

RESEARCH ARTICLE

Functional Ecology



Interacting effects of landscape and management on plant–solitary bee networks in olive orchards

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Abstract

1. Understanding how multi-scale environmental heterogeneity shapes the structure and functions of animal and plant communities is pivotal in agroecology. Our capacity to ensure the provision of ecosystem services (ES), the sustainability of agroecosystems and the efficiency of agri-environmental schemes (AES) relies on this knowledge.
2. There is growing interest in how biodiversity and ES are affected by the interplay between landscape characteristics and agricultural management (e.g., intermediate landscape complexity hypothesis; ILCH). However, studies have typically focused on classical measures of community structure (e.g., species abundance, richness and biodiversity), tending to neglect the effects on the structure and stability of ecological networks and the increased risk of biotic homogenization (i.e., loss of β -diversity).
3. In this work, we use bee trap nests to sample pollen–solitary bee mutualistic networks in 9 pairs of olive groves under different management regimes (conventional vs. organic) in a landscape complexity gradient in southern Spain. We analyse the mutualistic networks at farm level to test the ILCH and study how agricultural practices and landscape complexity interact to affect the properties of these networks. We also explore the effects on spatial biotic homogenization by performing multivariate analyses of the composition and abundance of bee–plant communities and their pairwise interactions.
4. The results show that solitary bee–plant networks have greater complexity and stability on organic olive farms embedded in relatively heterogeneous landscapes. Differences from conventional management were higher in landscapes of intermediate complexity but were non-significant on olive farms located in simpler landscapes. β -diversity of bees, plants and their pairwise interactions was also greater on organic olive farms.
5. In conclusion, human-induced environmental heterogeneity interacts at different scales to shape plant–solitary bee networks in olive groves, which may have important implications for ES provision and the effectiveness of agri-environmental measures.

KEYWORDS

biotic homogenization, landscape structure, mutualistic networks, network complexity, organic farming, plant–pollinator interactions, trap nests, β -diversity

1 | INTRODUCTION

The conversion of natural ecosystems into agricultural farmlands drives a loss of species and their interactions, thereby threatening the function of natural communities and the provision of important ecosystem services (ES; Landis, 2017) such as pollination. It is widely accepted that greater environmental heterogeneity at multiple scales usually enhances biodiversity and ES (Benton, Vickery, & Wilson, 2003). However, the scientific literature typically exploring differences at a single scale—for example, changes in local management methods—often reflects a variety of results (Batáry, Dicks, Kleijn, & Sutherland, 2015). This is relevant because it affects the success of conservation policies aimed at recuperating biodiversity in agroecosystems at individual farm scale (Froidevaux, Louboutin, & Jones, 2017). A good example is European agri-environmental schemes (AES) whose irregular successes and efficiency could be improved (Kaligarič, Čuš, Škornik, & Ivajnsič, 2019).

Some authors have proposed multi-scale approaches aimed at advancing understanding of processes and changing patterns in ecological communities (Moreira, Boscolo, & Viana, 2015). Tscharnkte et al. (2012) proposed eight hypotheses in which landscape complexity could play an important role in moderating the effects of local management on agroecosystems. One of them is the intermediate landscape complexity hypothesis (ILCH), which predicts greater effectiveness of agri-environmental measures at intermediate landscape complexities. Although the ILCH has been validated for certain taxa (including bees) in a number of agroecosystems and grasslands (Concepción et al., 2012), some aspects remain unclear. For instance, how do the studied taxa perceive heterogeneity (Birkhofer et al., 2018; Fahrig et al., 2011)? How do life-history traits and the dynamics of the systems under study (e.g., annual vs. perennial or savannah-like vs. bushy) affect the observed differences? Is the magnitude of the ecological contrast generated by the shifts in agricultural practices important (*sensu* Kleijn, Rundlöf, Scheper, Smith, & Tscharnkte, 2011)? At what scale does heterogeneity operate for a given group of organisms? For instance, Kohler, Verhulst, Van Klink, and Kleijn (2007) found that pollinators only benefitted from semi-natural areas within a radius of 150 m. Some studies have reported different multi-scale interactive effects of heterogeneity on pollinators. In a recent study, Nicholson, Koh, Richardson, Beauchemin, and Ricketts (2018) found that intensive local management and landscape simplification had a synergistically negative effect on pollination services. Likewise, Concepción et al. (2012) showed that bees were more benefitted from good local management in a landscape of intermediate complexity. However, studies trying to disentangle the interactive effects of agricultural management and landscape heterogeneity on pollinators have not yet incorporated interaction networks, which are a powerful tool for understanding ecosystems (Tylianakis & Morris, 2017). When considering the interplay between local practices and landscape, most studies have compared species biodiversity or abundance, even though habitat modification can have an impact on network properties (and therefore system stability) without affecting biodiversity (Tylianakis, Tscharnkte, & Lewis, 2007). Furthermore, many studies have focused on measuring α -diversity despite the fact

that environmental degradation is more likely to affect first community heterogeneity and species turnover (β -diversity) (Santana et al., 2017). Few authors have ever explored the effects of multi-scale heterogeneity gradients on interaction networks (Theodorou et al., 2017) and β -diversity (Gabriel, Roschewitz, Tscharnkte, & Thies, 2006; Moreira et al., 2015).

We conducted a study of the effects of contrasting agricultural management on plant-solitary bee networks in a permanent agroecosystem and tested for the first time the ILCH using a network approach that provides a more integrative and functional perspective. This important theoretical issue will also help answer pressing questions worldwide (Kaiser-Bunbury & Blüthgen, 2015). We used bee trap nests for sampling pollen-solitary bee interactions. Bee trap nests have recently started to be used as an appropriate tool for constructing plant-solitary bee networks (Staab, Pufal, Tscharnkte, & Klein, 2018); they target a very specific guild of pollinators—above-ground cavity-nesting solitary bees—that are good bioindicators of environmental quality as they depend on habitat heterogeneity (natural cavities and foraging resources) to survive (Wood, Holland, & Goulson, 2017). Moreover, their abundance correlates with floral visitation rates, density (Martínez-Núñez et al., unpublished) and the richness (Tscharnkte, Gathmann, & Steffan-Dewenter, 1998) of a wider community of pollinators.

This study was conducted in olive groves, a savannah-like permanent agroecosystem. We chose this system because it is one of the most important agroecosystems in Europe in terms of both socio-economic impact and surface area, and expanding in many temperate areas. Moreover, olive groves are present in many countries in the Mediterranean basin biodiversity hotspot (Medail & Quezel, 1999) and are a vital reservoir of this biodiversity. For instance, a study reported that olive groves can host as many bee species as certain semi-natural areas (Potts et al., 2006); likewise, a recent study found 549 different herb species on 40 olive farms (Rey et al., 2019), most pollinated by insects. Despite their importance for conservation and human societies, savannah-like agroecosystems are still under-represented in the literature.

We built plant-solitary bee networks on 18 paired olive farms with different local management regimes (organic vs. conventional) along a gradient of landscape complexity to test the combined effects of both factors. We hypothesized that (a) the structure of plant-solitary bee networks is better conserved on organic farms (i.e., networks have greater complexity and stability) than on conventional ones; (b) farms in complex landscapes have more complex and stable plant-solitary bee networks; (c) conventional agriculture promotes greater within-farm biotic homogenization (homogeneous communities and their interactions reflected in less β -diversity) than on organic farms; and (d) according to the ILCH, differences in networks due to agricultural management should be maximum in intermediate landscapes.

