Direct and indirect effects of agricultural practices, landscape complexity and climate on insectivorous birds, pest abundance and damage in olive groves

Carlos Martínez-Núñez [a],[*], Pedro J. Rey [a], Antonio J. Manzaneda [a], Rubén Tarifa [b], Teresa Salido [a], Jorge Isla [c], Antonio J. Pérez [a], Francisco M. Camacho [a], J.L. Molina [a]

[a] *Dept. Biología Animal, Biología Vegetal y Ecología, Universidad de Jaén, Jaén, Spain*
[b] *Estación Experimental de Zonas Áridas, Almería, Spain*
[c] *Integrative Ecology Group, Estación Biológica de Doñana, EBD-CSIC, Sevilla, Spain*

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ABSTRACT

Pesticides used in agriculture to prevent yield and economic loss are a threat for the natural heritage worldwide. Finding win-win solutions for pest control management in sustainable and profitable agriculture is a current yet elusive challenge for human societies. The main alternative to reduce pest damage in a sustainable manner consists in fostering natural enemies through the extensification of agricultural practices or the promotion of heterogeneous landscapes. However, very few studies have analyzed the combined effects of these components on natural enemies and pests simultaneously.

In this work, we fit meta-models (using Piecewise Structural Equation Models) aiming to understand the direct and indirect effects of agricultural management, landscape heterogeneity and climatic variables on insectivorous birds, pest abundance and crop damage. For this, we focus on olive groves, one of the most important woody agroecosystems worldwide, and its two main pest species.

We found that management extensification and landscape heterogeneity benefited pest control and supported more insectivorous birds. Also, high temperatures diminished pest damage. Compared to landscape and temperature effects, abundance/richness of insectivorous birds were poor predictors of pest abundance and damage, suggesting that other natural enemies might be currently more important for pest control in olive groves. Lastly, we found a decoupled response of pest abundance and pest damage that may be attributed to insecticide use. This suggests that predation pressure by birds might predict better pest abundance than pest damage in our system.

Current predation pressure by birds against pests in olive groves seems very low. Fostering extensive management and landscape heterogeneity increases the abundance of insectivorous birds in this system, potentially enhancing the pest control service.

1. Introduction

Pest species cause important yield and economic loss in crops worldwide (Oliveira et al., 2014; Savary et al., 2019). Promoting biodiversity-friendly agricultural practices and landscape heterogeneity is paramount to foster the biodiversity-mediated pest control service (Altieri, 1999; Dainese, 2019; Baker et al., 2020) and thus, achieve a sustainable agriculture for the future.

Agricultural extensification practices promote pest control, because they favor the presence of natural enemies that can maintain low pest populations, which usually increases yields (Garfinkel and Johnson, 2015; Muneret et al., 2019; Porcel et al., 2018). In contrast, agricultural intensification diminishes field and habitat suitability for natural enemies (Ricci et al., 2019), hindering their potential positive effects. Nonetheless, local management might not be the most important aspect affecting natural pest control in croplands. In turn, diversified landscapes, typically characterized by abundant semi-natural habitats, have a strong potential to host natural enemies and, therefore, increase predation pressure on pest species (Bianchi et al., 2006). However, there is a high inconsistency in the response of crop pests and their natural

enemies to surrounding landscape composition (Karp et al., 2018). Complex relationships such as intraguild predation (Lewis et al., 1997), or context-specific characteristics, which typically involve pest/predator life history traits and/or specific crop/semi-natural habitat features, could explain the contrasting results found in literature (Tscharntke et al., 2016). Landscape configuration (*i.e.* spatial arrangement of land use types), has also proven to affect the pest control provided by natural enemies (Martin et al., 2019). For instance, higher spatial heterogeneity is expected to increase pest suppression (Duarte et al., 2018), but again, these effects depend importantly on species-specific traits and the perception of spatial scales by the focal group (Haan et al., 2019).

Among pest control agents, insectivorous birds have received considerable attention due to their high mobility and potential for predation. Birds are frequently benefitted by extensive agricultural practices (Mangan et al., 2017; Rey et al., 2019) and are effective natural enemies in a variety of permanent woody agricultural systems, such as apple orchards (García et al., 2018), cacao plantations (Maas et al., 2013), coffee plantations (Karp et al., 2013) or vineyards (Barbaro et al., 2017). Several authors have explored landscape effects on insectivorous birds and the avian-mediated pest control (reviewed by Boesing et al., 2017), concluding that natural habitat cover, compositional heterogeneity and proximity to natural habitats generally promote pest control by birds. Less is known, however, about how the interplay of local management and landscape complexity can affect insectivorous birds and this ecosystem service. This is particularly true in Mediterranean woody agroecosystems, that are underrepresented in literature (Boesing et al., 2017; Peisley et al., 2015; Paredes et al., 2015) despite their great socio-economic importance, their century history and well-known pests, such as the olive moth, *Prays oleae* (Bernard, 1788) or the olive fly, *Bactrocera oleae* (Rossi, 1790). Moreover, very few studies have approached this topic from a holistic and integrative perspective, trying to identify combined (direct and indirect) effects of different multiscale environmental variables on natural enemies, pest abundance and crop damage.

