



# Intensive ground cover management and landscape simplification affect community-wide floral visitor-plant interactions in olive groves

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## ABSTRACT

Plant-pollinator interaction networks can provide insights about the impacts of agricultural practices on biodiversity. However, studies on the agricultural impact on these networks most often focus on specific pollinator guilds (i.e., wild bees), hindering our understanding of the effects at the entire insect visitor community level. Here, we evaluated the impact of intensive agriculture and the moderation effects of landscape context on the topology of community-wide plant-visitor interaction networks (381 insect species). We also compared the responses of wild bee-based networks and community-wide plant-floral visitor networks to agricultural intensification to examine whether the former can be a good proxy of the latter. To this aim, we sampled plant-pollinator interaction networks in 24 paired olive farms with contrasting herb cover management (low-intensity management, where ground herb cover is not removed during the flowering season, and intensive management, with herbs persistently removed by herbicides and/or recurrent tillage) across a gradient of landscape complexity in Andalusia (Spain).

Results show that the topology of whole floral visitor interaction networks was affected by the herb cover management and the landscape simplification. Furthermore, we found that the effects of the herb cover management were often moderated through the interaction with the landscape context at both floral stand and landscape scale. However, the landscape scale at which these interaction effects occurred varied with the network metric. Non-bee floral visitors were fundamentally redundant for the network topology.

We concluded that the implementation of low-intensity management of ground covers in olive groves, together with the enhancement of the flower stands at the local level (e.g., floral strips) and the maintenance and/or restoration of semi-natural habitats at the large landscape scale, would be beneficial to the preservation of healthy and robust floral visitor communities. Our study further supports that wild-bee based interaction networks may adequately reflect the response of the entire networks of plant-floral visitor, at least in this study system.

## 1. Introduction

Among all the drivers of pollinating insects' decline, intensive agriculture constitutes a prominent and widespread threat worldwide (Martínez-Núñez et al., 2020a; Potts et al., 2010; Raven and Wagner, 2021; Tilman et al., 2001). This threat can damage pollinator communities through two main different mechanisms acting at different scales. In one hand, landscape simplification, often associated with land

conversion to agriculture, involves reducing semi-natural habitats, decreasing the area available for pollinators to feed, nest, breed and find refuge from disturbances. On the other hand, intensive agricultural practices within farms, such as the use of pesticides or intensive ploughing, significantly reduce both floral resources and floral visitor populations (Brittain and Potts, 2011; Habel et al., 2019; Kennedy et al., 2013). Both landscape simplification and local agricultural intensification within farms might disrupt plant and pollinator communities as

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well as the interactions they establish, endangering whole communities and ecosystem functioning (Bloom et al., 2021; Goulnik et al., 2021; Martínez-Núñez et al., 2019; Saunders, 2016). However, even though the negative effects of agricultural intensification and landscape simplification are overall well documented, research on the relative importance and interacting effects of these two threats in disrupting and shaping community-wide plant-flower-visitors' interaction networks remains inconclusive.

In recent years, some studies have examined how structural properties of interaction networks (e.g. diversity of interactions, nestedness, specialization or modularity) change due to landscape simplifications and habitat quality loss in agricultural systems (e.g., Goulnik et al., 2021; Morrison et al., 2020; Olsson et al., 2021; Sritongchuay et al., 2022; Weiner et al., 2014). The effects of agricultural intensification on plant-visitor networks can be multiple. For instance, it can foster a reduction of cohesion in the interaction networks, leading to a weaker strength of the interactions and finally to a loss of links and/or species (Kay and Schemske, 2018). In this process, the networks often gain connectance, lose nestedness and acquire a more modular structure, which might increase the risk of extinction of species poorly connected in the network (Spiesman and Inouye, 2013; Thébault and Fontaine, 2010; but see Olesen et al., 2007). In addition, some studies have reported that communities tend to show a higher niche overlap in disturbed habitats where generalist plant species dominate (Marrero et al., 2017; Doublet et al., 2022) and the availability of diverse floral resources is scarce (Blüthgen and Klein, 2011), but see Rakosy et al. (2022) for the opposite trend when specialist species predominate in disturbed habitats. Yet, studies on agriculture effects in plant-pollinator networks have rarely focused on the whole plant-visitor community (e.g., Jauker et al., 2019; Martínez-Núñez et al., 2019; Ockermüller et al., 2023), probably due to the taxonomic challenge of identifying different groups. Although studying a single or few groups of pollinators in isolation has a high value, including the whole community of flower-visitors might provide a more holistic and complete picture about landscape and local effects of agriculture over these communities (Rader et al., 2016). This becomes particularly crucial as previous studies have documented varied responses among distinct groups to the same perturbations (Garibaldi et al., 2014; Jauker et al., 2019; Kennedy et al., 2013; Williams et al., 2010). For example, wild bees have been shown to be more sensitive than other groups such as beetles or hoverflies to habitat loss mainly due to differences in their natural history (Gómez-Martínez et al., 2022; Jauker et al., 2009; Spiesman and Inouye, 2013). The functional response of a given species or functional groups may also change along a gradient of landscape simplification (Traveset et al., 2018) or agricultural management intensification (Martínez-Núñez et al., 2020b).

Here, we study the community-wide plant-floral visitor interaction networks of olive grove landscapes, considering major areas of olive growing from Andalusia, southern Spain. Olive farming constitutes one of the most widespread and socio-culturally important perennial agroecosystems in Europe. In recent years, there is a growing trend towards the implementation of super intensive farming regime in olive crops (Vilar et al., 2018), which can increase the negative impact of olive farming on biodiversity and its functions in the agroecosystem. The agri-environment schemes (AES) of the European Union Common Agricultural Policy are trying to reverse this situation. The most common AES in olive groves consists of the low-intensity management of the herb cover (Villanueva et al., 2015), consisting mainly of its maintenance most of the year, only being removed in late spring by mechanic procedures. This has been shown to have a great positive impact on the plant community of the herb cover in this agroecosystem, and therefore equally so on the availability and diversity of floral resources for floral visitors (Rey et al., 2019; Tarifa et al., 2021). Olive groves under traditional cultivation practices, which involve mowing ground herb cover or superficially ploughing them in late spring, constitute a key crop for wild plant and pollinating insects' conservation in the