2 | MATERIALS AND METHODS

2.1 | Study sites and design

This study was conducted in 18 paired olive farms located in Andalucía, South Spain. The nine localities ranged from 5°53'46"W

to 2°64'87"W and 38°40'05"N to 36°78'36"N and represented a convex polygon area of ca. 18.142 km² (for detailed information about the sampled farms and localities, see Table S1 and Figure S1). The olive farms in the same pair shared many characteristics (e.g., size, landscape, locality, climate and other potential confounding factors) but differed in management. One was managed organically, that is no synthetic fertilizers or pesticides and with extensive herb cover; the other was managed conventionally, and synthetic fertilizers, insecticides, herbicides and/or systematic ploughing were employed. Localities were selected along a gradient of landscape complexity based on a single feature of landscape complexity, the percentage of semi-natural habitat cover (SNH). SNH in each locality was estimated within a 2-km radius buffer around the centroid of each pair of farms (organic vs. conventional). We used the most complete and recent land-use cartography for the region (SIOSE <http://www.siose.es>), which was processed using QGIS v.2.14 (QGIS Development Team, 2018) and FRAGSTATS (McGarigal, Cushman, & Ene, 2012). The landscape categories were roughly ascribed to degrees of landscape complexity as in Tscharrntke, Klein, Kruess, Steffan-Dewenter, and Thies (2005): simple (0%–5% SNH), intermediate (6%–20% SNH) and complex (>20% SNH). Although considering only one compositional aspect of landscape complexity might represent an oversimplification, SNH is one of the most straightforward indicators of habitat change and agricultural intensification. It has repeatedly been shown to have an impact on pollinator communities (Holland et al., 2017) and is widely used in studies of pollinators in landscape ecology (Cole, Brocklehurst, Robertson, Harrison, & McCracken, 2017). As well, it has been noted as decisive in the characterization of gradients of complexity in the region's olive grove landscapes (Rey et al., 2019). Nonetheless, we also considered 10 quantitative measures of landscape configuration and composition (in a 1-km radius around each farm) to explore finer landscape effects on network metrics (see Table S3).

2.2 | Sampling and sample processing

We used 96 bee trap nests to sample plant-solitary bee communities. Bee trap nests were chosen because they (a) target a bioindicator group (solitary bees that nest in cavities above-ground) that is highly dependent on environmental heterogeneity, (b) provide an easy and reliable method to detect and sample interactions, and (c) represent a fully standardized sampling method (Staab et al., 2018) previously proven to be applicable in our study system (Martínez-Núñez et al., 2019). On each pair of farms, we placed four or six bee trap nests depending on field size: small (<25 ha but frequently <10 ha) or big (>50 ha but frequently >100 ha), respectively. We placed bee trap nests in different microhabitats inside the farm (olive crop matrix, edges, non-productive areas and patches of semi-natural vegetation). Each nest had 84 nesting cavities and was built from different materials of varying diameters to target a wide community of cavity-nesting pollinators: 40× ca. 9 mm bamboo, 20× ca. 12 mm reed internodes, 20× ca. 15 mm reed internodes and 4× ca. 20 mm reed internodes. We set up nests in March 2017 and collected the colonized material

continuously until November 2017. Samples were opened and larvae individually reared inside plastic tubes at room temperature. Emerged adults were identified to species level. For every cavity colonized, samples of three (whenever possible) different pollen packs were extracted and dyed using fuchsine. Samples were identified under microscope to species or pollen-type level using expert knowledge and the University of Jaén's reference collection (see Lists A and B). In some cases, it was impossible to separate species of the same genera. This was not a drawback since the bees collected are not species-specific foragers and samples can still be compared between sites. Pollen and bee taxa from each cavity were considered an interaction event. We built quantitative mutualistic networks weighted by interaction frequency (i.e., the number of cavities in which two species co-occurred).

We also measured the availability of foraging resources for bees by estimating herb species richness and cover on each farm by monitoring monthly from March to June one 1-m² plot in six or ten 50-m radius permanent plots per farm (depending on field size). Herb species were identified and farm herb richness calculated using Chao's asymptotic estimator (Chao & Colwell, 2014).

2.3 | Network completeness

The comparison of interaction networks across environmental gradients requires equally representative sampling under all conditions. Despite a standardized sampling method, we still checked for network completeness across our environmental gradients to exclude any possible bias. We calculated sampling completeness by dividing the richness of pairwise interactions by Chao's asymptotic estimator of interaction richness (Chacoff et al., 2012). The completeness calculated for each network was used as a response variable and entered into a linear mixed model where management and landscape complexity were fixed factors and locality a random factor. The estimated sample completeness was $59 \pm 22\%$ (mean \pm SD), similar to other plant-pollinator network studies such as the 50% used by Grass, Jauker, Steffan-Dewenter, Tscharrntke, and Jauker (2018). Linear mixed models showed no differences in sampling completeness between management types ($\Delta\text{AIC}_{\text{null}} = 1.64$, $p\text{-value} = .57$, $R^2m = 0.019$), landscape complexities ($\Delta\text{AIC}_{\text{null}} = 3.73$, $p\text{-value} = .89$, $R^2m = 0.013$) or their interaction ($\Delta\text{AIC}_{\text{null}} = 5.32$, $p\text{-value} = .28$, $R^2m = 0.17$).

2.4 | Network indices

We analysed network indices to understand and compare variations in system properties in terms of complexity and stability. First, we explored differences in estimated interaction richness (Chao & Colwell, 2014) and interaction evenness, the two key components of biodiversity that describe system complexity and stability (Tylianakis et al., 2007). Since many studies of network ecology test environmental effects on complexity using the Shannon diversity of interactions (Kaiser-Bunbury et al., 2017), we also took this index into account (standardized using Chao's method). Interaction diversity embraces a richness of information and is a good indicator of functional diversity and system complexity

(Sabatino, Maceira, & Aizen, 2010). We also explored niche overlap, standardized using null models (keeping number of nodes, number of interactions and connectance constant) calculated for bees and plants separately. We considered this index as representative of functional redundancy (Peralta, Frost, Didham, Rand, & Tylianakis, 2017) and network stability (Cusser & Goodell, 2013). Finally, we measured stability through robustness, calculated for bees and plants, to explore vulnerability to secondary extinctions as a consequence of successive random deletions of interacting species (Memmott, Waser, & Price, 2004). Although some authors prefer to analyse robustness by focussing only on its structural component (Kaiser-Bunbury & Blüthgen, 2015), we believe that the number of species and number of interactions are legitimate variables that play an important role in a system's robustness against secondary extinctions. Sampling effort was balanced for the differing management systems and adapted to farm size. In addition, we ascertained that node richness and network completeness did not differ significantly across the gradients of our fixed factors. Hence, we are confident that the results from this unstandardized measure are not affected by a sampling bias. However, we also ran standardized versions of this index, using null models generated with Patefield's algorithm (Patefield, 1981) to explore differences in robustness due to exclusively topological characteristics.

Metric calculation details are given in Table S2. A correlogram showing relationships and potential redundancy between network indices is shown in Figure S4.

