seguí, A. Pérez-Delgado, M. Nogales, and A. Traveset. 2019. "Beta Diversity and Specialization in Plant–Pollinator Networks along an Elevational Gradient." *Journal of Biogeography* 46(7): 1598–1610. https://doi.org/10.1111/jbi.13615.

Leps, J., F. de Bello, S. Lavores, and S. Berman. 2006. "Quantifying and Interpreting Functional Diversity of Natural Communities: Practical Considerations Matter." *Preslia* 78(4): 481–501. https://www.researchgate.net/publication/279573477.

Maas, B., M. Brandl, R. I. Hussain, T. Frank, K. P. Zulka, D. Rabl, R. Walcher, and D. Moser. 2021. "Functional Traits Driving Pollinator and Predator Responses to Newly Established Grassland Strips in Agricultural Landscapes." *Journal of Applied Ecology* 58(8): 1728–37. https://doi.org/10.1111/1365-2664.13892.

Maglianesi, M. A., N. Blüthgen, K. Böhning-Gaese, and M. Schleuning. 2015. "Functional Structure and Specialization in Three Tropical Plant-Hummingbird Interaction Networks across an Elevational Gradient in Costa Rica." *Ecography* 38(11): 1119–28. https://doi.org/10.1111/ecog.01538.

Magrach, A., F. P. Molina, and I. Bartomeus. 2021. "Niche Complementarity among Pollinators Increases Community-Level Plant Reproductive Success." *Peer Community Journal* 1: e1. https://doi.org/10.24072/pci.

Martínez-Núñez, C., A. J. Manzaneda, J. Isla, R. Tarifa, G. Calvo, J. L. Molina, T. Salido, C. Ruiz, J. E. Gutiérrez, and P. J. Rey. 2020. "Low-Intensity Management Benefits Solitary Bees in Olive Groves." *Journal of Applied Ecology* 57(1): 111–120. https://doi.org/10.1111/1365-2664.13511.

Martínez-Núñez, C., A. J. Manzaneda, S. Lendínez, A. J. Pérez, L. Ruiz-Valenzuela, and P. J. Rey. 2019. "Interacting Effects of Landscape and Management on Plant–Solitary Bee Networks in Olive Orchards." *Functional Ecology* 33(12): 2316–26. https://doi.org/10.1111/1365-2435.13465.

Maruyama, P. K., J. Sonne, J. Vizentin-Bugoni, A. M. Martín González, T. B. Zanata, S. Abrahamczyk, R. Alarcón, et al. 2018. "Functional Diversity Mediates Macroecological Variation in Plant–Hummingbird Interaction Networks." *Global Ecology and Biogeography* 27(10): 1186–99. https://doi.org/10.1111/geb.12776.

Michener, C. D. 2000. *The Bees of the World*, Vol. 1. Baltimore, MD: JHU Press.

Müller, A. 2022. *Palaearctic Osmiine Bees*. Zürich: ETH Zürich. http://blogs.ethz.ch/osmiini.

Murray, T. E., Ú. Fitzpatrick, A. Byrne, R. Fealy, M. J. F. Brown, and R. J. Paxton. 2012. "Local-Scale Factors Structure Wild Bee Communities in Protected Areas." *Journal of Applied Ecology* 49(5): 998–1008. https://doi.org/10.1111/j.1365-2664.2012.02175.x.

Odanaka, K. A., and S. M. Rehan. 2019. "Impact Indicators: Effects of Land Use Management on Functional Trait and Phylogenetic Diversity of Wild Bees." *Agriculture, Ecosystems and Environment* 286: 106663. https://doi.org/10.1016/j.agee.2019.106663.

Oksanen, J., F. G. Blanchet, M. Friendly, R. Kindt, P. Legendre, D. McGlinn, P. R. Minchin, R. B. O'Hara, G. L. Simpson, and P.

Solymos. 2020. "Vegan: Community Ecology Package." R Package Version 2.5-7. 2020. https://CRAN.R-project.org/package=vegan.

