


Low-intensity management benefits solitary bees in olive groves

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Abstract

1. One of the current challenges for applied ecologists is to understand how to manage/restore agroecosystems in a sustainable and cost-effective way. The intermediate landscape complexity hypothesis (ILCH) predicts that the effectiveness of agri-environmental measures (AES) on biodiversity and ecosystem services recovery is often largest in landscapes of intermediate complexity. This hypothesis has rarely been tested in savanna-like permanent agroecosystems.
2. Focusing on pollinators, we test the ILCH at the regional scale in Mediterranean olive orchards, one of the most important permanent agroecosystems in the world. We inferred abundance of cavity-nesting pollinators in 40 paired olive orchards (extensively vs. intensively managed herbaceous cover) in 20 localities selected across a landscape complexity gradient. We also studied how different magnitudes in local management switches may affect pollinators by considering organic and intensive fields as management extremes in olive orchards. We used 208 trap nests for solitary bees to measure colonization rates. Additionally, we conducted pollinator surveys to ascertain that colonization rate was a representative proxy for pollinator activity.
3. Our results showed that (a) changes in colonization rates due to local herb cover management peaked at intermediate landscape complexity, with extensively managed fields rendering higher colonization rates. (b) Organic fields had higher colonization rates than their control farms regardless of landscape complexity. (c) There was a highly significant correlation between nest colonization rates and density of pollinators foraging on flowers, which suggests that colonization rate is a good estimator of pollinator activity.
4. *Policy implications.* The maintenance of ground herb cover (main agri-environmental measure in olive orchards) is a cost-effective investment allowing recuperation of pollinators when targeting olive farms located in landscapes of intermediate complexity. Additionally, fostering organic farming (still minority in olive groves) for the conservation of solitary bees should be a priority for policymakers since its effects are beneficial in any landscape.

KEYWORDS

AES, intermediate landscape complexity hypothesis, landscape complexity, management contrast, olive groves, organic farming, solitary bees, trap nests

1 | INTRODUCTION

Intensive agriculture is a major contributor to declines in pollinators and jeopardizes pollination service provisioning in agricultural and natural systems (Potts et al., 2010). Among insects, wild solitary bees are a very important group of pollinators. They are taxonomically and functionally diverse and are efficient pollinators of many plant species (Garibaldi et al., 2013). The value of diverse solitary bee communities is becoming increasingly clear as scientists acknowledge that pollination cannot rely on a single species, such as the domesticated honeybee (Garibaldi et al., 2013). Hence, the conservation of solitary bees is key to ensure consistent pollination services (Winfree et al., 2018). This goal is not, however, easy to achieve because solitary bees are particularly sensitive to agricultural intensification (Winfree, 2010) and the loss of foraging and nesting resources in extremely simplified farmlands (Wood, Holland, & Goulson, 2017).

Restoration methods (i.e., active or passive measures aimed to recuperate biodiversity) can be implemented in agroecosystems to benefit pollinators with, overall, good results (e.g., Barral, Rey Benayas, Meli, & Maceira, 2015). For instance, bee trap nests (also called bee hotels) have frequently been effectively used as a restoration tool to increase the number of cavities available for cavity-nesting pollinators (Dainese et al., 2018). Also, the provision of floral resources by semi-natural areas, field margins or extensive plant cover management is a common measure to ameliorate habitats for pollinators (Cole, Brocklehurst, Robertson, Harrison, & McCracken, 2017). The European agri-environmental schemes (AES) provide financial support to incentivize actions that enhance the sustainability and ecosystem services (ES) provision in farmlands (e.g. payments for switching from intensive to extensive plant cover management).

Considering only changes in local management (e.g. extensification of ground herb cover management) have shown contradictory outcomes on biodiversity and ecosystem services (Tschardt et al., 2016). Thus, the effectiveness of subsidies focused on farm scale only, like AES, has been questioned (Batáry et al., 2010). To explain these inconsistencies in the outcomes, other factors, such as socio-cultural framework or landscape complexity context, have gained attention over the last decade (Garratt, Senapathi, Coston, Mortimer, & Potts, 2017).

Tschardt et al. (2012) proposed that local restoration actions or shifts to agri-environmental management (i.e. AES) would maximize the biodiversity and ES gain when targeted areas are located in intermediate landscape complexity (termed Intermediate Landscape Complexity Hypothesis; ILCH hereafter). This is because the surrounding patches (e.g., semi-natural habitats) may provide a considerable amount of biodiversity by spillover, that would be very limited

in simpler landscapes. In contrast, in highly complex landscapes, spillover would occur even in the absence of restoration practices, overcoming the effects of local management.