2.5 | Statistical analyses

First, we explored differences in both bee species and pollen-type richness in the networks. We calculated the estimated richness of species/pollen types (Chao & Colwell, 2014) for every network at farm scale; we used these richness estimates as a response variable in mixed models (locality as a random factor to account for the paired nature of our field sampling design) and explored the fixed effects of management, landscape complexity and their interactions on pollen types and bee richness.

To compare pollination networks at farm level, we built mutualistic networks by accumulating data from all trap nests on each farm. Once we had deciphered one plant–solitary bee network for each olive farm ($N = 18$), we calculated their indices using the *bi-partite* package (Dormann, Gruber, & Fruend, 2008) in R. Then, we used each of the nine selected indices (detailed above) as dependent variables to run linear mixed-effects models (LMM), with local management (organic vs. conventional), landscape complexity (simple, intermediate or complex) and their interaction as fixed factors. We included locality as a random factor. Models were fitted using maximum likelihood and compared against null models. A simple two-step backward model selection was employed. Our first aim was to test the interaction between landscape complexity and local management regimes. Therefore, the first model considered included both these factors and their interaction. We also considered simpler models with simple main effects. We used Bayesian posteriors and checked for consistency and the stability of the models. For every dependent variable, we simulated 200

datasets generated with the selected model and compared the resulting posterior distributions with the observed (prior) data. We also inspected observed and posterior distributions grouped by the levels of each factor using the *bayesplot* package (developed by Jonah Gabry & Tristan Mahr, 2018).

To explore further possible effects of landscape on network metrics, we also ran polynomial regressions (using linear and quadratic terms) using 10 compositional and configurational quantitative landscape metrics, calculated in a 1-km radius buffer around each farm centroid (Table S3).

We also looked for differences in biotic homogenization at farm scale. To account for β -diversity within farms, we considered a network/assemblage for each bee trap nest ($N = 80$, because 16 were lost, damaged or not colonized). We compared the homogenization of the (a) plant (pollen) community, (b) solitary bee community and (c) bee–plant interactions. We followed Laliberté and Tylianakis (2010) to test for homogenization based on Anderson's method (Anderson, Ellingsen, & McArdle, 2006), a multivariate approximation of Levene's test. We measured multivariate distances between networks on the same farm using the Hellinger algorithm. This method is appropriate for our study because it ignores joint absences, gives less weight to rare species/interactions and focuses on relative rather than absolute differences in abundances (Legendre & Gallagher, 2001). We ran a principal coordinate analysis (PCoA) using the Hellinger distances between each pair of trap nests (for pollen community, bee community and their pairwise interactions) and calculated the distances in the multivariate space of each network (trap nest) to the farm centroid. We used distances to the farm centroid as a new dependent variable and ran LMM with 'locality' and 'farm' as random factors to test whether or not the interaction of landscape and local management—or any of these factors alone—could explain differences in the distances to centroid. To test for homogenization of bee–plant interactions, first we introduced into the model the distances of bees and plant communities to remove possible noise due to community composition. Hellinger's index consists of a number between 0 and 1; thus, we used arcsine square root transformation and ran linear models instead of the generalized variation for binomial variables. This decision was based on the goodness-of-fit. The inspection of the residuals confirmed that models met the assumptions.

To explore differences in foraging resource availability, we ran LMM for herb species richness estimates and LMM for the arcsine square root-transformed percentage of herb cover, using management, landscape complexity and their interaction as predictors and locality/farm as random factors.

Lastly, to check that the geographical dispersion of sampling units was not driving the observed differences, we followed the previous method and tested the homogeneity of distances to farm centroid across management types, landscapes and their interactions ($AIC_{\text{null}} < AIC_{\text{candidate model}}$, $p > .3$ in all cases) using Euclidean distances between pairs of geographic coordinates.

All statistical analyses were run using R, version 3.5.1 (R Core Team, 2018).

TABLE 1 Summary of items collected, pollen types, bee species, number and richness of interactions found in all sampled conditions

Local Management	Landscape complexity	Number of items collected	Pollen types	Bee species	Number of interactions (cumulative)	Number of different interactions
All	All	831	70	13	2,185	280
Organic	All	437	66	11	1,145	235
Conventional	All	395	53	11	1,040	156
Organic	Simple	138	38	8	332	115
Conventional	Simple	125	37	9	448	128
Organic	Intermediate	192	44	7	512	153
Conventional	Intermediate	173	39	9	413	91
Organic	Complex	107	49	8	301	123
Conventional	Complex	96	31	5	179	73

3 | RESULTS

A total of 70 pollen types, belonging to 23 different plant families and more than 40 plant genera, were identified (List A). Mean pollen-type richness per farm was 20 ± 8 (mean \pm SD; range: 5–33) and was slightly higher on organic farms (23 ± 8) than on conventional farms (18 ± 7). Thirteen cavity-nesting pollinator bee species from the family Megachilidae belonging to five different genera (*Anthidium*, *Heriades*, *Hoplitis*, *Megachile* and *Osmia*) were identified (List B). Mean farm bee richness was 4 ± 2 (range: 2–8). In organic and conventional orchards, the means were 4 ± 2 and 4 ± 1 , respectively. The 13 bee species interacted 2,185 times with the plant species, giving 280 different types of interactions. Models comparing bee and pollen richness between conditions showed no significant differences ($AIC_{\text{null}} < AIC_{\text{candidate model}}$ in all cases), which indicates that the richness (size) of the networks did not drive the patterns observed in their structure. Table 1 shows the number of items collected, number of pollen types identified, bee species, cumulative number of interactions and different types of interactions found per condition (Local Management * Landscape complexity).

The assessment of resource availability showed that organic farms had higher herb species richness than conventional farms ($t_{(8)} = 3.17$, $p = .013$; predicted mean \pm 1 SE: 72 ± 6.4 vs. 46 ± 6.4) and a higher percentage of herb cover in groves ($t_{(86)} = 10.21$, $p = .000$; 86 ± 0.05 on organic vs. 49 ± 0.05 conventional farms), thereby indicating that the shift in agricultural practices probably generates an important ecological contrast for solitary bees.

3.1 | Study of network parameters

Overall, the estimated Shannon diversity of interactions was higher in organic olive orchards (LMM; $t_{(9)} = 3.472$, $p = .007$), but this relationship depended on landscape complexity. At landscape level, interaction diversity was greater on farms embedded in intermediate landscapes (LMM; $t_{(9)} = 2.095$, $p = .066$). This latter pattern was even clearer for the evenness of interactions, which increased on organic farms of intermediate landscape complexity (LMM; $t_{(9)} = 3.829$,

$p = .009$) but decreased on conventional farms in intermediate landscapes (LMM; $t_{(9)} = -2.916$, $p = .015$). Networks had higher interaction richness on organic farms surrounded by complex landscapes (LMM; $t_{(9)} = 3.136$, $p = .020$).

Metrics for individual trophic levels showed that bees had a higher niche overlap in organic groves of intermediate landscape complexity (LMM; $t_{(12)} = 3.465$, $p = .005$). In addition, plant communities were more robust and less vulnerable to bee extinctions, although only in organic groves in intermediate landscapes (LMM; $t_{(9)} = 2.475$, $p = .048$) due to a loss of robustness on conventional farms in landscapes of intermediate complexity (driven by a steep decrease in interaction richness, see Table 1). Table 2 shows that the variances explained by most models were high. Results from the relevant models are plotted in Figure 1 and summarized in Table 2. Bipartite networks corresponding to each farm are illustrated in Figure S2 (organic farms) and Figures S3 (conventional farms).