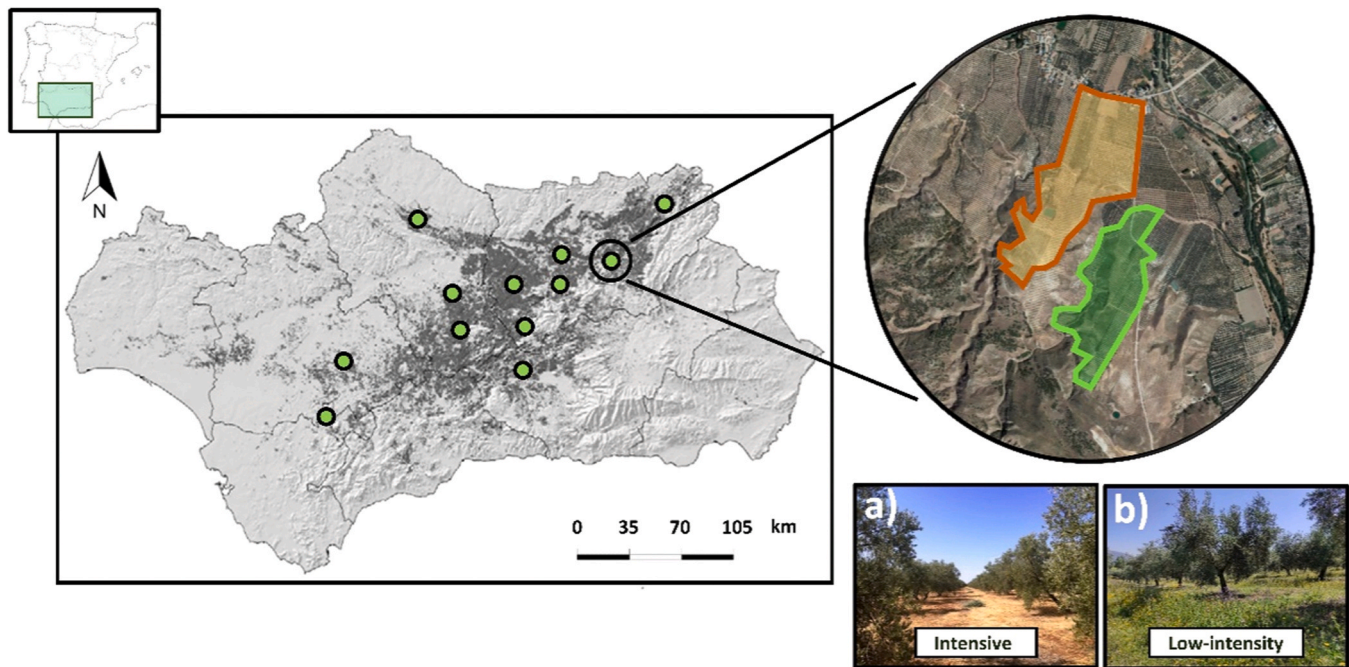
Mediterranean basin, despite olive trees not being a pollinator-dependent crop (Cano et al., 2022a; Martínez-Núñez et al., 2020a, b; Potts et al., 2016; Rey et al., 2019; Tscheulin et al., 2011). Preliminary studies have reported how organic management on olive farms benefits some groups of wild bees (Martínez-Núñez et al., 2020a), and how this effect is moderated by the landscape complexity at different landscape scales (Cano et al., 2022a; Martínez-Núñez et al., 2020b; Tscheulin et al., 2011). Likewise, studies focused on cavity-nesting solitary bee interactions with plants showed that the structure of networks became more complex and robust in olive farms with low-intensity herb cover management (Martínez-Núñez et al., 2019) even though the most important species to the network maintenance (i.e., core species) were the same irrespective of the intensity of herb cover management (Martínez-Núñez et al., 2020b). However, these studies were conducted with specific guilds of bees; we do not know to what extent the response to agricultural intensification of other pollinating insects and the community-wide networks of interactions with plants can be generalized from bees.

In this study, we explore the effects of agricultural intensification (i.e., intensity of herb cover management and landscape simplification) on the topology of interaction networks involving the entire visitor insect community and the flowers of the ground herb covers they visit in olive grove landscapes. We intend to test the following hypotheses a) low-intensity herb cover management will contribute to enhancing the structural complexity and stability of networks (i.e., we expect higher number of interacting species, diversity of interactions, nestedness, and niche overlap as well as lower modularity and specialization); b) the increased landscape complexity will moderate the effects of herb cover management on interaction network structure (i.e., the negative effects of intensive management will be mitigated by large-scale heterogeneity and the availability of diverse floral resources at a more local scale); and c) the structural properties of interaction networks based on the whole flower-visitor community will respond differently to agriculture intensification compared to those based only in bees.

## 2. Materials and methods

### 2.1. Study site and design

This study was conducted in 2020, in olive farm landscapes of Andalusia, southern Spain. Andalusia is the region with the largest area of olive-growing in the world, with more than 1.5 million hectares (Vilar et al., 2018). We selected a set of 24-paired olive farms located in 12 localities and spread throughout the main cultivation areas of olive groves in Andalusia across a large landscape transformation gradient (Fig. 1). The geographic distribution of the selected olive farms ranged from 5°47'66"W to 2°65'43"W and from 38°39'64"N to 36°9'10"N (ca. 40,000 km<sup>2</sup>). The pair of farms in each locality was within a 2 km buffer around the centroid of both farms, thus embedded in the same landscape complexity at a large scale (Fig. 1). Each pair of olive farms showed a contrasting herb cover management, a farm with intensive ground herb cover management (Fig. 1a) and a farm with low-intensity ground herb cover management (Fig. 1b). Intensive herb management consists of removing the ground herb cover permanently, usually by applying pre-emergence and/or post-emergence herbicides together with deep ploughing the soil several times a year, keeping the soil uncovered. In contrast, low-intensity herb cover management comprises the maintenance of the ground herb cover most of the year, only being removed in late spring, mainly by cattle or mechanic mowing (sometimes also with superficial ploughing). Concerning the use of pesticides, intensively managed farms used a high level of herbicides and insecticides, while olive farms with low-intensity management used low or no pesticides. It is worth mentioning that agriculture intensification associated with the use of pesticides should not be assimilated to conventional vs. organic farming in this study. All the olive farms selected were of at least 7 × 8 m tree plantation frames with a maximum of 14 × 14 m. In each locality,



**Fig. 1.** - Map of Andalusia (southern Spain) showing the 12 sampled localities (green dots) and the pair of farms sampled in each locality (right augmented view) with contrasting herb cover management: (a) intensive vs. (b) low-intensity. The dark shaded area in the map shows the occurrence of olive orchards in Andalusia.

the two paired olive farms shared the same size category, ensuring similarity in farm size between the two types of herb cover management. However, farm size varied substantially between localities. We differentiated between small farms (less than 10 ha) and large farms (greater than 100 ha). Considering intermediate-sized farms was logistically impractical. Yet, the farm size was found to have no relation with interaction network descriptors (Table S1), hence we opted to exclude it from the analyses to simplify the models (see Statistical analysis section). Detailed information about farm size, plantation frames, herb cover management, and pesticide application is provided in Table S2.