In this work, we assess, at the regional scale, how variations in landscape heterogeneity, local agricultural management and climatic variables affect insectivorous birds, pest abundance, and crop damage in olive groves. Several reasons justify the choice of Mediterranean olive groves as the study system. First, this agroecosystem is socioeconomically very important in Mediterranean countries (*e.g.* European Commission, 2012; Loumou and Giourga, 2003), and covers more than ten million hectares worldwide (http://www.fao.org/faostat). Second, although currently expanding in many regions of the world, it is still mainly located in the Mediterranean basin, an important biodiversity hotspot (Marchese, 2015). Third, Mediterranean olive groves have suffered a prolonged trend of increased management intensification during the last decades (Infante-Amate et al., 2016). Fourth, its semi-forestal structure provides structural complexity and stability, conferring to this agroecosystem a strong potential for conservation of biodiversity and ecosystem service recovery (Martínez-Núñez et al., 2019, 2020a; Rey et al., 2019). Finally, ecosystem services delivered by the fauna in this system are not well understood yet, and studies regarding pest control have mainly focused on arthropod natural enemies (Álvarez et al., 2019; Paredes et al., 2013). In fact, there is a noticeable gap of knowledge on the role of pest control exerted by insectivorous birds in olive groves. Although birds have been observed predating on these species occasionally, we only know about one study assessing their pest control effects in this system (Martínez-Núñez et al., 2020b). Some studies have suggested a deficient pest control by birds in this highly homogenized monoculture (Martínez-Núñez et al., 2020b; Rey Benayas et al., 2017). Understanding the extent of this deficit, and disentangling its underlying factors, is crucial to revert the loss of this important ecosystem service.

Here, we monitored insectivorous birds and the two most important olive insect pests in 40 paired olive groves with different management (intensive *vs.* extensive herb cover management) across a landscape complexity gradient in 20 localities in southern Spain (a pair of farms per locality). We used piecewise structural equation models (PSEM) to explore direct and indirect causal paths from the top driving variables (landscape complexity, management and climate), to the bottom (crop damage). We hypothesized that: i) extensive management, high landscape complexity, and warm-dry weather should reduce the abundance of pests and the damage they produce; ii) insectivorous bird abundance and richness should reduce pest abundance and damage to olive flowers and fruits; and iii) extensive management and landscape complexity should also indirectly diminish pest abundance and damage by increasing the abundance and richness of insectivorous birds.

2. Materials and methods

2.1. Study system and experimental design

The olive moth, *Prays oleae*, and the olive fly, *Bactrocera oleae*, are the two most widespread and important pest species associated to olive trees (Paredes et al., 2019; Ponti et al., 2014). Both species have a life cycle that matches the phenology of the olive trees. Briefly, the olive moth has three generations: the phyllophagous (larvae that develop in the leaves in winter-spring), the anthophagous (larvae that feed on the floral buttons and flowers during Spring) and the carpophagous (larvae that grow inside the fruit, causing production loss due to the premature fruit fall in Autumn). From late Spring to Autumn, adult flies oviposit their eggs inside the olive fruit. The larvae develop inside the fruit in Summer-Autumn, producing damage and necrosis to the fruit. Then, the larvae fall to the ground and spend the winter in the soil (Daane and Johnson, 2010).

This study was set in 40 olive farms that were paired in 20 localities distributed across the main cultivation areas of olive tree in Andalusia (southern Spain), comprising a wide landscape complexity gradient (see Fig. 1). These localities span 310 km between the two most distant ones (Mean distance ±1SD between localities: 105.5 ± 61.3 km). The paired design within each locality involved one farm in each of two contrasting management practices: intensive, implying the persistent removal of herbaceous cover by applying pre-emergence herbicides and/or by ploughing, *vs.* extensive herb cover management, with maintenance of herb cover most of the year (details in Rey et al., 2019). Mean distance between paired farms at the same locality was 1461 ± 796 m (mean ± 1SD). These two practices significantly differed in herb species richness and cover (about 20 more species and 30 % more cover in extensive farms compared to intensive ones; see details in Martínez-Núñez et al., 2020a). Regarding the pesticide/insecticide use, the twenty intensive farms were under conventional or integrated regimes, which implied the common use of herbicides and insecticides. The twenty extensive farms do not use herbicides but can use insecticides. Ten of these twenty extensive farms were in addition organic and thus, no agrochemicals were used in them. Although the use of synthetic insecticides is forbidden in organic farms, the application of natural insecticides (*e.g. Bacillus thuringiensis*) is common. The table S1 in supporting information shows detailed information about each farm.