Patterns for bee and plant standardized robustness and plant niche overlap were not satisfactorily explained by our models (worse than null models and/or with no significant terms) and are not reported for simplicity. Plots comparing the observed data and Bayesian posterior distributions were overall acceptable. Prior and posterior means did not differ significantly (Figure S5).

Polynomial regressions showed that farms surrounded by landscapes with a large dominant patch tended to host networks with lower diversity and evenness of interactions. High edge density slightly increased the diversity of interactions; interaction richness was higher in farms surrounded by landscapes with an intermediate mean patch area (see Table S3).

3.2 | Biotic homogenization

The analysis of the biotic homogenization (i.e., decrease in β -diversity) revealed that conventional olive groves were more homogenous than their organic counterparts in all three dimensions analysed (Figure 2). Plant communities became on average 17% more heterogeneous when switching to organic farming (LMM; $t_{(75)} = 3.410$,

TABLE 2 Summary of linear mixed models explaining variation in network metrics

Model	Terms	Estimate	SE	z-value	p-value	R ² M	R ² C
Shannon interaction diversity	Intercept	3.480	0.216	16.100	<.000	0.41	0.71
	Organic	0.172	0.213	0.809	.439		
	Intermediate L.	−0.467	0.306	−1.528	.148		
	Complex L.	−0.202	0.306	−0.662	.519		
	Organic: Intermediate L.	0.631	0.301	2.095	.066		
	Organic: Complex L.	0.424	0.301	1.409	.192		
Interaction evenness	Intercept	0.961	0.014	66.421	<.000	0.47	0.67
	Organic	0.023	0.016	−1.421	.205		
	Intermediate L.	−0.060	0.020	−2.916	.015		
	Complex LC	0.000	0.020	0.016	.987		
	Organic: Intermediate L.	0.088	0.023	3.829	.009		
	Organic: Complex L.	0.024	0.023	1.048	.335		
Interaction richness	Intercept	75.878	20.226	3.752	.005	0.25	0.72
	Organic	−15.688	17.538	−0.895	.405		
	Intermediate L.	4.227	28.603	0.148	.886		
	Complex L.	−43.945	28.603	−1.536	.160		
	Organic: Intermediate L.	12.731	24.802	0.513	.626		
	Organic: Complex L.	77.775	24.802	3.136	.020		
Niche overlap (bees)	Intercept	0.944	0.544	1.734	.108	0.48	0.48
	Organic	−1.403	0.770	−1.822	.093		
	Intermediate L.	−1.510	0.770	−1.961	.073		
	Complex L.	0.044	0.770	0.057	.956		
	Organic: Intermediate L.	3.774	1.089	3.465	.005		
	Organic: Complex L.	0.140	1.089	0.129	.900		
Robustness (plants)	Intercept	0.909	0.027	33.616	<.000	0.29	0.68
	Organic	0.002	0.026	0.069	.947		
	Intermediate L.	−0.063	0.038	−1.650	.133		
	Complex L.	−0.030	0.038	−0.787	.451		
	Organic: Intermediate L.	0.090	0.036	2.475	.048		
	Organic: Complex L.	0.031	0.036	0.868	.419		

Note: Models were fitted using maximum likelihood, considering local management (organic or conventional), landscape complexity (simple, intermediate or complex) and their interaction as fixed effects. Locality was used in the models as a random factor, and Conventional-Simple was the intercept. R² shows the marginal (M) and conditional (C) explained variance.

Bold values show significant differences for $\alpha < .1$.

$p = .003$, $R^2m = 0.12$, $R^2c = 0.32$). Bee assemblages were 27% more heterogeneous in plots on organic farms (LMM; $t_{(75)} = 1.801$, $p < .090$, $R^2m = 0.10$, $R^2c = 0.59$). Finally, the β -diversity of interactions was also higher (15%) on organic compared with conventional farms (LMM; $t_{(75)} = 2.420$, $p = .040$, $R^2m = 0.15$, $R^2c = 0.49$), even after accounting for variation in bee and plant communities (LMM; $t_{(75)} = 2.363$, $p = .031$, $R^2m = 0.16$, $R^2c = 0.49$).

The addition of the interaction term between local management and landscape complexity did not improve the models for the β -diversity of bees, pollen loads or bee–pollen interactions ($\Delta AIC < 2$, $p > .1$ in all cases). This indicated that farms under organic management had assemblages of solitary bees–pollen loads that were spatially more heterogeneous in all landscapes.

4 | DISCUSSION

4.1 | Effects of local farm management on plant–solitary bee network complexity and stability

As expected, overall organic farming increased the diversity of interactions and promoted the complexity and stability of pollen–solitary bee networks in olive groves. Although bee species richness did not decrease on conventional farms, the richness of the pollen types transported to the bee trap nests did decrease slightly (but not clearly; see Table 1). Interestingly, differences in the diversity of interactions diminished disproportionately according to differences in the richness of pollen loads (Table 1), which suggests that the loss of interaction diversity is not linked to community composition and that there is