In each olive farm, we considered two multi-floral stands scattered throughout the olive grove matrix. When the lack of flowering stands prevented the selection of appropriate multi-floral stands (e.g. some of the intensively managed olive orchards), they were located close to boundaries or gully edges and ravines. In any case, they were always within the crop matrix, avoiding farm edges and unproductive areas, that is, unmanaged semi-natural areas around the olive farm. They were always established in the largest and most flower-diverse stands on each farm, to cover as many singular plant-floral visitor interactions as possible. The area sampled in each multi-floral stand was 10 m<sup>2</sup> (normally 2 × 5 m). Whenever possible, each pair of multi-floral stands on each farm was separated at least 150 m. We tried to use the same stand in each sampling round, but new ones had to be used when there were no more flowers in the original ones (e.g., due to phenology or management).

We employed two different scales considering several landscape metrics to characterise the landscape complexity surrounding the olive farms: 1 km radius centred on each farm and 100 m around each multi-floral stand. We used recent land-use cartography (data from SIOSE 2016 available at <http://www.juntadeandalucia.es/medioambiente/site/rediam/>) to estimate the proportion of semi-natural habitat (including field edges, flowering shrubs, grasslands, hedgerows, and road verges) as landscape metric at 1 km radius scale using GIS platform (QGIS v.2.14). At the 100 m radius scale, we measured the proportion of floral habitat (involving the floral elements located on farm boundaries, field margins, and small semi-natural meadows) by manual digitalization using the most current orthophotos in Google Earth®. Moreover, we also surveyed, by visual inspection, the flower cover and the occurrence

of each flowering species for the 10 m<sup>2</sup> area of each sampling floral stand as quality floral stand metrics.

## 2.2. Interactions surveys

Plant-floral visitor interaction surveys were conducted in 48 multi-floral stands (two flowering stands per olive farm), to build interaction networks. Surveys were carried out from March to June, in three sampling rounds separated by 5–6 weeks each. The period covered provides a good representation of the floral visitor community and their interactions, since the study area is characterized by Mediterranean climate where the flowering season of most herbaceous species is coincident with a rainy period between the beginning of spring and the beginning of summer. We sampled during rain-free days with a minimum temperature of 18°C and wind speed below 5 km/h to maximize detection of insect activity. The survey of interactions consisted of recording the contacts between flowers and floral visitors for 15 minutes in the morning (until 13 h pm) and 15 minutes in the afternoon (until 17 h pm) in each sampling round. The contact of a floral visitor individual with the reproductive part of a flower was considered an interaction event. Most of the insects were visually identified to genus level in the field, but after finishing the pollinator censuses many individuals (at least one of each morphotype) were collected with a sweep net for later identification to species or morphospecies level in the laboratory. Morphospecies were assigned to insects belonging to genus for which identification keys are not available in the Iberian Peninsula (but see Cano et al. 2022b for updates on the identification process). In any case, for the genera with a higher number of morphospecies (e.g. *Andrena* and *Lasioglossum* genera), we tried to be as conservative as possible and considered only females to define morphospecies to not overestimate species richness.

## 2.3. Network metrics

To characterize the topology of the plant-floral visitor networks, we built a matrix of interaction frequency for each olive farm (interactions were grouped by farm across floral stands and rounds) considering as interaction counts the number of contacts between flower reproductive



organs and each floral visitor.

Then, we calculated network metrics from these quantitative mutualistic networks (weighted by interaction frequency) and explored the effects of agricultural intensification at different scales on their topology. To this aim, we used six quantitative network metrics widely used to describe changes in interaction networks (Kaiser-Bunbury and Blüthgen, 2015).

Firstly, we used two diversity metrics which are closely related to community stability (Kaiser-Bunbury and Blüthgen, 2015) and the quality of the ecosystem functions (Tylianakis et al., 2007).

Floral visitor richness in networks:

This metric refers to the number of floral visitor species.

Shannon diversity of interactions:

This index calculates the diversity of interactions in a manner analogous to the Shannon diversity of species.

Secondly, we used four distribution metrics which refer to the connectivity of interacting species in networks, thus describing generalisation-specialisation gradients in the networks (Kaiser-Bunbury and Blüthgen, 2015) that could be suitable indicators to assess changes in networks due to environmental disturbances (Dunne et al., 2002).

### 2.3.1. Modularity

Modularity measures the organizational structure of interaction network by assessing the degree to which a network is divided into modules (i.e., set of species interacting among each other). Modularity can decrease due to the increase of intersection across modules or due to the loss of species that represent whole modules. Theoretically, high modularity implies a lower resistance to disturbances (Thébault and Fontaine, 2010).

### 2.3.2. Network specialization ( $H_2$ )

$H_2$  measures the specificity of the interaction network across the interacting species (Blüthgen et al., 2008), closely linked to network robustness and vulnerability (Kaiser-Bunbury and Blüthgen, 2015).

### 2.3.3. Nestedness

Nestedness is interpreted as the tendency for specialist species (less connected) to interact with generalist species (highly connected), a pattern underlying important ecological and evolutionary relationships (Hoeppke and Simmons, 2021). Here, we measured nestedness as NODF (nestedness metric based on the overlap and decreasing fill) (Almeida-Neto et al., 2008).

### 2.3.4. Niche overlap of floral visitors

Niche overlap measures the mean similarity in interaction patterns among species (floral visitors in this case). It is calculated as Horn's index and it refers to similarities in the interaction patterns between floral visitor species. Values close to 0 show that niche is virtually not shared among species, whereas values close to 1 indicate a large degree of overlap (Horn, 1966).

We computed all these network metrics both using the interactions of the entire community of floral visitors and the subset of interactions conducted by the guild of wild bees only, to compare the topology of the two types of networks across agricultural gradients.

Since network size may affect the network metric values, we built 1000 networks for each farm that were standardized to the size of the smallest network across sites by randomly deleting floral visitor species (Vanbergen et al., 2014). Then, we recalculated all the metrics in each randomized network to use the mean value as the standardized value for each network (Lázaro et al., 2015; Vanbergen et al., 2014). We did not use standardized values for  $H_2$  as this metric can be used directly for comparisons across networks due to its robustness against network sizes and sampling effort (Blüthgen et al., 2006). Floral visitor richness in networks also did not require standardisation, as it inherently represents one of the dimensions of network size.