2.2. Landscape complexity

Landscape complexity is a human abstraction, rather difficult to characterize by a single variable. This explains why some authors claim for a functional classification of the landscape heterogeneity using multiple variables that define different aspects of heterogeneity (*e.g.* Fahrig et al., 2011). This has led to the frequent use of categories to describe landscapes, especially in agroecology studies (see for example: Batary et al., 2011; Concepción et al., 2012) leading to test landscape effects on biodiversity or ecosystem functions (Tscharntke et al., 2012). We followed a similar approach, classifying landscape from a multivariate and systematic perspective, which is consistent with previous research conducted in this same study system (Rey et al., 2019;
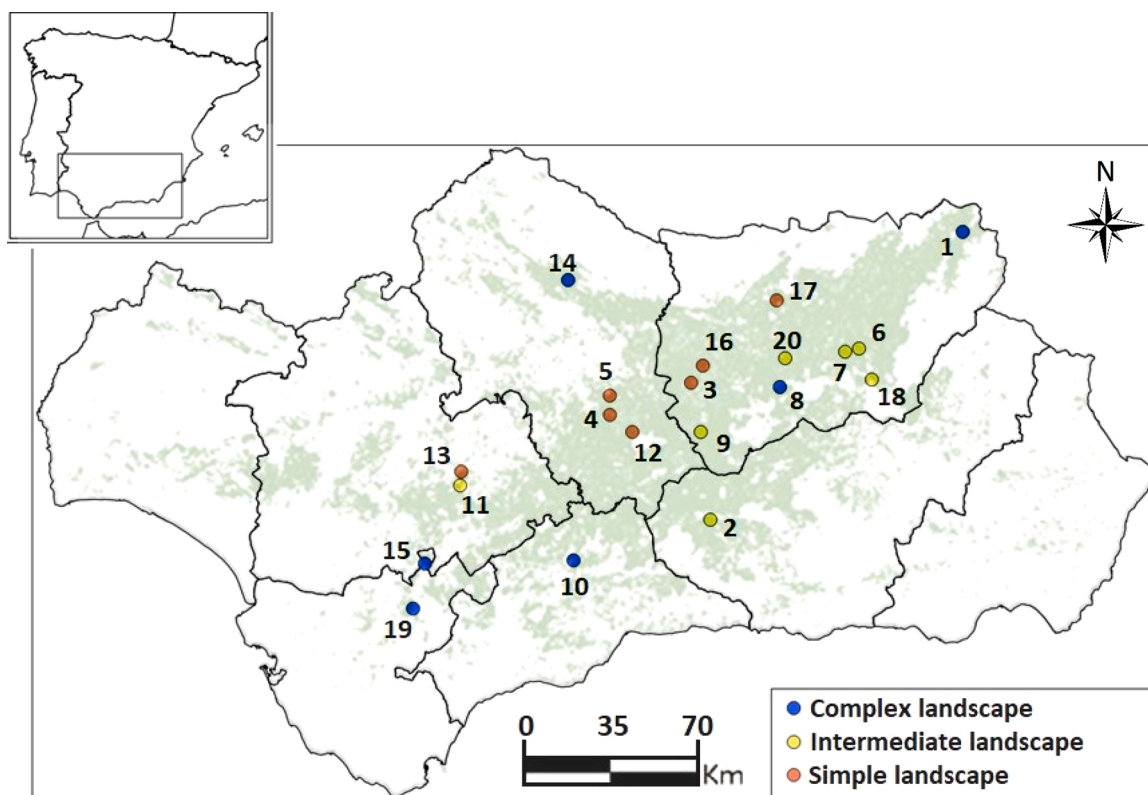
Fig. 1. The 20 localities of study distributed across the region of Andalusia. Shadow represents the area covered by olive farms. In each locality, two farms with different management regimes are sampled. Numbers are linked to Table S1, where further information about each specific farm and locality is provided. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article).

Martínez-Núñez et al., 2020a) about landscape and agricultural management effects on bird, ant, herb and pollinator biodiversity. Thus, localities were firstly chosen using *in situ* exploration and ortho-photos inspection to encompass most of the landscape complexity gradient of olive grove landscapes in Andalusia, and classified into three categories (simple, intermediate and complex landscapes). To validate such perceptual classification, landscape complexity was subsequently quantitatively assessed in the 20 localities at the scale of 2 km radius from the centroid of each pair of farms and using a multivariate approach. For that, we used recent land use cartography (SIOSE, http://www.siose.es) of Andalusia to measure twelve variables of compositional and configurational landscape heterogeneity typically used to describe more realistically how animals perceive and respond to landscape (Fahrig et al., 2011): patch richness, diversity and evenness, percentage of semi-natural habitat cover, percentage of olive groves cover, edge density, largest patch area, mean patch area, shape of the mean patch, Euclidean distance between nearest neighbor patches of similar uses, contagion and interspersion/juxtaposition index. With this information, we used the method of classification and regression tree (CART, De'ath and Fabricius, 2000), which does not assume linear relationships and provides specific thresholds among categories, to validate the *a priori* created landscape complexity groups. The CART correctly classified the 20 localities into the three perceptually established groups (Simple, Intermediate and Complex) just using three variables: percentage of area covered by semi-natural habitat (SNH; a compositional heterogeneity metric), distance to nearest neighbor patch of similar use (NND), and mean patch size (MPS) (two configurational heterogeneity metrics; see Rey et al., 2019 for more details). Simple landscapes were characterized for having less than 9 % of semi-natural area. Intermediate landscapes had more than 9% of semi-natural area and NND higher than 85 m. Last, complex landscapes had more than 9 % of SNH and a mosaic of land uses (less than 85 m NND).