Studies aiming to understand how local and landscape components impact biodiversity and ES are still very scarce in the Mediterranean basin, an area considered a hotspot of biodiversity (Marchese, 2015). To our knowledge, no study has tested ILCH in a permanent savanna-like agroecosystem, such as olive tree orchards (see Froidevaux, Louboutin, & Jones, 2017 for vineyards, permanent non-savanna-like agroecosystems). Olive orchards are the most widespread and socioeconomically important permanent crop in Europe and the Mediterranean region (<https://ec.europa.eu/eurostat/statistics-explained/>). The structural complexity and stability of this agroecosystem confers strong potential for biodiversity conservation (Rey et al., 2019). Efforts to strategically improve biodiversity in olive orchards would likely increase the ES provided in extensive areas. Olive orchards have a significant potential to be the habitat for numerous pollinator and plant species (Potts et al., 2006), but few studies have focused on pollinators in this cropland, particularly in the context of landscape heterogeneity or agricultural management variation (but see Tschudin, Neokosmidis, Petanidou, & Settele, 2011). Olive trees are pollinated by wind, but pollinators sustain wild plant communities that deliver key ecosystem services such as preventing soil erosion, contributing to control pest species and crop diseases or providing natural soil fertilization (Palese et al., 2014; Paredes, Cayuela, & Campos, 2013).

Here, we aim to test the ILCH, quantifying the relative benefit to pollinators by extensification of the ground herb cover management. That is, whether maintaining plant cover in the orchards (the most common AES in olive agriculture) over most of the year (compared to their persistent removal by herbicides or mechanical means) is most beneficial to pollinators in landscapes of intermediate complexity. Kleijn, Rundlöf, Scheper, Smith, and Tschardt (2011) hypothesized that different magnitudes in local management switches—for example, contrast in only herb cover maintenance versus contrast in herb cover plus no application of pesticides and fertilizers as in organic farming—mediate the effectiveness of AES to recover biodiversity and ecosystem services. Therefore, we not only examine the moderating effects of landscape regarding changes in herb cover management (extensive vs. intensive) but also explore the differences between organic extensive (a further step in extensification) and intensive practices, which represent two extremes of olive crop management.

We collected a robust and unique dataset at the regional scale across southern Spain (Andalucía). We sampled 40 paired olive farms in 20 localities of olive cultivation (one olive farm under extensive vs. another under intensive herb cover management per locality)

distributed along a wide landscape complexity gradient. We adopt a novel approach using data from cavity occupation in trap nests and validating it with pollinator surveys to test the following predictions. (a) The difference in colonization rates between extensive and intensive practices is maximized in localities with intermediate landscape complexity. (b) Nests have higher colonization rates in organic fields compared to intensive fields, regardless of landscape complexity. (c) Pollinator foraging activity is closely correlated with colonization rates in nests, proving that this measurement can be used as a proxy for pollinator activity.

2 | MATERIALS AND METHODS

2.1 | Study sites and study design

This study was carried out in 2017, in Andalucía (southern Spain). We sampled 40 olive farms covering altogether a cultivated area of circa 35 km². The sampled farms ranged from 5°53'46"W to 2°6'48"W and 38°40'05"N to 36°7'836"N (ca. 28.000 km²). The 40 farms were situated in 20 localities embedded in a gradient of different landscape complexity (Figure 1). ILCH is typically tested through paired designs using farms under different managements surrounded by the same landscape (Rey et al., 2019). Hence, in each study locality, a pair of olive orchards with different herb cover managements (extensive vs. intensive) was selected (see details on study sites in Table S1). Mean distance between localities was 105.5 ± 61.3 km (mean ± 1SD), ranging from 2.8 km to 310 km. Mean distance between paired olive farms at the same locality was 1,461 ± 796 m (mean ± 1SD), with only one pair ('Gascón') separated by less than 0.5 km (specifically, 335 m). Given the restricted dispersal of these solitary bees (Zurbuchen et al., 2010), the study localities and the paired orchards within each locality, can be considered to a large extent independent for solitary bee abundance and nest colonization.

Extensively managed orchards maintain natural herbaceous cover most of the year, before eventually removing vegetation in late spring by grazing or mowing. Conversely, intensive management involves the persistent removal of herbs by using herbicides (pre- and post-emergence) and/or ploughing the field several times per year. In addition, 10 out of the 20 extensive farms were managed according

to organic guidelines (extensive cover management plus no use of pesticides nor synthetic fertilizers) while their 10 respective paired farms were managed intensively (use of pesticides and inputs of synthetic fertilizers). In one location (Cañada del Duz), both orchards had extensive herb cover management but only one was organic.

2.2 | Bee trap nests

Bee trap nests were used to assess colonization rates and sample the community of solitary wild bees nesting inside above-ground cavities. Since different cavities are able to support a large diversity of cavity-nesting bees (Dainese et al., 2018), we built bee trap nests (208 in total) using three different materials and six cavity diameters, providing a total of 104 nesting cavities per nest (Figure S1). In each farm, four to six nests (depending on farm size) were set in March, matching the period of activity in the phenology of these solitary bees and the flowering plants they pollinate (Molina & Bartomeus, 2019, and authors' personal observation). Bee trap nests were set in different microhabitats (i.e. olive orchard matrix, non-productive areas, edges and small semi-natural patches) to sample as much variability as possible within each farm. Trap nest colonization was monitored monthly, from April to September. Colonization rate was calculated counting the number of cavities occupied during the sampling period.