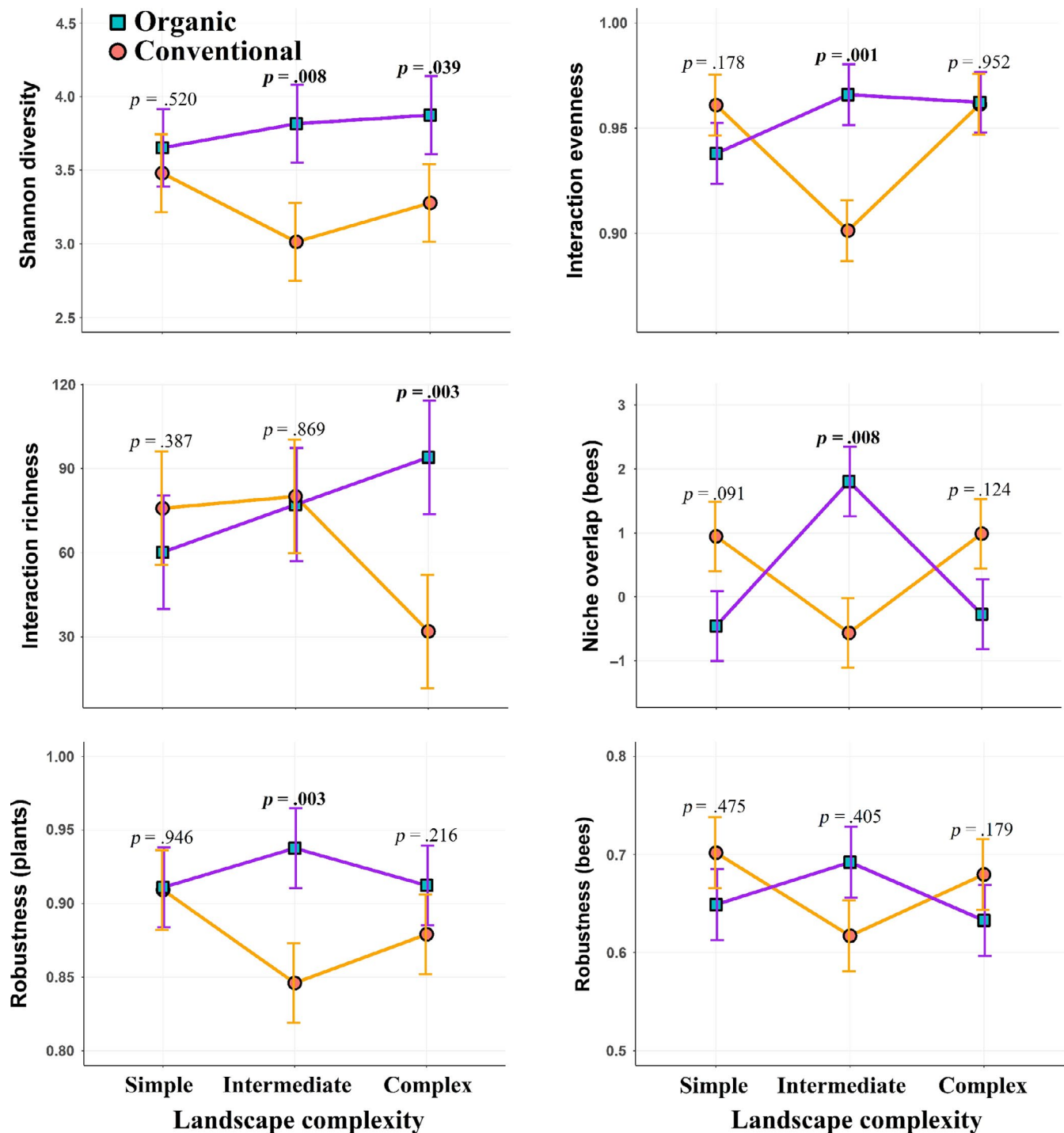


FIGURE 1 Predicted means (mean \pm 1 SE) after linear mixed effect models for the interaction network metrics. *p*-Values show comparisons between management across landscapes (slice test)

a nonlinear loss of functionality with the loss of plant species. This might be due to unsuccessful foraging by bees in intensive conventional olive groves as a consequence of decreased floral availability, a hypothesis that is supported by our results for herb richness and herb cover. Carman and Jenkins (2016) report the same pattern for native bees in disturbed habitats.

The plant community pollinated by these bees was more robust to bee extinctions on organic olive farms, which indicates

greater stability and resilience to perturbations. The fact that standardized robustness (removing the effect of network size and number of interactions) did not show the same pattern suggests that observed differences are due to a richer community and a higher density of links. Our study agrees with Winfree et al. (2018) since in general, more complex networks (e.g., with more diversity of interactions) were also more robust to secondary extinctions.

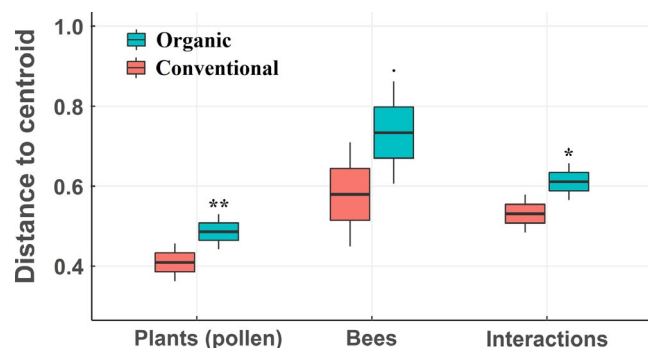


FIGURE 2 Differences in multivariate distance to centroid (β -diversity) between traps within groves under different management types. Mean \pm 1 SE, whiskers represent confidence intervals (95%). Significant differences between groups shown by $p < .1$ (.), $p < .05$ (*), $p < .01$ (**)

The patterns found in our networks are mainly resource-mediated. The diversity of interactions and complexity are limited by plant species, as seen in tropical systems (Hagen & Kraemer, 2010), and confirmed by our results regarding floral resource availability. This suggests a bottom-up disturbance effect triggered by intensive herb-cover management. Parallel patterns have been reported in other systems. For instance, Vollstädt et al. (2018) found that interaction diversity in seed-dispersal networks increased with fruit diversity and availability.

In a related study, Power and Stout (2011) concluded that organic farming benefits insect-flower pollination networks on dairy farms. However, more studies addressing the impact of different agricultural practices on plant-pollinator interaction networks are still needed before generalized conclusions can be drawn.

4.2 | Fine-grained landscape configuration affects interaction diversity and stability in olive grove plant-solitary bee networks

There were no patterns in networks linked only to landscape heterogeneity, measured as the percentage of semi-natural habitat at locality scale (2-km radius around the centroid of each pair of farms). However, configurational landscape measures calculated at smaller scales (1-km radius around each farm centroid) did reveal interesting patterns. Landscapes dominated by a large patch and low edge density had less interaction diversity and evenness. Similar patterns have been found in other systems, suggesting that edge density and landscape heterogeneity could be very important for conserving pollinators (Hass, Kormann, et al., 2018). Interestingly, landscapes with intermediate mean patch size had greater diversity and richness of interactions, probably because these landscapes possess more natural areas, unlike landscapes dominated by olive groves or other types of highly anthropic fragmented landscapes. To date, most published studies report a positive relationship between landscape complexity and network stabilizing properties (reviewed by Ferreira, Boscolo, & Viana, 2013). For instance, Hass, Liese, et al. (2018) studied the effect of different land uses on pollination networks, concluding that

agroforests were beneficial for pollination networks in rice-dominated landscapes. Likewise, Schrader, Franzén, Sattler, Ferderer, and Westphal (2018) report that plant-pollinator networks were more complex in sites surrounded by complex habitats.

4.3 | Conventional agriculture in olive groves promotes the homogenization of plant-solitary bee networks

We confirmed that organic management in olive groves increased the heterogeneity of bees, pollen-load types and their interactions at farm scale. Local management and landscape complexity have frequently been linked to an increase in species β -diversity in agroecosystems. Gabriel et al. (2006) found that β -diversity explained most of the variance in species richness at both meso- and macroscales. Studies of biotic homogenization consistently show how environmental simplification under different systems and scales leads to a loss of β -diversity in terms of species richness. For example, Rey et al. (2019) showed that landscape simplification diminished both the β -multi-diversity and β -diversity of birds in landscapes dominated by olive groves. Likewise, intensification caused a loss of β -diversity in plants (Gabriel et al., 2006) and butterflies (Ekroos, Heliölä, & Kuussaari, 2010) in other agroecosystems. Biotic homogenization by agricultural management, land conversion and deforestation may be more insidious; it may occur at species richness level and also affect previously ecosystem functions by modifying biotic interactions and the structure of interaction networks (Valiente-Banuet et al., 2014). Thus, Laliberté and Tylianakis (2010) showed that deforestation homogenized parasitoid-host interactions in coffee plantations and grasslands in Central America. Kehinde and Samways (2014) reported biotic homogenization of insect-flower interaction networks in vineyards in South Africa. We report similar results for plant-pollinator systems in olive groves. We also warn of the consequences that the homogenization of pollination interactions might have for bees, wild and cultivated plants in intensively managed olive-dominated landscapes in southern Spain.