2.3. Climatic variables

Climate (especially extreme temperatures) plays a key role in the distribution and life cycles of the olive moth and the olive fly (Ponti et al., 2014). Therefore, we included two climatic variables in the models, namely average maximum temperature (which is correlated with mean annual temperatures, Spearman rank test; rho = 0.53, P = 0.000), and annual precipitation. Together, extreme temperatures and low humidity can diminish pest reproduction success and egg/larvae survival (Barranco Navero et al., 2017). For instance, the eggs of the olive fly do not develop below 7.5−10 °C or above 30−32 °C (Tsitsipis, 1977). We obtained the annual historical average of these variables from maps with a resolution of 1 × 1 km, in REDIAM (http://www.juntade andalucia.es/medioambiente/site/rediam/). Maximum temperatures varied between 29.3 °C and 32.7 °C, while annual precipitation ranged between 359 and 695 mm.

2.4. Bird surveys and functional classification

Birds were surveyed by means of point censuses, by recording the singing of the species heard, or recording birds directly by sight. Censuses were performed for five minutes at six or ten point census plots, depending on farm size (N = 336 plots), separated at least 200 m. Monthly censuses were conducted from March 2016 to April 2017 (except July and August), within three hours after sunrise (ten rounds, N = 4036 total censuses). For this study, only insectivorous birds were accounted. Bird ascription to the insectivore guild (see Table S3, in Supporting Information) was based on our own expertise and existing functional traits database (Storchová and Horák, 2018 and Wilman et al., 2014). We did not consider different guilds of insectivorous birds because the focal pests live on the tree, on the ground and flying around. Surveys were aggregated for the whole year, at the plot level, because

these pests are available for predators during the most part of the year at different life-cycle stages. We followed a conservative approach and did not weight abundances by specie's degree of insectivory, because percentage of insectivory might not reflect predation incidence on (or appetence for) olive pests and because no information is available on consumption of these pests by different bird species. However, for completeness, we also ran models using weighed bird abundance (results are presented in Fig. S1, Supporting Information).

2.5. Pest monitoring

The olive moth was monitored in the 40 olive farms considering the same sampling plots used for birds (N = 336). In this case, we used funnel traps baited with the specific pheromone z-7-tetradecen-1-ol and a pill of insecticide (2,2-dichlorovinyl dimethyl phosphate, DDVP), which attracts and collects adult males (Mazomenos et al., 1999). These traps were used from April to July 2017, coinciding with the strongest peak of adult activity in our range. We conducted monthly rounds to count moths. We renewed the insecticide and the pheromone after 8 weeks. Monthly abundances were aggregated and total mean abundance per trap for the whole sampling period was calculated. Finally, we used the total abundance per trap and farm (N = 336 in total). Adult olive flies were recorded from July to November of 2016 in the 40 olive farms using McPhail traps baited with diammonium phosphate diluted (4 %) in water, a known attractant for flies (Paredes et al., 2015). At each olive farm, we used 6 (in small farms, < 25 ha) or 10 (in big farms, >50 ha) McPhail traps, hanging in olive trees widespread throughout the whole farm, which were coinciding with (or close to, in the case of non-crop plots) the bird point census plots. All McPhail traps (N = 336) were monthly checked and refilled after counting the olive flies. Due to logistic constraints, we were not able to sample the birds and both the olive fly and the olive moth simultaneously. There is a one-year delay between bird (April 2016 – March 2017) and olive moth data (April 2017 – July 2017). Nonetheless, we believe that this is not an important constraint in order to detect true inter-relationships between pest abundance/damage, avian predator abundance and environmental variables (local landscape, agricultural management and climate) for several reasons: First, the response of organisms with discrete generations (like the insect pests studied here) to predator abundance is inherently delayed for at least one generation (Gilg et al., 2003), which makes one-year-delayed comparisons between predators and pests more realistic. Second, our sampling and modeling entail that the stability of environmental predictors (local landscape, agricultural management, climate) is, in the short term, largely independent of the year. It also implies the assumption that avian predator abundance is more influenced by site-specific conditions than by short term stochastic year variations. We believe that these assumptions are widely acceptable. Finally, we study differences between sites/conditions for the same period (time is not a confounding factor for these comparisons).