2.3 | Pollinator surveys

Bee trap nests are used only by a specialized guild of pollinators, so we linked cavity-nesting pollinator data with pollinator activity by relating colonization rates to density of foraging pollinators assessed through in situ surveys. Pollinator surveys were conducted in thirty-two 10-m² flowering patches belonging to 8 different localities and 16 farms (two patches per farm). Twenty-two of these patches were close (<200 m) to 30 randomly chosen bee trap nests (at least one in each farm). Solitary bees have relatively limited foraging ranges (Zurbuchen et al., 2010), thus these last patches were used to link colonization rates to pollinator abundance and activity in the flowering patches. Also, we related mean infield foraging activity (pooling every survey conducted in the farm) with mean colonization rates

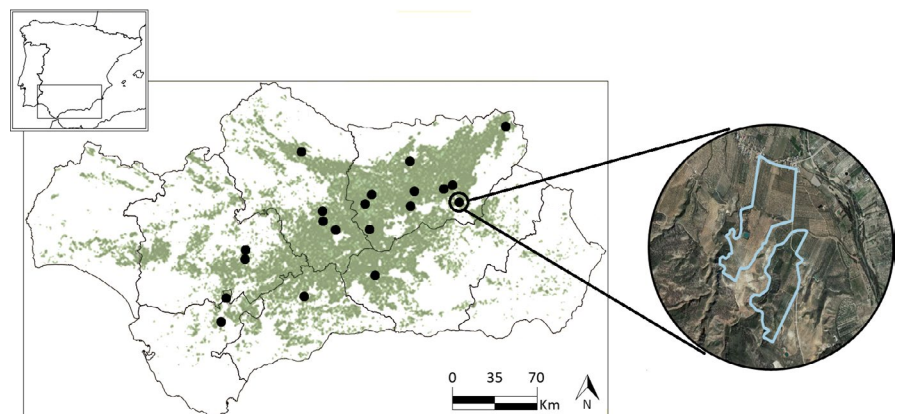


FIGURE 1 Map of Andalucía showing the 20 sampled localities (black dots) and the pair of farms sampled in each locality (right augmented view). Green area shows occurrence of olive orchards in Andalucía

(pooling information from all trap nests) at the farm scale. This enabled us to explore whether management or farm conditions can also explain correlation between foraging activity and colonization rates.

Surveys consisted of two 15-min rounds (30 min total) doing focal observations on pollinator visits in standardized patches of *Sinapis alba* (L.). We selected this species because it blooms in early spring (when we set the bee trap nests and 95% of the final colonization was observed), attracts many pollinator species and is abundant in olive orchards. It has also ecological and economic importance (Alcántara, Pujadas, & Saavedra, 2011). *Sinapis alba* decreases soil erosion, prevents diseases in olive trees (e.g. verticilosis) and is used for biofuel production (Jaime, Alcántara, Manzaneda, & Rey, 2018). In each farm, we selected the two biggest patches of *S. alba*, most frequently ca. 10–15 m². In these patches, five 1-m² plots were selected and the total open flowers counted. In each plot we recorded the abundance of active pollinators contacting floral reproductive structures and the number of flowers contacted during 3 min. From these observations we calculated pollinator density (number of active pollinators per flower unit). Observations were conducted between 11:30 hr (around 3 hr after sunrise) and 17:00 hr in sunny days, with a temperature of >15°C and a wind speed < 5 km/hr. Combining data from surveys and colonization rates allowed us to assess whether this variable was a representative proxy for pollinator foraging activity (i.e. higher colonization rates means more pollinators are active).

2.4 | Foraging resources

To explore how different managements affect foraging resources for bees, we quantified herb species richness and cover in each olive farm. We conducted monthly surveys from March to June. Herb species richness was evaluated in four or six 1-m² plots (depending on farm size) embedded each in a 100-m² square from which we visually estimated the herb cover (percentage). Herb species were identified, and richness estimated at the farm scale using the Chao's method, extrapolating to the double the minimum sample size (i.e., 8 units) (as recommended by Chao & Colwell, 2014).

2.5 | Landscape complexity assessment

The 20 study localities were initially classified into 'low', 'intermediate' and 'high' landscape complexity categories based on visual inspection of the localities in the field and ortho-images (Figure S2). As described in Rey et al. (2019), this perceptual classification was corroborated using metrics of landscape compositional (five indices: land use or patch richness, diversity, evenness, percentage of semi-natural habitat cover and percentage of olive groves in the landscape) and configurational heterogeneity (seven indices: proportion of the total landscape occupied by the largest patch; edge density of the mean patch; mean patch area; shape of the mean patch; Euclidean distance between nearest neighbour patches of similar uses; contagion and interspersed/juxtaposition index) (Fahrig et al., 2011). These metrics were derived from the most recent and complete land