Finally, in order to test to what extent the distribution metrics (nestedness, modularity and niche overlap) in the observed networks were significantly different from those expected by chance, we calculated a z-score for each observed network (Dormann and Strauss, 2014; Ulrich and Gotelli, 2009; Vanbergen et al., 2014) controlling for species richness and number of links using the Patefield algorithm in 1000 networks (Patefield, 1981).

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

## 2.4. Statistical analysis

First, we assessed the effect of herb cover management and landscape simplification on the structure of community-wide interaction networks (those comprising the entire community of floral visitors). We ran multi-level mixed Bayesian models, fitted through MCMC (Markov Chain Monte Carlo) with the parameters set to 4 chains, 50,000 iterations (with the first 10,000 being burned) in the 'brms' R package (Bürkner, 2017) that rendered stable outputs. We used uninformative diffuse priors, which means that we did not provide previous information about the expected posterior to bias the calculation of posterior probabilities. We decided to use these models because they perform better and have less convergence issues than frequentist methods for low-moderate sampling sizes ( $N=24$ ;  $n=12$  low-intensively managed farms and  $n=12$  intensively managed farms).

In these models, we used each observed network metric as a response variable and the herb cover management, the landscape variables and the quality of floral stand metrics as descriptors with the locality always as a random factor. Due to the nature of the data, we used: a) Gaussian distribution and log link function for NODF and the diversity of interactions; b) Poisson distribution and log link function for floral visitor richness; and c) Beta distribution with logit link function for the rest of the metrics.

Landscape variables used as predictors were: the proportion of floral habitats at the scale of 100 m radius buffer around the floral stands, and the proportion of semi-natural areas at the large scale of 1 km radius buffer around the centroid of each olive farm.

Quality floral stand metrics used as predictors: the flowering herb richness and the floral cover measured within the 10 m<sup>2</sup> floral stand.

To avoid multicollinearity, we previously checked the variance inflation factor (VIF) of the explanatory variables for each response variable in the models. VIF values informed about negligible collinearity among the explanatory variables (Table S3).

Because we were interested in the effects of herb cover management and landscape at different scales, and how the landscape context moderates the intensity of herb cover management effect on the interaction network properties, for modelling of variation of each response variable we considered a series of alternative competing models including, separately: simple main effects of herb cover management; simple main effects of each of the descriptors of landscape complexity and quality of floral stands; and additive and interactive effects of herb cover management with each descriptor of landscape complexity and quality of floral patches. These sets of competing models were computed for each of the two landscape scales considered and the floral stand level (see Tables S2-3). Model validation was performed using the approximate leave-one-out (LOO) cross-validation method in the 'loo' package (Vehtari et al., 2017). Likewise, the leave-one-out validation allowed us to perform model selection against null models (i.e., models fitted without fixed factors) for each response variable based on the variation in the LOO information criterion (LOOIC; lower LOO indicates better model fit and parsimony). However, it is essential to examine the difference between each model and the best one to determine whether the best model is different from the rest or whether they are equivalent in terms of their predictive power for the dataset. 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). Models can be compared based on the difference between their ELPD-LOO and the one in the best model (ELPD-Diff) and the standard error of such difference. We considered that a model cannot be distinguished from the best one regarding their predictive performance when the interval  $\text{ELPD-Diff} \pm \text{SE}$  contained the zero estimate (Bürkner, 2017). When several models were equivalent to the best one, we opted for the model with the highest  $R^2$  which showed estimates for the response variable whose 95 % credible interval did not include 0. For the local level, when the additive and the interaction models were equivalent to each other, we used complete models (i.e. including both the additive and interaction effects between herb cover management and the two descriptors of landscape) in order to determine which of the two descriptors had the greater effect.

We checked the normality of model residuals by visual inspection, convergence via  $\hat{R}$  (all equal to 1 or 10.01), and stability of the results by visual examination of chains.

The standardized values of the network metrics were used as response variables in a second set of models, following the same structure and methodology as the previous one for determining the best models. By comparing the best models resulting from the two sets (standardized networks and observed ones), we can determine if the size of networks influenced the observed values of the network metrics. If the best models differ between the two sets, it suggests an effect of network size on observed values; conversely, consistent best models in both sets imply no such influence.

To assess if the response of network topology across the agricultural intensification gradient differed between wild bees and the entire floral visitor assemblage, we also ran multi-level mixed models with the same parameters mentioned above (i.e., fitted through MCMC with the parameters set to 4 chains, 50,000 iterations with the first 10,000 being burned), using uninformative diffuse priors and the same distribution and link functions as above for the response variables. We employed network metrics as response variables and tested the interaction effect between network type (i.e. including the whole floral visitor assemblage or wild bees only) and herb cover management, and network type and landscape variables. Locality was considered always a random factor in these analyses. Models selection was carried out as described above for the set of models that evaluate the structure of the community-wide interaction networks.

### 3. Results

Overall, interaction networks in this study were built from a total of 16,147 plant-floral visitor interactions, which represented 1473 unique interactions between 381 species and morphospecies of flower-visitor insects belonging to 4 orders (Hymenoptera, Diptera, Coleoptera and Lepidoptera) (List S1; see also Cano et al., 2022b), and 135 flowering herb species belonging to 33 families (List S2). The majority of interactions (62.94 % of the total) were carried out by bees (Anthophila group), which were also the most frequent group of the flower-visitor community (167 species/morphospecies). They were followed by the Diptera (16.75 % of interactions), in which Bombyliidae and Syrphidae families stand up above the rest of them (11.82 %, 3.43 % and 1.50 % of interactions; and 36, 13 and 29 species/morphospecies respectively). Coleoptera (57 species/morphospecies) performed 11.05 % of the interactions and the non-bee Hymenoptera group, represented by 55 species/morphospecies, performed 4.12 % of interactions. Finally, the least represented group of this study were the Lepidoptera, comprising 24 species that carried out 5.14 % of the interactions.