2.6. Pest damage monitoring

To measure the actual impact of pest species on olive trees, we counted the number of olive fruits damaged by the olive fly (in 40 farms and 336 trees during 2016). We also monitored the damage produced to flowers and fruits by the olive moth (in 40 farms and 336 trees during year 2017). The damage caused by the olive fly, was assessed from September to December, by inspecting 100 olive fruits per tree (six to ten trees depending on farm size, trees located in the bird census plots). For the olive moth, during May and June (depending on the locality), we collected 100 inflorescences from each tree (25 on branches facing each cardinal point) in six or ten trees (depending on farm size, trees located in or near to the bird census stations). We inspected these flowers in the lab, looking for moth larvae presence as a proxy of flower damage (incidence). From October to December, we further inspected 100 fruits in the same 6–10 olive trees, checking for olive moth damage. Because

the damage caused by the olive moth implies that the olive fruit may eventually fall to the ground, we also collected 100 olives from the ground to find evidences of the olive moth attack.

2.7. Statistical analyses

Our causal models (Figs. 2–4) aim to detect relationships between relatively temporally stable site-specific predictors (landscape, agricultural management and climate) and final target response variables (pest abundance and damage), hypothesized to be further influenced by avian predation pressure. We built meta-models considering direct and indirect links between four manifest exogenous variables (management, landscape complexity, maximum temperature and annual precipitation), and the abundance/richness of insectivorous birds, the abundance of pests and finally the flower and fruit damage caused by pests. Paths linking climatic variables with bird abundance/richness were omitted in this model. Climatic variables could also determine differences in seasonality and thus, a contrasting response of bird communities at the regional scale (Pérez-Tris and Tellería, 2002). However, landscape heterogeneity is highly correlated with climatic variables in the study system. Therefore, to avoid collinearity, we did not include climatic paths to bird abundance/richness while paths from landscape to these variables were included. Thus, our main model hypothesizes a stronger ecological effect of landscape complexity (instead of temperature) on birds in the study range. This decision was further supported by results of the model simplification (see details on the procedure bellow; see also final optimized model in results) which removed climatic variables because landscape heterogeneity explained more variance. Further, general linear models confirmed that maximum temperature and precipitation are not important variables to explain bird abundance or richness, once introduced landscape heterogeneity (Table S2). In contrast, because it is clearly documented that climate may limit olive pests (Ponti et al., 2014), paths from climate to abundance and damage of pests were allowed. In any case, for completeness, we present also alternative models, forcing a model simplification in which we retain temperature and paths to birds and pests, instead of landscape complexity.

Each pest may respond differently to biotic and abiotic correlates, hence we built three separate meta-models (one for both pests considered together, and two others considering each pest separately) (see Figs. 2–4, respectively). These models were fitted using piecewise structural equation models (PSEM), that allow to incorporate hierarchical sampling designs (for example, nested random factors) using the package *piecewiseSEM* (Lefcheck, 2016) in R (R Core Team, 2019). Management and Landscape complexity were originally factor variables, and we converted them to ordinal numeric variables from intensive (1) to extensive (2) management, and from simple (1), to intermediate (2), and complex (3) landscape. We treat them as ordinal variables to facilitate the interpretation of the coefficients in a conceptually clear ordinal direction congruent with our environmentally-friendly gradient of the agricultural management and landscape complexity levels. Abundance and richness were log-transformed and damage (as percentage) arcsine square-root transformed to run normal linear mixed models using the package *nlme* (Pinheiro et al., 2020) because models with transformed variables performed better (better fit and no convergence issues) than generalized linear models. Performance and predictability by normalized models was good (see Fig. S2). Farm ID and Locality ID were included in the models as nested random variables. We firstly fitted the *a priori* predicted model (named "complete" model) specifying all predicted relationships. We tested the completeness and goodness of fit of the model through "tests of direct separation", using the Fisher C test, which also assists to detect potential missing paths and informs about how well the model reflects the data (Lefcheck, 2016).