use cartography of the region (SIOSE, <http://www.siose.es>) and were recorded considering 2-km radius circular buffer centred between the two paired farms of each locality and calculated with QGIS v.2.14 (QGIS Development Team, 2018) and FRAGSTATS software (McGarigal et al., 2012). Classification and Regression trees analyses (CART, De'ath & Fabricius, 2000) confirmed that 3 of the 12 metrics—semi-natural land cover (*cobnat*), mean patch size area (*pa*) and nearest neighbour distance between patches of same use (*NND*)—correctly classified the 100% of study localities as perceptually defined. Simple landscapes were characterized by low representation of natural habitat (*cobnat* < 9%), intermediate landscapes by *cobnat* larger than 9% (except one with 8.7% of *cobnat* that segregated from simple ones by *pa* > 7.5 ha) and *NND* higher than 85 m, and complex landscapes by *cobnat* larger than 9% and a mosaic of uses with *NND* < 85 m (further details in Rey et al., 2019). Quantitative landscape metrics are provided in Mendeley data archive (<https://doi.org/10.17632/dchz48kfbh.1>) associated with Rey et al. (2019).

2.6 | Statistical analysis

Our experimental design may potentially confound the effects of organic versus intensive management with the effects of extensive versus intensive ground herb cover management. To solve this, we analysed three sets of data (Figure S3): (a) the whole dataset (extensive vs. intensive ground herb cover management), (b) 10 non-organic extensive versus their intensive pair farms, and (c) 10 organic extensive farms and their intensive pairs.

Management effects on foraging resource availability were tested using linear mixed effects models (LMM) with herb species richness and percentage of herb cover (arcsine square root transformed) as response variables, management as predictor and locality as a random blocking factor.

To test the effect of agricultural management and landscape complexity on colonization rates, we fitted generalized linear mixed effects models (GLMM). The explanatory variables were herb cover management (extensive/intensive; non-organic extensive/intensive or organic extensive/intensive, depending on the dataset used) and landscape complexity, with locality incorporated as a random blocking factor. Response variable (Colonization rate) was treated as a proportion, and consequently models were run with binomial error distribution and logit link function. Models suffered overdispersion, thus we also included an observation level random effect factor (OLRE) (Harrison, 2015). We ascertained that patterns observed in extensive versus intensive comparisons (dataset a, detailed above) were not caused by the effect of the 10 organic extensive versus intensive pairs by controlling for the effect of 'organic' (i.e. entering the term first in the model). Subsequently, we reran the tests separately for each subset (b and c, detailed above). In all these analyses, candidate models were compared against null models (model including only random terms) via ANOVA, using Δ AIC to assess the validity of each candidate model. Valid models were analysed to identify significant terms. Model assumptions were checked by inspection of residuals.

Because landscape heterogeneity may also be considered as continuous rather than categorical, we further conducted linear and quadratic regressions (general linear models) to analyse separately the influence of each continuous landscape metrics on colonization rates at the farm (1 km radius) and locality scale (2 km radius). Linear and quadratic terms were incorporated in these regressions to explore the possibility of nonlinear relationships.

To test whether colonization rates at trap nest (number of cavities colonized in spring) and farm level (mean colonization rate averaged across all trap nests of the farm over the season) are a good proxy for pollination density, we ran Spearman's rank correlation tests between the colonization rate and variables obtained from pollinator surveys conducted during March–April, at close-to-nest patches and farm level respectively.

Analyses were run with R v.3.4.3 (R Core Team, 2013) using the packages: 'lme4' (Bates, Mächler, Bolker, & Walker, 2015), 'INEXT' (Hsieh, Ma, & Chao, 2016), 'DHARMA' and 'GGPLOT2' (Wickham, 2016).

3 | RESULTS

Nest occupation ranged between 3% and 33% (22% mean) among olive farms and was strongly biased towards wood material and small-medium size cavities (see Table S2). We found 15 species of pollinators, belonging to 5 different genera of the family Megachilidae (see List S1 for species and keys consulted).

Estimated herb richness ranged between 18 and 89 (mean of 49) and herb cover between 5%–80% (mean of 29%) in olive farms. Herb richness ($\Delta AIC_{NULL} = 10$; $t_{(36)} = 4.074$, $p < .000$; effect size: 18.8 ± 4.3 species of difference in predicted means ± 1 SE) and especially cover ($\Delta AIC_{NULL} = 57$; $t_{(205)} = 11.06$, $p < .000$; effect size: 0.28 ± 0.03 , as proportion) were higher in extensive than in intensive herb management (whole dataset). The comparison with the subset of 10 non-organic extensive versus 10 intensively managed (excluding the organic

extensive vs. intensive pairs) rendered quasi-significant results for richness ($\Delta AIC_{NULL} = 2.2$; $t_{(16)} = 2.17$, $p = .058$; effect size: 10.0 ± 4.8) and significant effects for cover ($\Delta AIC_{NULL} = 43$; $t_{(101)} = 7.5$, $p < .000$; effect size: 0.22 ± 0.03). As expected, such differences were even higher when comparing the 10 organic extensive versus their 10 intensive pairs (for richness, $\Delta AIC_{NULL} = 7.7$; $t_{(16)} = 3.87$, $p = .003$; effect size 27.6 ± 6.0 ; for cover, $\Delta AIC_{NULL} = 70$; $t_{(101)} = 10.4$, $p < .000$; effect size 0.34 ± 0.04).