#### 3.1. Community-wide networks topology

Floral visitor richness in networks was not affected by any of the descriptors of landscape scales or stand-level quality considered or by herb cover management (null models were equivalent to the best models

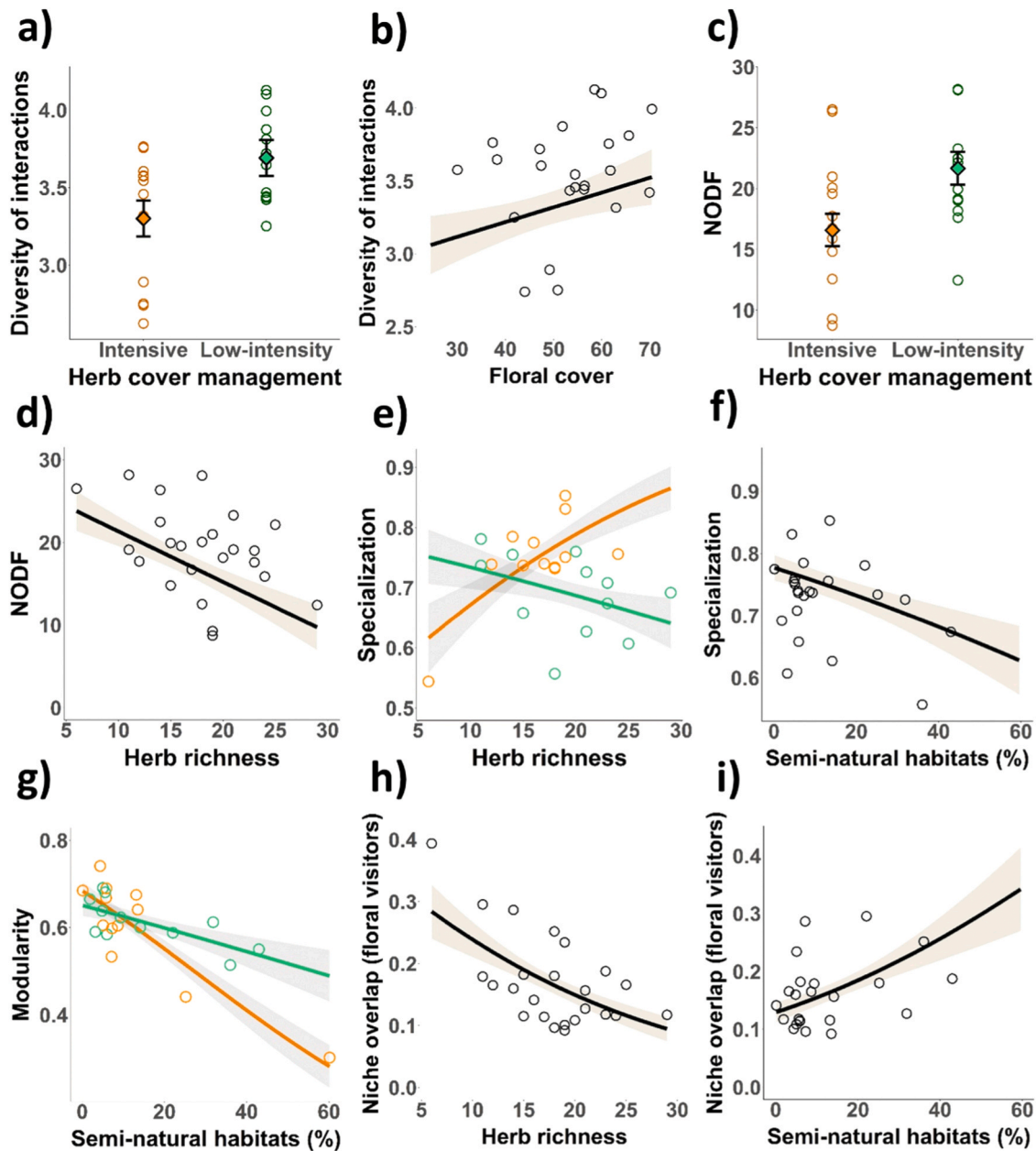
in each landscape level; see Table S4). Since none of the predictor variables tested showed a definite relationship with floral visitor richness in networks, we will assume that the effect of the size of networks does not mediate the effect of predictors on the network metric values in this study. Moreover, this is congruent with the results obtained for the models fitted with the standardized metrics, in which the best models are consistent with the models with the raw network metrics (see Table S5).

Herb cover management was the best predictor for the diversity of interactions across all landscape levels (Table S4), showing higher values in farms with low-intensity management (Table 1; Fig. 2a). At the floral stand level, diversity of interaction was also positively affected by the floral cover of sampling stand independently of the effect of herb cover management (Table 1; Fig. 2b; see also Table S4). Effects on nestedness were only detected at the floral stand level, with the best model considering the additive effect of herb cover management and the herb richness in the sampling stands (Table S4). Nestedness in networks was higher in low-intensity olive farms (Table 1; Fig. 2c), while the increase in herb richness in the floral stands had a negative effect on this network property (Table 1; Fig. 2d). This pattern agrees with the response of  $H_2$ , since the best model for  $H_2$  at local level shows a positive effect on the response of this metric in intensively managed farms, especially when flower richness in multi-floral stands is high (Table 1; Fig. 2e).  $H_2$  was also negatively affected at large scale through the increase of the proportion of semi-natural habitats (Table 1; Fig. 2f). Modularity in the networks was only affected at the largest scale (i.e., at 1 km radius buffer). The best model shows an interaction between herb cover management and the landscape context at the larger scale (Table S4). Network modularity decreased with the increase in the proportion of semi-natural habitats, but this decrease was slower in olive farms under low-intensity management (Fig. 2g). Niche overlap in floral

**Table 1**

Estimates for the selected best Bayesian mixed model for each network metric. The table displays the posterior estimate, standard error, 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 (diversity of interactions (mDI), NODF (mNODF),  $H_2$  (mH), modularity (mMod) and niche overlap (mNO)). FC = Floral cover at the floral stand level, HR = Herb richness at the floral stand level, SNA = Proportion of semi-natural area at 1 km radius buffer. All models tested for each network metric are shown in Table S4. The model codes correspond to those used in Table S4.

Model code	Fixed factor	Estimate	Standard error	95 % LCI	95 % UCI
<b>mDI-M</b>	Intercept	3.30	0.12	3.06	3.54
	Low-intensity	0.39	0.14	0.12	0.66
<b>mDI-8</b>	Intercept	2.81	0.37	2.08	3.54
	Low-intensity	0.31	0.14	0.03	0.60
	FC	0.01	0.01	0.00	0.02
<b>mNODF-11</b>	Intercept	27.49	3.57	20.43	34.50
	Low-intensity	5.11	1.87	1.38	8.78
	HR	-0.61	0.20	-1.01	-0.21
<b>mH-2</b>	Intercept	1.25	0.12	1.01	1.50
	Low-intensity	-0.26	0.13	-0.52	0.01
	SNA	-0.01	0.00	-0.02	0.00
<b>mH-12</b>	Intercept	0.11	0.39	-0.65	0.89
	Low-intensity	1.13	0.53	0.09	2.18
	HR	0.06	0.02	0.01	0.11
	Low-intensity: HR	-0.08	0.03	-0.14	-0.02
<b>mMod-3</b>	Intercept	0.77	0.10	0.58	0.97
	Low-intensity	-0.15	0.13	-0.41	0.11
	SNA	-0.03	0.01	-0.04	-0.02
	Low-intensity: SNA	0.02	0.01	0.00	0.03
<b>mNO-1</b>	Intercept	-1.92	0.17	-2.30	-1.62
	SNA	0.02	0.01	0.01	0.04
<b>mNO-10</b>	Intercept	-0.58	0.32	-1.22	0.05
	HR	-0.06	0.02	-0.09	-0.02