Starting from the complete model, we conducted a backward simplification by removing non-significant relationships until the final
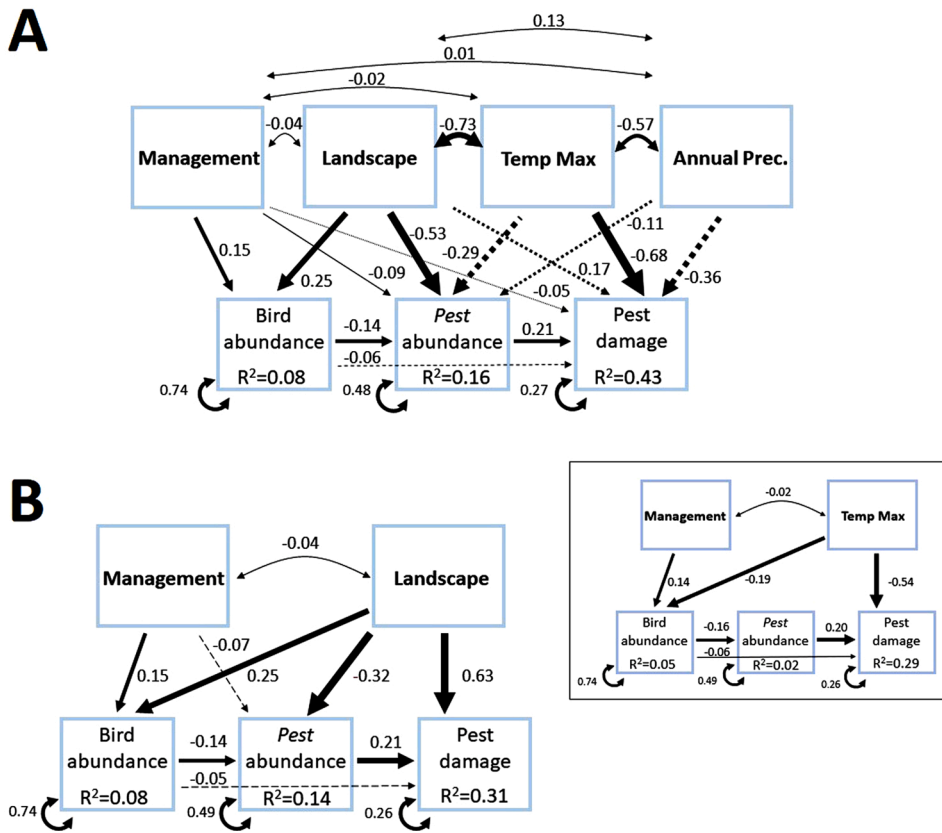
Fig. 2. Structural equation model showing all predicted relationships between the exogenous variables, abundance of insectivorous birds, pest abundance (olive moth plus olive fly), and pest damage (olive moth plus olive fly) (A) and the optimized model according to AIC (B). Double headed arrows show correlated errors between exogenous variables. Arrows show directional relationships. Their width represents the strength of the coefficient (standard coefficients). Non-significant (p-value ≥0.1) paths are depicted with a dashed line. The inset in B shows an alternative final model in which we forced the maintenance of the variable maximum temperature during model simplification.
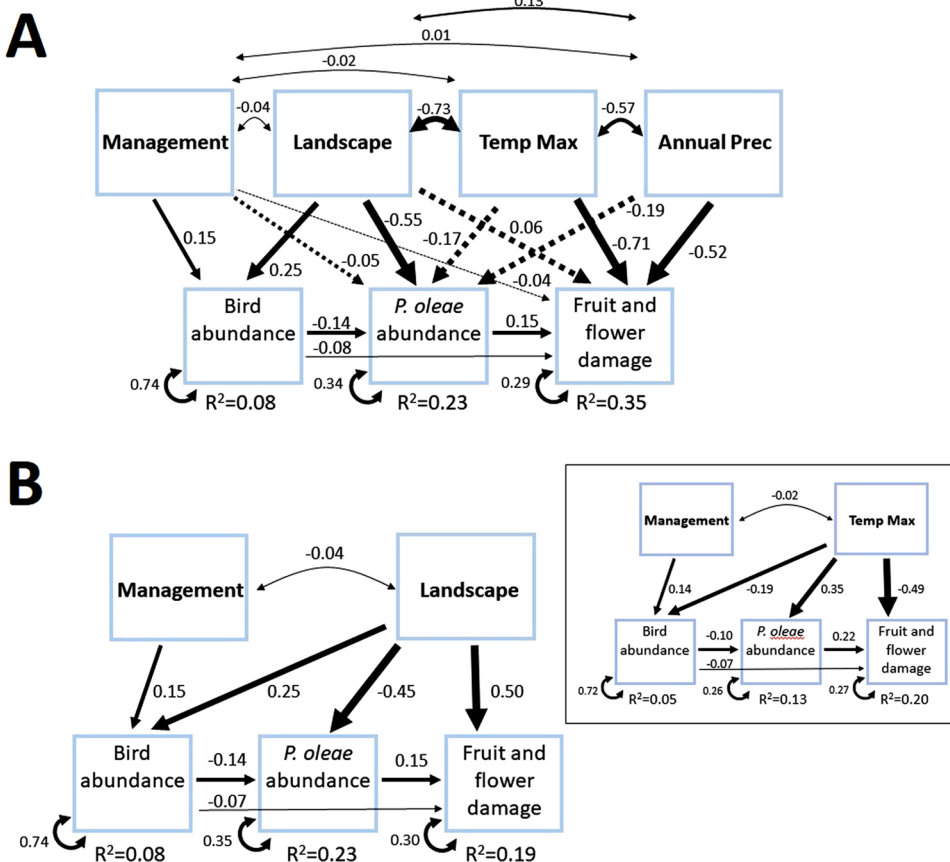

Fig. 3. Structural equation model showing all predicted relationships between the exogenous variables, abundance of insectivorous birds, pest abundance (olive moth), and pest damage (olive moth) (A) and the optimized model according to AIC (B). Arrow width and pattern interpretation follows that of Fig. 1. Non-significant (p-value ≥0.1) paths are depicted with a dashed line. The inset in B shows an alternative final model in which we forced the maintenance of the variable maximum temperature during model simplification.