4.4 | Landscape complexity moderates the effects of agriculture intensification on plant-solitary bee networks

We found that for most network indices, organic and conventional farms located in simpler and in more complex landscapes did not differ significantly. Nonetheless, differences between agricultural management types for solitary bee-plant networks were strong in intermediate landscapes and drove the overall pattern found in organic versus conventional local management. Therefore, our general results support the idea that landscape complexity moderates the effects of local agricultural management (Tscharntke et al., 2012). Concepción et al. (2012) reported the same results for bee species richness in an extensive study of arable fields and grasslands in six European countries. Scheper et al. (2013) ratified these outcomes in a meta-analysis that supports the ILCH for pollinators and pollination ecosystem services. Our study

complements this work by showing how the effectiveness of agricultural extensification for improving plant-solitary bee network complexity (interaction diversity and evenness) and stability (niche overlap and robustness) could be maximized in intermediate landscapes. Although our results coincide with the ILCH in a final analysis, different mechanisms may underlie these patterns. The ILCH predicts a theoretical nonlinear increase in biodiversity or ecosystem function with increasing landscape complexity up to a saturation threshold in intermediate-to-complex landscapes. Such a threshold is reached sooner along the landscape complexity gradient in organic than in intensively managed systems (Concepción et al., 2012). Nevertheless, we found no increase across the landscape complexity gradient but maximum differences between management types in intermediate landscapes. This pattern might be explained by a combination of resource availability (nesting and foraging resources) and habitat use preference. Foraging resources (driven by management) might be more important for solitary bees in intermediate landscapes because in simpler landscapes they are rather limited by other factors such as nesting resources or anthropic disturbances. By contrast, more complex landscapes provide both foraging and nesting resources, and bees use these habitats preferentially, spilling over into agricultural areas with similar (but relatively low) frequencies.

Few studies have explored the multi-scale effects of heterogeneity on plant-pollinator networks. Moreira et al. (2015) reported an improvement in plant-pollinator network stability with increasing heterogeneity at different scales, which especially affects nestedness. Theodorou et al. (2017) emphasized the key positive effects of local environments for plant-pollinator interactions. Overall, our study supports the need to include information about landscape complexity in future work. Moreover, our results suggest that it might not be possible to counteract the effects of landscape simplification on solitary bee-pollen networks merely with good local agricultural management (i.e., organic management) if we do not previously conserve or restore an appreciable level of SNH cover in the landscape mosaic, as previously shown in hymenopteran-based food webs (Fabian et al., 2013). This task should not be difficult because even small amounts of natural vegetation provide great benefits for pollinators and the plants they forage (Sabatino et al., 2010). A study has experimentally demonstrated how ecosystem restoration (removal of exotic shrubs) benefits pollination networks (Kaiser-Bunbury et al., 2017). In olive groves, possible and successful solutions could be the enrichment of field margins (Rands & Whitney, 2011) and the leaving of unproductive areas with local woody and herb species on farms (see also Rey et al., 2019).

5 | CONCLUSIONS

The analysis of solitary bee-plant interaction networks enables us to conclude that on olive farms, (a) organic management favours more complex and stable plant-solitary bee networks; (b) landscape complexity moderates the effects of local management by maximizing

differences at intermediate complexities; and (c) conventional farms homogenize bee and plant communities, and their pairwise interactions, thereby diminishing β -diversity. Therefore, we urge the conversion to organic farming (especially efficient in intermediate-to-complex landscapes) and adoption of landscape heterogenization measures, particularly needed in simple landscapes as help efficient conversion to organic farming. These policies will also ensure the structure, stability and function of plant-solitary bee networks and preserve their spatial heterogeneity in permanent savannah-like agroecosystems in general and in olive groves in particular.

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AUTHORS' CONTRIBUTIONS

C.M.-N., P.J.R. and A.J.M. conceived the ideas, designed the methodology, analysed the data and led the writing of the manuscript; C.M.-N., S.L., A.J.P. and L.R.-V. collected the data and identified the samples. All authors contributed critically to the final version of the manuscript and gave final approval for its publication.

DATA AVAILABILITY STATEMENT

Data that support these results are available in the Mendeley Data repository <http://dx.doi.org/10.17632/2m3y6z53y3.1> (Martínez et al. 2019).

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REFERENCES

- Anderson, M. J., Ellingsen, K. E., & McArdle, B. H. (2006). Multivariate dispersion as a measure of beta diversity. *Ecology Letters*, 9(6), 683–693. <https://doi.org/10.1111/j.1461-0248.2006.00926.x>
- Batáry, P., Dicks, L. V., Kleijn, D., & Sutherland, W. J. (2015). The role of agri-environment schemes in conservation and environmental management. *Conservation Biology*, 29(4), 1006–1016. <https://doi.org/10.1111/cobi.12536>
- Benton, T. G., Vickery, J. A., & Wilson, J. D. (2003). Farmland biodiversity: Is habitat heterogeneity the key? *Trends in Ecology & Evolution*, 18(4), 182–188. [https://doi.org/10.1016/S0169-5347\(03\)00011-9](https://doi.org/10.1016/S0169-5347(03)00011-9)