**Fig. 2.** - Marginal effects of agricultural intensification variables for the best Bayesian mixed model on each network metric. Plots showing the relationship between: diversity of interactions and (a) herb management, and (b) floral cover at stand level; NODF and (c) herb management, and (d) herb richness at stand level; (e) the interaction of herb management with the herb richness at stand level and specialization; (f) specialization and the proportion of semi-natural habitats (1 km radius buffer); (g) the interaction of the herb cover management with the semi-natural habitats (1 km radius buffer) and modularity; niche overlap in floral visitors and (h) herb richness at stand level, and (i) proportion of semi-natural habitats (1 km radius buffer). Boxplots represent the predicted means with the standard error, lines represent the posterior estimates, circles represent the original raw data and the shaded area represents the standard error (green colour represents the response for the low-intensity olive farms, while the orange colour represents the response for the intensively managed olive farms. Black colour represents the overall response.

visitor was affected by the proportion of semi-natural habitat at the landscape level, and simultaneously by the herb richness in sampling floral stands at local level (Table S4). Niche overlap showed a negative response to the increase in the herb richness in the floral stands (Table 1; Fig. 2h), and conversely, it showed a positive response to the increase in the proportion of semi-natural habitats at landscape scale (Table 1; Fig. 2i). Fig. S1 shows the tendency for all the interaction effects between herb cover management with the landscape and floral stand descriptors for all the network metrics contemplated (irrespective of whether the interaction was included in competitive models selected as the best).

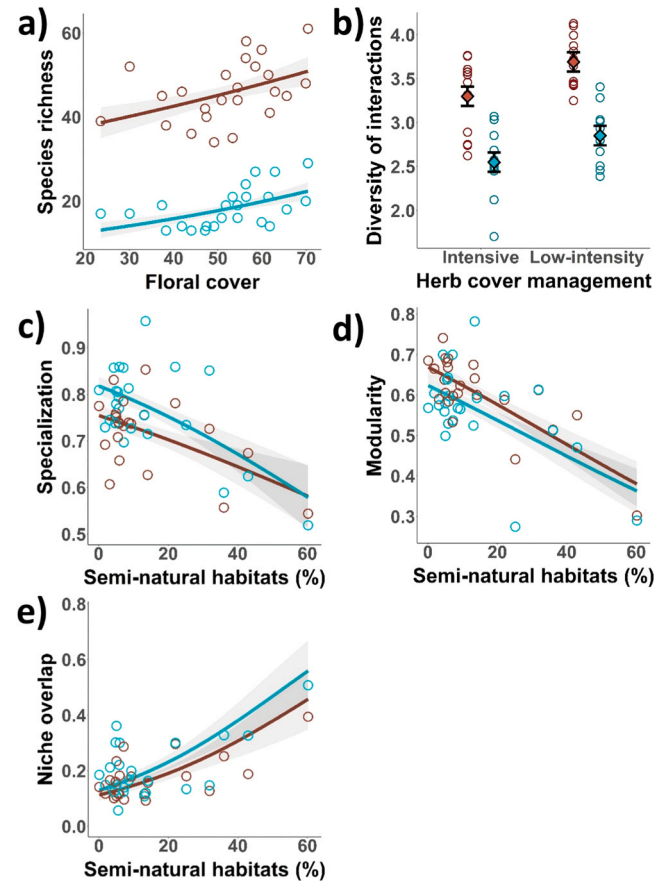
Z-scores from null-model analyses computed for the distribution

metrics (i.e., nestedness, modularity and niche overlap) for all the observed networks showed that all of them were significantly less nested, more modular and with a lower degree of niche overlap than expected by chance (Table S6).

### 3.2. Community-wide networks vs. wild bee-based networks

No interaction between the floral visitor group and the environmental variables was detected (Fig. 3; Table S7). Hence, results showed that there were no differences between the response of the network metrics of the entire community of floral visitors and the bee community to agricultural intensification (either through herb cover management,





**Fig. 3.** - Comparisons of the response to agricultural intensification (management type and landscape variables) of community-wide network and bee-based network metrics (considering the best Bayesian mixed model on each network metric). These comparisons are represented as the interaction effect of floral visitor group (either the entire floral visitor community or only bees) and the intensification variables incorporated in the respective models. Boxplots represent the predicted means with the standard error, lines represent the posterior estimates, circles represent the original raw data and the shaded areas represent the standard error (blue colour represents the response of the bee-based network metrics, while brown colour represents the response of the community-wide network metrics).

landscape or floral stand quality effects). In fact, Fig. 3 showed that the pattern of variation for each network metric for the community-wide interaction network resembled that of wild bee-based network.

Number of species of both groups (all floral visitor insects and bees) responded positively to floral cover in the floral stands (Table 2; Fig. 3a; see also Table S7). The best predictor of the diversity of interactions was the herb cover management (i.e., intensive vs. low-intensity) (Table 2; see also Table S7). Both types of networks (including the entire flower-visitor community or only bees), tended to have a higher diversity of interactions in olive farms with low-intensity management (Fig. 3b). None of the landscape variables explained the response of nestedness in networks for the interaction between groups (all floral visitors and bees) since the best models were equivalent to the null model (Table S7). For the rest of network descriptors, the best models were those incorporating the simple effect of the proportion of semi-natural area (Table 2; see also Table S7).  $H_2$  and modularity decreased as the proportion of semi-natural area increased (Figs. 3c and 3d respectively), while niche overlap in floral visitors showed an opposite tendency (Fig. 3e).

4. Discussion

We confirmed that both dimensions of intensification (i.e., the farm-

**Table 2**

Estimates for the best interaction Bayesian mixed model (floral visitor group x management type and landscape variables) for each landscape level. The table displays the posterior estimate, standard error and 95 % credible intervals. In bold, estimates with credible intervals not including 0. First column identifies the code of the best model for each response variable (diversity of interactions (iDI),  $H_2$  (iH), modularity (iMod) and niche overlap (iNO)). FC = Floral cover at floral stand level, HR = Herb richness at floral stand level, SNA = Proportion of semi-natural area at 1 km radius buffer. All models tested for each network metric are shown in Table S7. The model codes correspond to those used in Table S7.