Fig. 4. Structural equation model showing all predicted relationships between the exogenous variables, abundance of insectivorous birds, pest abundance (olive fly) (A) and the optimized model according to AIC (B). Arrow width and pattern interpretation follows that of Fig. 1. Non-significant (p-value ≥0.1) paths are depicted with a dashed line. The inset in B shows an alternative final model in which we forced the maintenance of the variable maximum temperature during model simplification.
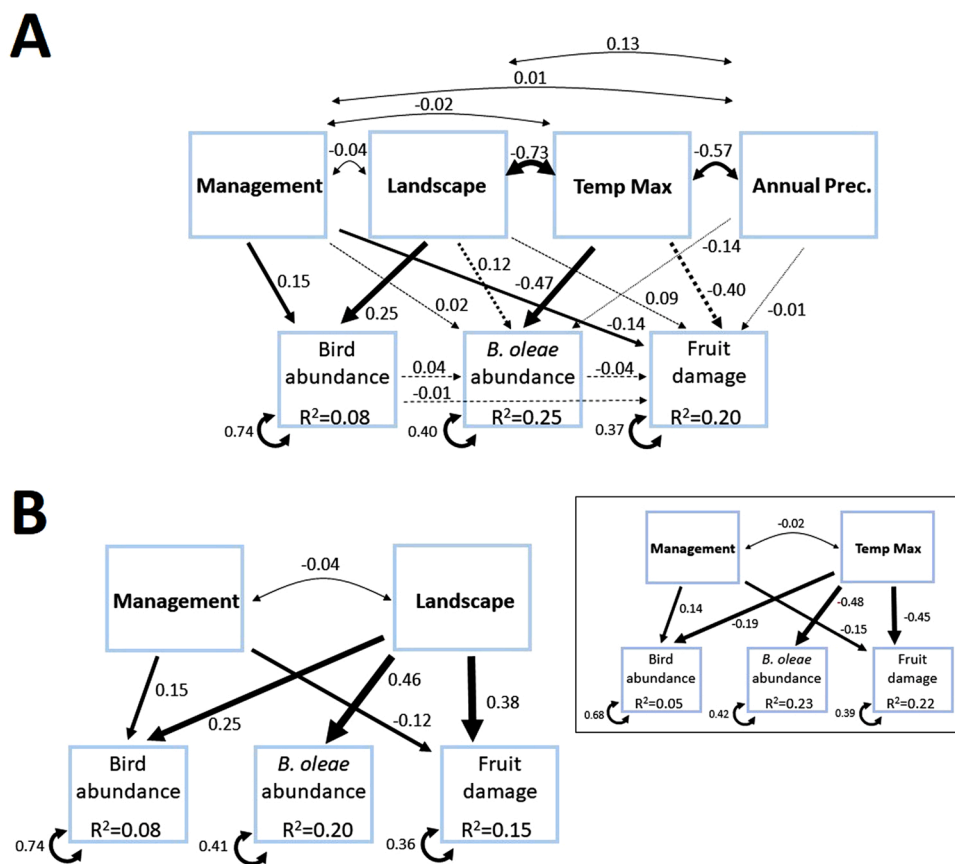
best model (lower AIC) was achieved. Finally, we intentionally compared meta-models including and excluding the effect of birds on pests, to test their relative importance as pest control agents. We ran three sets of models, considering the two pests together, then the olive moth and the olive fly separately. The 'complete' models are shown in Figs. 2–4A. Their respective chosen simplified models are shown in Figs. 2–4B. Because some exogenous variables were inherently correlated due to characteristics of the studied system (*i.e.*, olive farms in complex landscapes are often found in montane colder and humid sites), we analyzed the presence of collinearity. Hence, we calculated the variation inflation factor of variables in each component model, using the *vif* function in the *car* package (Fox and Weisberg, 2019), finding vif < 5 in all cases. Also, the model simplification process used, leading to our final models (the one we discuss), always removed redundant variables, as recommended in case of collinearity, and had no correlated exogenous variables.

Our study sites spanned large geographic distances; whereby observed patterns might be influenced by spatial autocorrelation. Therefore, we ascertained that residuals of all component models did not have any spatial pattern (no trend with latitude or longitude) (Dormann et al., 2007).

3. Results

We found 165 bird species, from which 99 were insectivores (Table S3). Bird abundance throughout the year was 148 ± 28 individuals; Mean ± SD per point census plots, ranging from 85 to 215 across olive groves. Mean bird richness was 21 ± 4 (17–26).

Pest abundance was high (2006 ± 1309 reproductive males/trap for the sampling period for olive moth, and 158 ± 184 adults/trap for the olive fly), and highly variable across farms, ranging from 147 to 6119 adult males/trap for olive moth, and from 8 to 624 adults/trap for olive

fly (mean of 158). Damage caused by the olive moth was on average (5% of flowers/fruits, ranging from 0 to 15 %). The olive fly caused more damage to production, being on average 7 % of fruits (0–37 %).