- Birkhofer, K., Andersson, G. K. S., Bengtsson, J., Bommarco, R., Dänhardt, J., Ekblom, B., ... Smith, H. G. (2018). Relationships between multiple biodiversity components and ecosystem services along a landscape complexity gradient. *Biological Conservation*, 218, 247–253. <https://doi.org/10.1016/j.biocon.2017.12.027>
- Carman, K., & Jenkins, D. G. (2016). Comparing diversity to flower-bee interaction networks reveals unsuccessful foraging of native bees in disturbed habitats. *Biological Conservation*, 202, 110–118. <https://doi.org/10.1016/j.biocon.2016.08.030>
- Chacoff, N. P., Vázquez, D. P., Lomáscolo, S. B., Stevani, E. L., Dorado, J., & Padrón, B. (2012). Evaluating sampling completeness in a desert plant-pollinator network. *Journal of Animal Ecology*, 81(1), 190–200. <https://doi.org/10.1111/j.1365-2656.2011.01883.x>
- Chao, A., & Colwell, R. K. (2014). Rarefaction and extrapolation with Hill numbers: A framework for sampling and estimation in species diversity studies. *Ecological Monographs*, 84(1), 45–67. <https://doi.org/10.1890/13-0133.1>
- Cole, L. J., Brocklehurst, S., Robertson, D., Harrison, W., & McCracken, D. I. (2017). Exploring the interactions between resource availability and the utilisation of semi-natural habitats by insect pollinators in an intensive agricultural landscape. *Agriculture, Ecosystems & Environment*, 246, 157–167. <https://doi.org/10.1016/j.agee.2017.05.007>
- Concepción, E. D., Díaz, M., Kleijn, D., Báldi, A., Batáry, P., Clough, Y., ... Verhulst, J. (2012). Interactive effects of landscape context constrain the effectiveness of local agri-environmental management. *Journal of Applied Ecology*, 49(3), no-no. <https://doi.org/10.1111/j.1365-2664.2012.02131.x>
- Cusser, S., & Goodell, K. (2013). Diversity and distribution of floral resources influence the restoration of plant-pollinator networks on a reclaimed strip mine. *Restoration Ecology*, 21(6), 713–721. <https://doi.org/10.1111/rec.12003>
- Dormann, C. F., Gruber, B., & Freund, J. (2008). Introducing the bipartite Package: Analysing ecological networks. *R News*, 8(2), 8–11.
- Ekroos, J., Heliölä, J., & Kuussaari, M. (2010). Homogenization of lepidopteran communities in intensively cultivated agricultural landscapes. *Journal of Applied Ecology*, 47(2), 459–467. <https://doi.org/10.1111/j.1365-2664.2009.01767.x>
- Fabian, Y., Sandau, N., Bruggisser, O. T., Aebi, A., Kehrl, P., Rohr, R. P., ... Bersier, L.-F. (2013). The importance of landscape and spatial structure for hymenopteran-based food webs in an agro-ecosystem. *Journal of Animal Ecology*, 82(6), 1203–1214. <https://doi.org/10.1111/1365-2656.12103>
- Fahrig, L., Baudry, J., Brotons, L., Burel, F. G., Crist, T. O., Fuller, R. J., ... Martin, J.-L. (2011). Functional landscape heterogeneity and animal biodiversity in agricultural landscapes. *Ecology Letters*, 14(2), 101–112. <https://doi.org/10.1111/j.1461-0248.2010.01559.x>
- Ferreira, P. A., Boscolo, D., & Viana, B. F. (2013). What do we know about the effects of landscape changes on plant-pollinator interaction networks? *Ecological Indicators*, 31, 35–40. <https://doi.org/10.1016/J.ECOLIND.2012.07.025>
- Froidevaux, J. S. P., Louboutin, B., & Jones, G. (2017). Does organic farming enhance biodiversity in Mediterranean vineyards? A case study with bats and arachnids. *Agriculture, Ecosystems & Environment*, 249, 112–122. <https://doi.org/10.1016/J.AGEE.2017.08.012>
- Gabriel, D., Roschewitz, I., Tscharnke, T., & Thies, C. (2006). Beta diversity at different spatial scales plant communities in organic and conventional agriculture. *Ecological Applications*, 16(5), 2011–2021. [https://doi.org/10.1890/1051-0761\(2006\)016\[2011:BDADSS\]2.0.CO;2](https://doi.org/10.1890/1051-0761(2006)016[2011:BDADSS]2.0.CO;2)
- Grass, I., Jauker, B., Steffan-Dewenter, I., Tscharnke, T., & Jauker, F. (2018). Past and potential future effects of habitat fragmentation on structure and stability of plant-pollinator and host-parasitoid networks. *Nature Ecology & Evolution*, 2(9), 1408–1417. <https://doi.org/10.1038/s41559-018-0631-2>
- Hagen, M., & Kraemer, M. (2010). Agricultural surroundings support flower-visitor networks in an Afrotropical rain forest. *Biological Conservation*, 143(7), 1654–1663. <https://doi.org/10.1016/j.biocon.2010.03.0361417>; <https://doi.org/10.1038/s41559-018-0631-2>
- Hass, A. L., Kormann, U. G., Tscharnke, T., Clough, Y., Baillod, A. B., Sirami, C., ... Batáry, P. (2018). Landscape configurational heterogeneity by small-scale agriculture, not crop diversity, maintains pollinators and plant reproduction in western Europe. *Proceedings of the Royal Society B: Biological Sciences*, 285(1872), 20172242. <https://doi.org/10.1098/rspb.2017.2242>
- Hass, A. L., Liese, B., Heong, K. L., Settele, J., Tscharnke, T., & Westphal, C. (2018). Plant-pollinator interactions and bee functional diversity are driven by agroforests in rice-dominated landscapes. *Agriculture, Ecosystems & Environment*, 253, 140–147. <https://doi.org/10.1016/J.AGEE.2017.10.019>
- Holland, J. M., Douma, J. C., Crowley, L., James, L., Kor, L., Stevenson, D. R. W., & Smith, B. M. (2017). Semi-natural habitats support biological control, pollination and soil conservation in Europe. A review. *Agronomy for Sustainable Development*, 37(4), 31. <https://doi.org/10.1007/s13593-017-0434-x>
- Kaiser-Bunbury, C. N., & Blüthgen, N. (2015). Integrating network ecology with applied conservation: A synthesis and guide to implementation. *AoB Plants*, 7, plv076. <https://doi.org/10.1093/aobpla/plv076>
- Kaiser-Bunbury, C. N., Mougil, J., Whittington, A. E., Valentin, T., Gabriel, R., Olesen, J. M., & Blüthgen, N. (2017). Ecosystem restoration strengthens pollination network resilience and function. *Nature*, 542(7640), 223–227. <https://doi.org/10.1038/nature21071>
- Kaligarič, M., Čuš, J., Škornik, S., & Ivajnšič, D. (2019). The failure of agri-environment measures to promote and conserve grassland biodiversity in Slovenia. *Land Use Policy*, 80, 127–134. <https://doi.org/10.1016/j.landusepol.2018.10.013>
- Kehinde, T., & Samways, M. J. (2014). Effects of vineyard management on biotic homogenization of insect-flower interaction networks in the Cape Floristic Region biodiversity hotspot. *Journal of Insect Conservation*, 18(3), 469–477. <https://doi.org/10.1007/s10841-014-9659-z>
- Kleijn, D., Rundlöf, M., Scheper, J., Smith, H. G., & Tscharnke, T. (2011). Does conservation on farmland contribute to halting the biodiversity decline? *Trends in Ecology & Evolution*, 26(9), 474–481. <https://doi.org/10.1016/J.TREE.2011.05.009>
- Kohler, F., Verhulst, J., Van Klink, R., & Kleijn, D. (2007). At what spatial scale do high-quality habitats enhance the diversity of forbs and pollinators in intensively farmed landscapes? *Journal of Applied Ecology*, 45(3), 753–762. <https://doi.org/10.1111/j.1365-2664.2007.01394.x>
- Laliberté, E., & Tylianakis, J. M. (2010). Deforestation homogenizes tropical parasitoid-host networks. *Ecology*, 91(6), 1740–1747. <https://doi.org/10.1890/09-1328.1>
- Landis, D. A. (2017). Designing agricultural landscapes for biodiversity-based ecosystem services. *Basic and Applied Ecology*, 18, 1–12. <https://doi.org/10.1016/j.baae.2016.07.005>
- Legendre, P., & Gallagher, E. D. (2001). Ecologically meaningful transformations for ordination of species data. *Oecologia*, 129(2), 271–280. <https://doi.org/10.1007/s004420100716>
- Martínez, C., Manzaneda, A. J., Lendínez, S., Pérez, A. J., Ruiz-Valenzuela, L., & Rey, P. J. (2019). Data for: Interacting effects of landscape and management on plant-solitary bee networks in olive orchards (Functional Ecology), Mendeley Data, v1. <http://dx.doi.org/10.17632/2m3y6z53y3.1>
- Martínez-Núñez, C., Manzaneda, A. J., Isla, J., Tarifa, R., Calvo, G., Molina, J. L., ... Rey, P. J. (2019). Low-intensity management benefits solitary bees in olive groves. *Journal of Applied Ecology*, 1365–2664, 13511. <https://doi.org/10.1111/1365-2664.13511>
- McGarigal, K., Cushman, S. A., & Ene, E. (2012). FRAGSTATS v4: Spatial Pattern Analysis. Program for Categorical and Continuous Maps. Amherst, MA: University of Massachusetts.