Overall colonization rates responded positively to extensive herb cover management (Tables 1 and 2; Models CR-1, CR-3 and CR-4), although the response depended clearly on landscape complexity context (Tables 1 and 2; Model CR-3 and CR-4). Differences in colonization rates in response to different local herb cover management peaked at intermediate landscape complexity, while farms located in landscapes with low or high complexity did not exhibit clear differences in colonization rates (Figure 2). Switching to extensive management in intermediate landscape complexity would increase colonization rates more than 80%. Both models CR-4 (Tables 1 and 2) and CR-2-ExO (a model with subset b: excluding the olive farm pairs that have an organic extensive farm member, Tables S3 and S4) showed that the pattern found in the comparison of extensive versus intensive management is not driven by the 10 organic farms.

Organic management positively affected colonization rates (Figure 3, Tables 1 and 2; Model CR-1-O). The effect of organic management on colonization rates was not significantly moderated by landscape complexity (Table 1; Model CR-1-O has significant smaller AIC than Model CR-2-O; i.e., $\Delta AIC > 2$). Thus, bee trap nests placed in organic farms had greater colonization rates than those placed in intensive farms, in all landscapes. A change from non-organic to organic management provided a mean increase of 53% in colonization rates. Relatively low values of R^2 (Table 1) for all the models suggest that most variability occurs at farm/bee trap nest scales. For completeness, we included the estimates for all the valid models (better than null) in Table S4.

TABLE 1 Generalized linear mixed models for colonization rates (CR). Section A corresponds to models fitted using the whole dataset (40 paired farms). Section B, models fitted using only organic farms and their intensive pairs (20 paired farms). Locality and bee nest entered the models as random factors. LC = Landscape complexity. *P*-value indicates significant differences between a model and the null model (attending to ΔAIC). Significant terms at $p < .05$ appear in bold

| Model code | Fixed factors | AIC | df | Deviance | <i>p</i> -value | R ² m | R ² c |
|--------------------------------------|--------------------------------|-------|-----|----------|-----------------|------------------|------------------|
| (a) Whole dataset | | | | | | | |
| CR-Null | None | 1,618 | 199 | 1,612 | – | | |
| CR-1 | Herb management | 1,614 | 198 | 1,606 | .019 | 0.005 | 0.226 |
| CR-2 | Landscape Complexity | 1,621 | 197 | 1,611 | .642 | 0.004 | 0.226 |
| CR-3 | Herb management * LC | 1,610 | 194 | 1,593 | .003 | 0.018 | 0.226 |
| CR-4 | Organic + Herb management * LC | 1,610 | 193 | 1,592 | .002 | 0.020 | 0.226 |
| (b) Subset: organic versus intensive | | | | | | | |
| CR-Null-O | None | 816 | 98 | 810 | – | | |
| CR-1-O | Organic management | 807 | 97 | 799 | <.001 | 0.017 | 0.234 |
| CR-2-O | Organic * Landscape Complexity | 810 | 93 | 795 | .297 | 0.044 | 0.234 |

| Model code | Terms | Estimate | SE | z-value | p-value |
|---|--|----------|-------|---------|-------------|
| (a) Whole dataset | | | | | |
| CR-3 | Intercept (HM intensive, LC low) | -1.289 | 0.256 | -5.032 | 0 |
| | HM (extensive) | -0.262 | 0.212 | -1.232 | .218 |
| | LC (intermediate) | -0.508 | 0.346 | -1.436 | .151 |
| | LC (High) | -0.568 | 0.372 | -1.529 | .126 |
| | HM (extensive): LC (Intermediate) | 0.992 | 0.286 | 3.467 | 0 |
| | HM (extensive): LC (high) | 0.546 | 0.301 | 1.813 | .069 |
| CR-4 | Intercept (HM intensive, LC low, O no) | -1.305 | 0.252 | -5.182 | 0 |
| | O (yes) | 0.334 | 0.221 | 1.51 | .131 |
| | C (extensive) | -0.315 | 0.214 | -1.471 | .141 |
| | LC (intermediate) | -0.49 | 0.347 | -1.408 | .16 |
| | LC (High) | -0.554 | 0.365 | -1.519 | .13 |
| | HM (extensive): LC (Intermediate) | 0.846 | 0.3 | 2.82 | .005 |
| | HM (extensive): LC (high) | 0.374 | 0.32 | 1.189 | .242 |
| (b) Subset: organic versus intensive farming | | | | | |
| CR-1-O | Intercept (not organic) | -1.686 | 0.228 | -7.388 | 0 |
| | Organic management | 0.534 | 0.158 | 3.392 | 0 |

TABLE 2 Estimates for best models. Sections A and B as in Table 1. O = Organic Management, HM = Herb cover Management, LC = Landscape Complexity. Significant terms at $p < .05$ are in bold

Analyses of the variation in colonization rates according to the 12 quantitative landscape heterogeneity metrics measured at 1 km radius (farm scale) and 2 km radius (locality scale) showed that no single landscape metric influenced colonization rates (Table S5).