Olsson, R. L., M. R. Brousil, R. E. Clark, Q. Baine, and D. W. Crowder. 2021. "Interactions between Plants and Pollinators across Urban and Rural Farming Landscapes." *Food Webs* 27: e00194. https://doi.org/10.1016/j.fooweb.2021.e00194.

Peat, J., J. Tucker, and D. Goulson. 2005. "Does Intraspecific Size Variation in Bumblebees Allow Colonies to Efficiently Exploit Different Flowers?" *Ecological Entomology* 30(2): 176–181. https://doi.org/10.1111/j.0307-6946.2005.00676.x.

Potts, S. G., T. Petanidou, S. Roberts, C. O'Toole, A. Hulbert, and P. Willmer. 2006. "Plant-Pollinator Biodiversity and Pollination Services in a Complex Mediterranean Landscape." *Biological Conservation* 129(4): 519–529. https://doi.org/10.1016/j.biocon.2005.11.019.

Rey, P. J., A. J. Manzaneda, F. Valera, J. M. Alcántara, R. Tarifa, J. Isla, J. L. Molina-Pardo, et al. 2019. "Landscape-Moderated Biodiversity Effects of Ground Herb Cover in Olive Groves: Implications for Regional Biodiversity Conservation." *Agriculture, Ecosystems and Environment* 277: 61–73. https://doi.org/10.1016/j.agee.2019.03.007.

Ricotta, C., and M. Moretti. 2011. "CWM and Rao's Quadratic Diversity: A Unified Framework for Functional Ecology." *Oecologia* 167(1): 181–88. https://doi.org/10.1007/s00442-011-1965-5.

Souza, D. M., R. F. M. Teixeira, and O. P. Ostermann. 2015. "Assessing Biodiversity Loss Due to Land Use with Life Cycle Assessment: Are We There Yet?" *Global Change Biology* 21(1): 32–47. https://doi.org/10.1111/gcb.12709.

Tarifa, R., C. Martínez-Núñez, F. Valera, J. P. González-Varo, T. Salido, and P. J. Rey. 2021. "Agricultural Intensification Erodes Taxonomic and Functional Diversity in Mediterranean Olive Groves by Filtering out Rare Species." *Journal of Applied Ecology* 58(10): 2266–76. https://doi.org/10.1111/1365-2664.13970.

Tscharntke, T., A. M. Klein, A. Kruess, I. Steffan-Dewenter, and C. Thies. 2005. "Landscape Perspectives on Agricultural Intensification and Biodiversity – Ecosystem Service Management." *Ecology Letters* 8(8): 857–874. https://doi.org/10.1111/j.1461-0248.2005.00782.x.

Tscheulin, T., L. Neokosmidis, T. Petanidou, and J. Settele. 2011. "Influence of Landscape Context on the Abundance and Diversity of Bees in Mediterranean Olive Groves." *Bulletin of Entomological Research* 101(5): 557–564. https://doi.org/10.1017/s0007485311000149.

Vallejos, M. A. V., A. A. Padial, J. R. S. Vitule, and E. L. D. A. Monteiro-Filho. 2020. "Effects of Crowding Due to Habitat Loss on Species Assemblage Patterns." *Conservation Biology* 34(2): 405–415.

Vehtari, A., A. Gelman, and J. Gabry. 2017. "Practical Bayesian Model Evaluation Using Leave-One-Out Cross-Validation and WAIC." *Statistics and Computing* 27(5): 1413–32. https://doi.org/10.1007/s11222-016-9696-4.

Ward, L. T., M. L. Hladik, A. Guzman, S. Winsemius, A. Bautista, C. Kremen, and N. J. Mills. 2022. "Pesticide Exposure of Wild Bees and Honey Bees Foraging from Field Border Flowers in Intensively Managed Agriculture Areas." *Science of the Total Environment* 831: 154697. https://doi.org/10.1016/j.scitotenv.2022.154697.

Williams, N. M., E. E. Crone, T. H. Roulston, R. L. Minckley, L. Packer, and S. G. Potts. 2010. "Ecological and Life-History Traits Predict Bee Species Responses to Environmental Disturbances." *Biological Conservation* 143(10): 2280–91. https://doi.org/10.1016/j.biocon.2010.03.024.

SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.