- Medail, F., & Quezel, P. (1999). Biodiversity hotspots in the Mediterranean basin: Setting global conservation priorities. *Conservation Biology*, 13(6), 1510–1513. <https://doi.org/10.1046/j.1523-1739.1999.98467.x>
- Memmott, J., Waser, N. M., & Price, M. V. (2004). Tolerance of pollination networks to species extinctions. *Proceedings of the Royal Society of London. Series B: Biological Sciences*, 271(1557), 2605–2611. <https://doi.org/10.1098/rspb.2004.2909>
- Moreira, E. F., Boscolo, D., & Viana, B. F. (2015). Spatial heterogeneity regulates plant-pollinator networks across multiple landscape scales. *PLoS ONE*, 10(4), e0123628. <https://doi.org/10.1371/journal.pone.0123628>
- Nicholson, C. C., Koh, I., Richardson, L. L., Beauchemin, A., & Ricketts, T. H. (2018). Farm and landscape factors interact to affect the supply of pollination services. *Agriculture, Ecosystems & Environment*, 250, 113–122. <https://doi.org/10.1016/j.agee.2017.08.030>
- Patefield, W. M. (1981). Algorithm AS 159: An efficient method of generating random $R \times C$ tables with given row and column totals. *Applied Statistics*, 30(1), 91. <https://doi.org/10.2307/2346669>
- Peralta, G., Frost, C. M., Didham, R. K., Rand, T. A., & Tylianakis, J. M. (2017). Non-random food-web assembly at habitat edges increases connectivity and functional redundancy. *Ecology*, 98(4), 995–1005. <https://doi.org/10.1002/ecy.1656>
- Potts, S. G., Petanidou, T., Roberts, S., O'Toole, C., Hulbert, A., & Willmer, P. (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>
- Power, E. F., & Stout, J. C. (2011). Organic dairy farming: Impacts on insect-flower interaction networks and pollination. *Journal of Applied Ecology*, 48(3), 561–569. <https://doi.org/10.1111/j.1365-2664.2010.01949.x>
- QGIS Development Team. (2018). QGIS Geographic Information System. Open Source Geospatial Foundation Project. <http://qgis.osgeo.org>
- R Core Team. (2018). R: A language and environment for statistical computing. Vienna, Austria: R Foundation for Statistical Computing. <http://www.R-project.org/>
- Rands, S. A., & Whitney, H. M. (2011). Field margins, foraging distances and their impacts on nesting pollinator success. *PLoS ONE*, 6(10), e25971. <https://doi.org/10.1371/journal.pone.0025971>
- Rey, P. J., Manzaneda, A. J., Valera, F., Alcántara, J. M., Tarifa, R., Isla, J., ... Ruiz, C. (2019). Landscape-moderated biodiversity effects of ground herb cover in olive groves: Implications for regional biodiversity conservation. *Agriculture, Ecosystems & Environment*, 277, 61–73. <https://doi.org/10.1016/j.agee.2019.03.007>
- Sabatino, M., Maceira, N., & Aizen, M. A. (2010). Direct effects of habitat area on interaction diversity in pollination webs. *Ecological Applications*, 20(6), 1491–1497. <https://doi.org/10.1890/09-1626.1>
- Santana, J., Porto, M., Reino, L., Moreira, F., Ribeiro, P. F., Santos, J. L., ... Beja, P. (2017). Using beta diversity to inform agricultural policies and conservation actions on Mediterranean farmland. *Journal of Applied Ecology*, 54(6), 1825–1835. <https://doi.org/10.1111/1365-2664.12898>
- Scheper, J., Holzschuh, A., Kuussaari, M., Potts, S. G., Rundlöf, M., Smith, H. G., & Kleijn, D. (2013). Environmental factors driving the effectiveness of European agri-environmental measures in mitigating pollinator loss - a meta-analysis. *Ecology Letters*, 16(7), 912–920. <https://doi.org/10.1111/ele.12128>
- Schrader, J., Franzén, M., Sattler, C., Ferderer, P., & Westphal, C. (2018). Woody habitats promote pollinators and complexity of plant-pollinator interactions in homegardens located in rice terraces of the Philippine Cordilleras. *Paddy and Water Environment*, 16(2), 253–263. <https://doi.org/10.1007/s10333-017-0612-0>
- Staab, M., Pufal, G., Tscharntke, T., & Klein, A.-M. (2018). Trap nests for bees and wasps to analyse trophic interactions in changing environments-A systematic overview and user guide. *Methods in Ecology and Evolution*, 9(11), 2226–2239. <https://doi.org/10.1111/2041-210X.13070>
- Theodorou, P., Albig, K., Radzevičiūtė, R., Settele, J., Schweiger, O., Murray, T. E., & Paxton, R. J. (2017). The structure of flower visitor networks in relation to pollination across an agricultural to urban gradient. *Functional Ecology*, 31(4), 838–847. <https://doi.org/10.1111/1365-2435.12803>
- Tscharntke, T., Gathmann, A., & Steffan-Dewenter, I. (1998). Bioindication using trap-nesting bees and wasps and their natural enemies: Community structure and interactions. *Journal of Applied Ecology*, 35, 708–719. <https://doi.org/10.1046/j.1365-2664.1998.355343.x>
- Tscharntke, T., Klein, A. M., Kruess, A., Steffan-Dewenter, I., & Thies, C. (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>
- Tscharntke, T., Tylianakis, J. M., Rand, T. A., Didham, R. K., Fahrig, L., Batáry, P., ... Westphal, C. (2012). Landscape moderation of biodiversity patterns and processes - eight hypotheses. *Biological Reviews*, 87(3), 661–685. <https://doi.org/10.1111/j.1469-185X.2011.00216.x>
- Tylianakis, J. M., & Morris, R. J. (2017). Ecological networks across environmental gradients. *Annual Review of Ecology, Evolution, and Systematics*, 48(1), 25–48. <https://doi.org/10.1146/annurev-ecolsys-110316-022821>
- Tylianakis, J. M., Tscharntke, T., & Lewis, O. T. (2007). Habitat modification alters the structure of tropical host-parasitoid food webs. *Nature*, 445(7124), 202–205. <https://doi.org/10.1038/nature05429>
- Valiente-Banuet, A., Aizen, M. A., Alcántara, J. M., Arroyo, J., Cocucci, A., Galetti, M., ... Zamora, R. (2014). Beyond species loss: The extinction of ecological interactions in a changing world. *Functional Ecology*, 29(3), 299–307. <https://doi.org/10.1111/1365-2435.12356>
- Vollstädt, M. G. R., Ferger, S. W., Hemp, A., Howell, K. M., Böhning-Gaese, K., & Schleuning, M. (2018). Seed-dispersal networks respond differently to resource effects in open and forest habitats. *Oikos*, 127(6), 847–854. <https://doi.org/10.1111/oik.04703>
- Winfrey, R., Reilly, J. R., Bartomeus, I., Cariveau, D. P., Williams, N. M., & Gibbs, J. (2018). Species turnover promotes the importance of bee diversity for crop pollination at regional scales. *Science*, 359(6377), 791–793. <https://doi.org/10.1126/science.aao2117>
- Wood, T. J., Holland, J. M., & Goulson, D. (2017). Providing foraging resources for solitary bees on farmland: Current schemes for pollinators benefit a limited suite of species. *Journal of Applied Ecology*, 54(1), 323–333. <https://doi.org/10.1111/1365-2664.12718>

SUPPORTING INFORMATION

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