Colonization rate at the trap nest level was correlated with the density of foraging pollinators (Figure 4a) recorded during the censuses (Spearman's rank correlation: = 0.56; $p = .001$; $N = 30$). Moreover, at farm scale, mean occupation was correlated with the density of active foraging pollinators recorded with censuses (Figure 4b) (Spearman's rank correlation: = 0.55; $p = .03$; $N = 15$). No correlation was found with absolute number of flowers contacted or absolute number of active pollinators.

4 | DISCUSSION

4.1 | Verifying the intermediate landscape complexity hypothesis

The main results from this study concur with the general trends observed for annual crops and support the ILCH in permanent savanna-like agroecosystems. We recorded a strong interaction between landscape complexity and herb cover management on pollinators, in olive orchards. The fields embedded in intermediate-complexity landscapes benefited most from extensive herb management. This is a clear case where landscape complexity can determine the effectiveness of AES in relatively stable orchards. Given this result,

we suggest that AES implementation (extensification of ground herb cover management) in olive groves should be prioritized in areas with intermediate landscape complexity. Our results also show that local measures of extensification of herb cover management should be accompanied by strategies seeking to increase landscape heterogeneity in extremely simple landscapes. Our results agree with studies conducted in other agroecosystems (see review by Scheper et al., 2013), including perennial ones. For instance, Nicholson, Koh, Richardson, Beauchemin, and Ricketts (2017) found in highbush blueberry plantations that landscape simplification interacted with intensive local management to provide less pollination service. However, contradictory results are still found (Batáry, Baldi, Kleijn, & Tschardtke, 2011). Contradictions may arise from pollinator-specific response to microenvironmental heterogeneity (Garratt et al., 2017); differences among studies in the focal groups of pollinators, which would respond differently to landscape or local variables due to distinct functional traits (De Palma et al., 2015); differences in the landscape complexity metric used in each particular study and in its range of variation; and/or the relative attractiveness of the floral resources of semi-natural and olive field patches that may vary considerably with the landscape context.

Limited availability of cavities and foraging resources combined could explain our results. Our data suggest that floral resource availability (shown by higher herb cover and richness in extensive management) is not the primary limiting factor for cavity-nesting bees in landscapes with low and high complexity (Figure 2). In

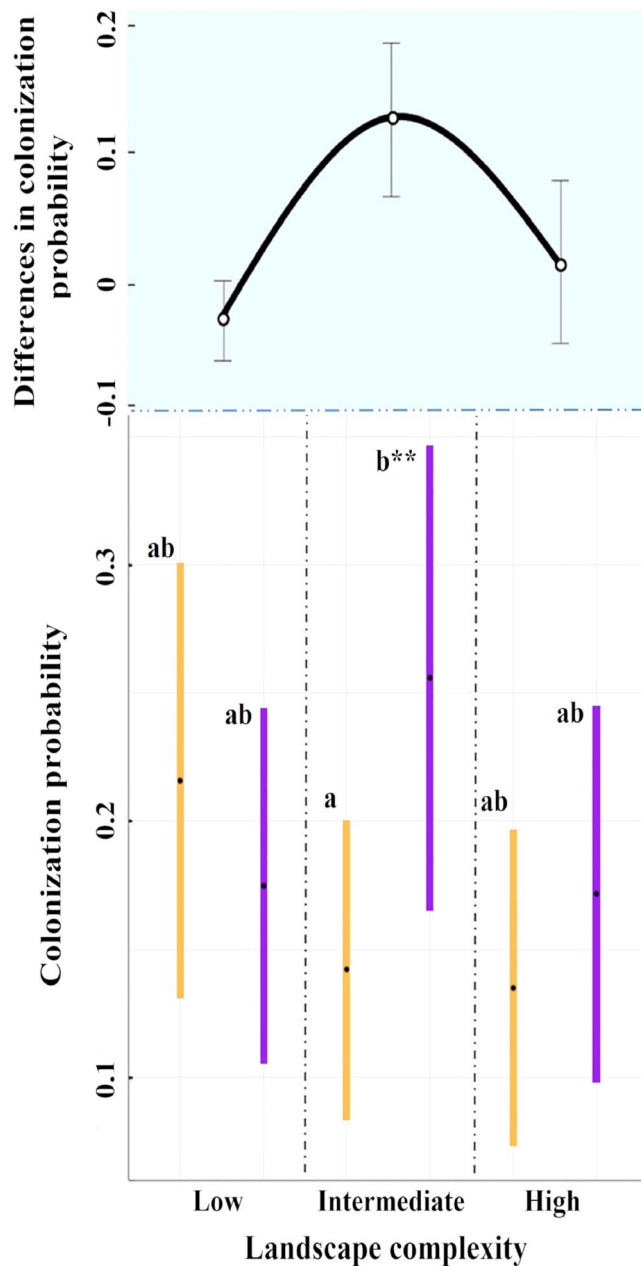


FIGURE 2 Differences in probability of colonization between paired farms with different herb cover managements (Extensive–Intensive) along a gradient of landscape complexity (whole dataset considered). Predicted means and 95% confidence intervals are plotted. Letters show group assigned after post hoc Tukey's test. $**p < .01$. Orange colour depicts intensive management and purple colour extensive management