Model code	Fixed factor	Estimate	Estandard error	95 % LCI	95 % UCI
iDI-1	Intercept	3.30	0.12	3.07	3.53
	Low-intensity	0.39	0.11	0.18	0.61
	Bees	-0.75	0.11	-0.96	-0.54
	Low-intensity: Bees	-0.09	0.15	-0.39	0.21
iH-2	Intercept	1.13	0.13	0.88	1.38
	SNA	-0.01	0.01	-0.03	-0.01
	Bees	0.38	0.17	0.05	0.71
	SNA: Bees	-0.01	0.01	-0.02	0.01
iMod-2	Intercept	0.71	0.11	0.50	0.92
	SNA	-0.02	0.01	-0.03	-0.01
	Bees	-0.20	0.13	-0.46	0.06
	SNA: Bees	0.00	0.01	-0.01	0.01
iNO-2	Intercept	-2.08	0.22	-2.54	-1.69
	SNA	0.03	0.01	0.01	0.05
	Bees	0.16	0.14	-0.12	0.44
	SNA: Bees	0.00	0.01	-0.01	0.02

level intensification management through ground herb cover removal and the landscape simplification by land conversion to agriculture) affected plant-floral visitor networks. Moreover, we found frequently an interactive effect between herb cover management with landscape simplification and the quality of floral stands on network topology, meaning that the small-scale and landscape context of the floral stands influence the effect that the herb cover management of each farm has on the networks, although the scale at which this influence works varied with the network metric. We also found that wild bees are the main contributors to plant-floral visitor networks and that to a large extent shape the response of the entire floral visitor network to agricultural intensification.

4.1. Community-wide patterns of variation in network topology in response to agricultural intensification

We expected to find a positive effect of the low-intensity herb cover management on the floral visitor richness as found in similar studies (Bengtsson et al., 2005; Gaspar et al., 2022; Samnegård et al., 2019; Weiner et al., 2014), but in contrast, we did not find any effect. These findings are in line with Cano et al., (2022a), where no effects of herb cover management of olive farms in the same study area on the richness of the entire floral visitor community were detected either. However, both studies are not fully comparable since we here assessed the floral visitor community in floral patches inside the olive crop matrix, unlike Cano et al., (2022a) who conducted the study in floral stands within unmanaged semi-natural patches of the olive grove landscape where the herb cover management is not so evident. The absence of herb management effects could be partly attributed to our active search for relatively rich flowering patches in both intensively and low-intensively managed farms, thereby minimizing apparent differences between the farms. Conducting surveys at random sites within the farm would likely have resulted in stronger differences due to management. However, we dismissed this option in favour of comparing maximums due to the scarcity of flower patches on intensively managed farms. A possible limitation of our conclusion in this regard is that this result may be inconsistent between years, something not explored in a one-year study

such as this one. However, the detection of effects of intensification of landscape and herbaceous cover management despite using floral patches of the highest quality makes it likely that these results are relatively consistent in the face of stochastic between-years variation in climatic conditions (i.e., more or less favorable conditions for plant growth).

The diversity of interactions in the observed networks was lower in intensively managed olive farms, as reported in other studies (e.g., Martínez-Núñez et al., 2019; Olsson et al., 2021). Apart from that, the increase in the diversity of interactions was not dependent on network size. In other words, even after controlling for floral visitor species richness, the interactions are more diverse on olive farms with low-intensity management, as we hypothesized. A possible explanation for this could be that even floral visitor species that behave like specialist foragers can act opportunistically when the availability of rewarding flowering herb species increases (Chittka et al., 1997; Goulson, 1999; Goulson et al., 1997; Waser et al., 2009). Such behaviour would explain the positive relationship detected between floral cover at stand level and the diversity of interactions. This would therefore lead to the construction of more diverse (less specialized) interaction networks in less intensively managed farms than would be expected simply from the increase in floral visitor species.

As expected, low-intensity management in olive farms shaped less specialized plant-floral visitor interaction networks. This trend became more pronounced as the number of herb species increased in the floral stands. Rakosy et al., (2022) also found this pattern for intensively managed grasslands, arguing that this could be due to the functional filtering caused by the intensity of grazing on the herb community. However, our results suggest that it is the overall loss of diversity of interactions on intensively managed farms that causes the increase of  $H_2$  rather than the loss of plants with which they interact in the floral stands. The loss of unique interactions in the networks will result in a greater specificity of those that persist, or in other words, in an increase of the  $H_2$ . On the other hand, while  $H_2$  rises with the increase in herb richness in the floral stands in intensively managed farms, it decreases in low-intensity ones (Fig. 2e). A possible explanation could be the availability and distribution of the floral resources due to the intensity of herb cover management. Floral resources are usually arranged in small stands scattered throughout the matrix of the olive crops, especially in intensively managed olive farms, which causes a local concentration effect on floral visitors, increasing interspecific competition among them, and leading them to specialize their trophic niche (Blüthgen and Klein, 2011). On the contrary, we found the opposite situation in low-intensity farms, so here floral visitor species had more opportunities to interact with more types of flowers since interspecific competition was lower. Specialization was also affected by the proportion of semi-natural areas at the landscape scale (1 km radius buffer), so that specialization in networks decreased as the proportion of semi-natural areas in the olive farms increased. Semi-natural areas here involve flowering shrub species and grasslands, so this pattern could also be caused by a concentration effect of floral visitors in the sampled floral stands when the proportion of semi-natural areas is low in olive farms (Vallejos et al., 2020). Thus, in olive orchards with a lower proportion of semi-natural areas, floral visitors would be more concentrated in the floral stands of the crop matrix, leading them to specialize their trophic niches increasing specialization in the network.

Regarding network architecture, nestedness is one of the most usual properties that arise in mutualistic networks (Bascompte et al., 2003). By contrast, all the interaction networks observed in this study were less nested than expected by chance, suggesting that the assemblage of floral visitor-plant interactions showed high flexibility during the sampling period due to the disturbances to which the olive crop matrix is subjected (mainly mowing and/or ploughing). These disturbances, which also occur in the low-intensity management farms (although less intensive and less recurrent), cause changes in the abundance of floral

resources in the herb cover, leading to the organization and disorganization of the interaction networks over time, thus contributing negatively to nestedness (CaraDonna and Waser, 2020). Moreover, we found that networks became even less nested in intensively managed farms, where the herb cover management is much more aggressive. Since nestedness in networks is supposedly related to a higher resilience (Thébault and Fontaine, 2010) and robustness (Mémott et al., 2004) in plant-pollinator communities, our results suggest that, although the networks here are less nested than expected, the maintenance of the herb cover in olive farms makes them more resistant to environmental disturbances. At the floral stand level, we also detected additive effects of herb richness on nestedness in networks. Theoretically, the addition of herb species should increase the nestedness values, but we observed the opposite trend. It has already been repeatedly found that floral pollinators are able to reduce their niche breadth when floral resources are concentrated at small scales, thus focusing their interactions on fewer plant species (Gómez-Martínez et al., 2022). Therefore, it seems that it is this process that operates at the small scale, thus decreasing the nestedness values in our networks.