very simple landscapes bees might be limited primarily by natural cavities for nesting (e.g. wood, hollow stems, etc.), justifying adding bee trap nests in many agricultural systems to increase cavity availability (Maclvor, 2017). In highly complex landscapes, solitary bees are likely not limited by lack of floral resources or nesting sites. Therefore, adding floral resources via extensive management has little effect as bees spillover to agricultural areas from natural habitats where they forage and nest preferentially. In intermediate landscape

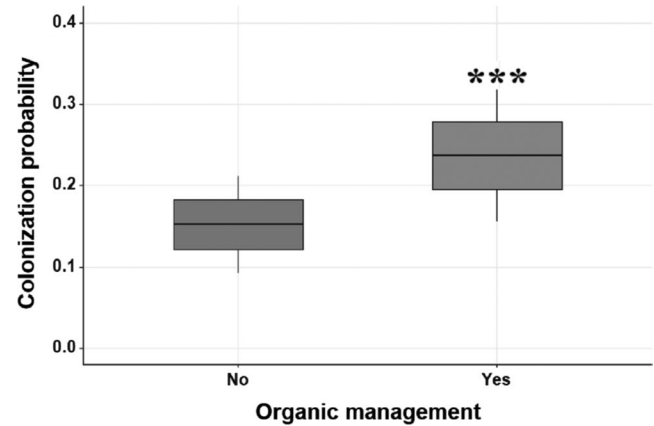


FIGURE 3 Differences in probability of cavity colonization by solitary bees between the 10 farms with organic management and their 10 corresponding intensive pairs. Mean \pm 1 SE. Vertical lines show CI (95%). $***p < .001$ generalized linear mixed effects models (GLMM)

complexity, cavity-nesting bees seem to have enough cavities but might be limited by foraging resources and thus are more dependent on herb cover management, driving the pattern observed in our results.

We did not find a significant effect of quantitative nor categorized metrics of landscape heterogeneity alone. This result seems to contradict some postulates of the ILCH that expect higher biodiversity and ES in intermediate to complex landscapes compared to simple ones (Tscharntke et al., 2012). Inconsistent results are, however, reported in literature. For example, Breitbach et al., (2012) found in wild cherries that structurally simple habitats held higher bee richness and flower visitation rates than more complex habitats. Also, other studies found non-significant effects of landscape variables on pollinators (Ekroos et al., 2015). However, in a meta-analysis, Kennedy et al. (2013) found overall positive effects of landscape heterogeneity on pollinators in agroecosystems. Our results could be due to a bee preference for the use of available natural areas for nesting that limits the use of farmlands and trap nests in more complex landscapes. We suggest that bees in olive orchards could be less likely to colonize trap nests as landscape complexity increases and more natural cavities are available in semi-natural patches, although they could be still foraging in floral patches adjacent to olive fields. Also, the finding of high colonization rates in organic farms in simple landscapes (see next subsection) could dampen the differences among landscapes. Alternatively, the landscape scales selected (1 and 2 km radius) might be too coarse to detect changes in these communities, if they responded more tightly to fine-scale variables (e.g., Lindgren, Lindborg, & Cousins, 2018). In fact, most of the variation in colonization rates in our study remains unexplained, supporting the idea that fine-scale determinants (non-explored here) of colonization rates were also important and merit further attention. The low variance explained in the models could be expected because, ultimately, predictions here are at the cavity scale and thus are inherently more stochastic than at bee trap nest scale.

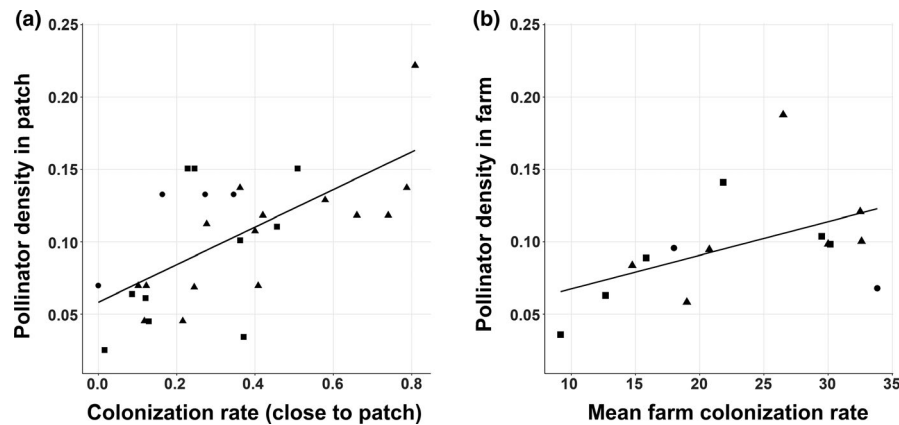


FIGURE 4 (a) Correlation between colonization rates at trap nest level (CR) in spring (until May) and pollinator density (number of active pollinators divided by number of flowers) in nearby patches (surveys in March–April). Results show significant positive correlation ($N = 30$, $p = .001$, $r = 0.56$). (b) Correlation between mean trap nest colonization rate and pollinator density at farm level across the whole season. Results show significant positive correlation ($N = 15$, $p = .03$, $r = 0.55$). Shape of symbols represents different landscape complexity. Regression lines are presented only to facilitate visualization of the trend in the figure; however, no statistical fit is intended since data are not normally distributed

4.2 | The magnitude of the management contrast: Organic versus intensive agriculture

Organic fields had greater colonization rates than the intensive fields regardless of landscape complexity. This suggests that the strong effect of organic management on pollinators may be obscuring the effect of landscape complexity. We argue that landscape moderation capacity depends on the magnitude of the effect caused by the local management itself (i.e. the magnitude of the ecological contrasts between managements induced by AES, as proposed by Kleijn et al., 2011; Marja et al., 2019). We further propose that under certain scenarios (e.g. organic management), the permanent agroecosystem could behave like an attractive zone itself (e.g. semi-natural area), not like a passive sink dependent on external sources of biodiversity. Thus, there might be a threshold of management intensity over which neutral or inverted patterns occur. Once the deficit of natural cavities is ameliorated by nest supply, organic olive farms might behave more like semi-natural areas for these cavity-nesting bees; since they do not have pesticides and provide more resources, functioning as a concentration zone where higher abundance of species is found regardless of landscape complexity. We name it the 'Biodiversity Concentration Effect Hypothesis' (BCEH) and it is an idea worth exploring further in permanent agroecosystems. In any case, our results concerning organic management contribute to overwhelming evidence that organic farming benefits biodiversity and pollination services (Kennedy et al., 2013).

4.3 | Bee trap nests, an effective tool for bioindication

Twenty years ago, Tscharntke, Gathmann, and Steffan-Dewenter (1998) recognized the potential of using trap nests for bioindication and sampling. These authors highlighted the possibility of doing quick evaluations focusing on the number of cavities colonized because this metric was

closely related to species richness. However, most studies that currently use trap nests constrain their use to a destructive sampling, emptying their content to identify the cavity-nesting insects and characterize the community (reviewed in MacIvor, 2017). In this study, we successfully used a non-destructive approach combining in situ surveys and bee-nest colonization rates to benefit from both the restoration and sampling function bee trap nests can offer simultaneously. Colonization rate is correlated with pollinator density in flower patches in our study system. We interpret this correlation as strong because we correlated samples from different localities, landscape complexities, herb cover managements and zones (semi-natural patches, olive orchards) without controlling for any of these factors. These significant correlations suggest that colonization rate is a useful indicator of density of foraging pollinators. We are aware that cavities could also be colonized by parasite wasps (Steckel et al., 2014; Tscharntke et al., 1998). In this study, we assumed that the proportion of cavities occupied by pollinators and non-pollinators were stable among the sampled fields (Steckel et al., 2014). Moreover, the main objectives of this study were to test the ILCH and the agricultural management contrast effect, so the framework and results would be equally valid if both pollination and biological control were considered.

5 | CONCLUSIONS

As hypothesized, the effect of herb cover management on colonization rates was strongly moderated by landscape complexity. Only farms embedded in landscapes of intermediate complexity showed a clear positive response of bee trap nest colonization rate to herb cover management extensification. This study represents a solid case where the effectiveness of the main AES in olive orchards (extensification of herb cover management) can depend critically on greater scales than only farm level. Therefore, we recommend focusing efforts on olive orchards located in intermediate landscape complexity. As we expected, organic management of olive farms

led to higher colonization rates in trap nests. Moreover, this happened regardless of landscape complexity, which suggests that the importance of landscape context depends on the ecological contrast induced by the local practices. Based on this result, we suggest that fostering organic farming, a rather minority practice in olive groves, should be a priority for policymakers. Last, our results supported our expected outcome that colonization rates in trap nests are a rightful measure in our system, closely correlated with pollinator density and can be used as an effective bioindication tool in our system.

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AUTHORS' CONTRIBUTIONS

C.M.-N., P.J.R. and A.J.M. conceived the ideas and designed the methodology; C.M.-N., J.I., R.T., G.C., J.L.M., J.E.G. and C.R. collected the data; T.S. processed the land use cartography data and produced metric of landscape heterogeneity; C.M.-N., P.J.R. and A.J.M. analysed the data and led the writing of the manuscript. All authors contributed critically to the final version of the manuscript and gave final approval for publication.

DATA AVAILABILITY STATEMENT

Data are available via the Mendeley Data Repository, <https://doi.org/10.17632/93mkr28hpk.1> (Martínez-Núñez et al., 2019).

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