Niche overlap of floral visitors was lower than expected by chance. As mentioned for nestedness, the disturbances that occur in the olive crop matrix would result in a reassembly of interactions, and consequently would hinder both nestedness and niche overlap. However, niche overlap in the floral visitor community decreased with the increase in floral richness at stand level since, as previously mentioned, floral visitors can segregate their trophic niches when the diversity of resources is available (Blüthgen and Klein, 2011). Moreover, this is congruent with our findings of the response of network nestedness and  $H_2$  to flowering herb species at the stand level. In addition, the niche overlap of floral visitors also showed a positive response to the proportion of semi-natural areas at the landscape scale. As the response for the specialization at the landscape scale, the concentration effect on the floral stands in olive farms with a low proportion of semi-natural areas could be the reason for this pattern. The narrowing of the trophic niche that occurs when interspecific competition increases as a result of the local concentration of floral visitors in attractive floral stands (Blüthgen and Klein, 2011) would result in a lower degree of niche overlap. This is consistent with the findings for the response of the specialization in networks at this landscape scale since the decrease in specialization would be linked to an increase in the niche overlap.

Modularity analysis revealed that all the networks in our study system showed this topological feature, which is frequent in mutualistic networks (Bascompte and Jordano, 2013). Large-scale landscape context moderated the effect of herb cover management on modularity (that is, the only significant effect on modularity was the interaction between the proportion of semi-natural area and herb cover management), thereby the difference in modularity among different intensities of herb cover management occurs only when the proportion of semi-natural areas was high. In any case, modularity tended to decrease as the proportion of semi-natural areas increased (Fig. 2g). Spiesman and Inouye (2013) also reported the same relationship between landscape simplification and modularity mainly mediated by the species loss. By contrast, in our study, the proportion of semi-natural areas did not affect floral visitor richness, so one possible mechanism for this pattern would be a change in the floral visitor species composition as a result of a greater influence of a large proportion of semi-natural areas surrounding the olive crops, a pattern typically found (e.g., González-Robles et al., 2020). However, in this study, we did not examine the effect of the floral visitor composition on modularity, so it is challenging to find an explanation in this direction. The decrease in the concentration of floral visitors on floral stands as the proportion of semi-natural areas increases could be a more plausible cause for this pattern. Floral visitors are not forced to reduce their trophic niches when the concentration is low (Blüthgen and Klein, 2011), thus the cohesion between modules in networks rises, decreasing the modularity.



Moreover, this is consistent with the patterns obtained for both specialization and niche overlap at a large scale. On the other hand, repeated removal of herbaceous cover in intensively managed olive orchards could be expected to mitigate this decrease in modularity since these disturbances would shorten and stagger the flowering phenology, thus increasing compartmentalization in networks (Martín González et al., 2012). However, we found the opposite, probably because the floral stands that persist under intensive management are dominated by generalist and common (herbicide-tolerant) herb species. Abundant generalist species tend to have a higher degree (number of species to which they interact) in networks, which increases the cohesion between modules (Vázquez et al., 2009), so a floral stand of flowering herbs that becomes more homogeneous would render a decrease in the modularity. The interplay between landscape and herb cover management effects would explain a much more pronounced decrease in the modularity in the intensively managed olive farms in comparison to the low-intensively managed ones as landscape heterogeneity increases.

#### 4.2. Community-wide vs. bee-based networks

Contrary to our expectations, bees shaped, to a large extent, the topology of the plant-floral visitor interaction networks and their response to agricultural intensification in olive grove landscapes. Bees were the most diverse group of floral visitors and accounted for most floral visits and most interactions in these networks (62.9 % of the total interactions). Moreover, the comparison among the responses of the entire floral visitor versus bee network topology to agricultural intensification revealed that they were virtually the same. That is, the community-wide interaction network metrics followed the same trend as the wild bee-based network metrics, so we can attribute the structural properties of the networks to the wild bee assemblage. Jauker et al., (2019) reported similar results when analysing the contribution of hoverflies and wild bees to network structure. As in the mentioned study, we suggest that this is indicative that non-bee species were mostly redundant for the interaction network properties, at least when bees are present. This may be explained by the great foraging flexibility that wild bees can display so that the role of wild bees in preserving the network structure would be filling in the gaps resulting from the loss of species and interactions (Frund et al., 2013; Spiesman and Gratton, 2016) caused by agriculture intensification.

#### 5. Conclusions

In conclusion, this study demonstrates that the promotion of friendly conditions through low-intensity herb cover management positively influences interaction networks within olive groves. Specifically, these conditions contribute to the development and maintenance of complex and robust floral visitor-plant communities. Moreover, some of the interaction network properties were negatively affected by the landscape simplification and the depletion of floral resources in stands, although this effect was smoothed out in olive groves under low-intensity management. Avoiding the removal of herb cover and increasing landscape complexity together with the enhancement of floral stands at the local (small-scale) level (e.g., flower strips) and increasing the landscape complexity on a larger scale, would be key actions that could help to recover and conserve floral visitor communities in this important agro-ecosystem. Monitoring the success of such actions in preserving or improving plant-flower visitor networks can focus on bees (the most common flower visitors in most agroecosystems) since non-bee taxa were redundant in terms of the response of the topological network properties to agriculture intensification when bees are present. These findings underscore the importance of sustainable land management practices in shaping ecological interactions and biodiversity dynamics in agricultural landscapes.

#### CRedit authorship contribution statement

**Pedro José Rey Zamora:** Writing – review & editing, Supervision, Project administration, Investigation, Funding acquisition, Formal analysis, Conceptualization. **María Teresa Salido Ramírez:** Methodology. **Julio Manuel Alcántara Gámez:** Writing – review & editing, Supervision, Investigation, Formal analysis, Conceptualization. **Antonio Jesús Pérez Milla:** Methodology, Data curation. **Carlos Martínez Núñez:** Writing – review & editing, Supervision, Investigation, Formal analysis, Conceptualization. **Domingo Cano:** Writing – review & editing, Writing – original draft, Methodology, Investigation, Formal analysis, Data curation, Conceptualization.

#### Declaration of Competing Interest

Domingo Cano, on behalf of all co-authors, declares that there is no conflict of interest.

#### Data Availability

Data will be made available on request.

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#### Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.agee.2024.109124.

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