3.1. Model for both pest species

The complete meta-model adequately explained the causal relationships proposed between environmental correlates (management, landscape and climatic variables and bird abundance, pest abundance and damage as suggested by the overall fit of the model (see Table 1; overall goodness of fit: $C_4 = 0.682$; P = 0.953). Two exogenous variables, landscape complexity and maximum temperature were strongly negatively correlated (Pearson correlation test; r = −0.73, P = 0.000). Also, maximum temperature and precipitation were negatively correlated (Pearson correlation test; r = −0.57, P = 0.000). The abundance of insectivorous birds increased importantly both with landscape complexity (Linear Mixed Model; standardized coefficient, hereafter beta, = 0.25, P = 0.016) and extensive agricultural practices (beta = 0.15, P = 0.043) (see Fig. 2A and Table 1). Landscape complexity strongly diminished the abundance of pests (standardized coefficient=−0.53, P = 0.034). Higher bird abundance diminished the abundance of pests significantly (beta = −0.14, P = 0.002), but not pest damage (beta=−0.06, P = 0.104). Higher maximum temperatures diminished observed damage caused by pests (beta=−0.68, P = 0.012). Finally, pest abundance increased the observed pest damage (beta = 0.21, P = 0.000).

The best model (see Fig. 2B and Table 1) did not include the effects of precipitation but included bird abundance and its negative direct effects on pest abundance and pest damage. Landscape complexity (highly correlated with maximum temperature) negatively affected pest abundance beta=−0.32, P = 0.035) and higher temperatures reduced pest damage (beta = 0.63, P = 0.000). Both management and landscape

Table 1
Piecewise structural equation models for olive pests (olive moth plus olive fly), Fisher C (measure of goodness of fit), AIC, and Marginal R^2 for each endogenous variable.

Model	Description	Fisher C (p-value)	AIC	Marginal R^2
Complete		0.682 (0.95)	50.7	Bird abundance 0.08
	Complete model with all predicted paths (Fig. 2A)			Pest abundance 0.16
				Pest Damage 0.43
1		0.51 (0.77)	40.5	0.08
	Best model based on AIC (including bird abundance) (Fig. 2B)			0.14
				0.31
2		4.87 (0.30)	42.9	0.08
	Model 1 without the path from birds to pest damage			0.14
				0.31
3		27.04 (0.09)	53.0	0.08
	Model 2 without the path from birds to pest abundance			0.13
				0.31

Table 2
Piecewise structural equation models for *P. oleae* (olive moth), Fisher C (a measure of goodness of fit), AIC, and Marginal R^2 for each endogenous variable. Note that only AIC values of saturated models (Fisher C p-value $\geq$ 0.05) are legitimately comparable.

Model	Description	Fisher C (p-value)	AIC	Marginal R^2
Complete	Complete model with all predicted paths (Fig. 3A)	0.682 (0.953)	50.7	Bird abundance 0.08
				P. oleae abundance 0.23
				Damage 0.35
P1	Best model based on AIC (including bird abundance) (Fig. 3B)	5.53 (0.24)	43.5	0.08
				0.23
				0.19
P2	Model P1 without the path from birds to fruit and flower damage	11.34 (0.08)	47.3	0.08
				0.23
				0.19
P3	Model P2 without the path from birds to pest abundance	27.06 (0.00)	61.1	0.08
				0.21
				0.19

Table 3
Piecewise structural equation models for *B. oleae* (olive fly), Fisher C (a measure of goodness of fit), AIC, and Marginal R^2 for each endogenous variable.

Model	Description	Fisher C (p-value)	AIC	Marginal R^2
Complete	Complete model with all predicted paths (Fig. 4A)	0.68 (0.953)	50.7	Bird abundance 0.08
				B. oleae abundance 0.25
				Damage 0.20
B1	Best model based on AIC (including bird abundance)	3.03 (0.55)	41.0	0.08
				0.20
				0.15
B2	Model B1 without the path from birds to fruit damage	3.06 (0.80)	39.1	0.08
				0.20
				0.15
B3	Model B2 without the path from birds to pest abundance (Fig. 4B)	6.12 (0.63)	40.1	0.08
				0.20
				0.15

complexity had an indirect negative effect on pest abundance by increasing bird abundance (Table S4). These two variables and bird abundance also indirectly diminished pest damage through decreasing pest abundance (Table S5).

This model was replicated using insectivorous bird richness as endogenous variable instead of bird abundance (Table S5 and Fig. S3). Results showed that neither extensive management (t_{19} = 0.67, P = 0.507) nor landscape complexity (t_{18} = 0.82, P = 0.420) affected bird richness. Also, bird richness was not an important variable for explaining variation in pest abundance nor pest damage (see Table S5 and Fig. S3B). The indirect effects found in this model were weak (see Table S6). Only landscape complexity diminished pest damage indirectly, through decreasing pest abundance.

3.2. Model for the olive moth

The complete model was rather similar to the previous SEM (Fig. 3A). Landscape complexity decreased the abundance of the moth (beta=−0.55, P = 0.042), but in this case did not affect pest damage (beta = 0.27, P = 0.792). Maximum temperature negatively affected the observed damage (beta = −0.71, P = 0.014) and annual precipitation too (beta=−0.52, P = 0.012). Bird abundance diminished pest numbers (beta=−0.14, P = 0.001) and slightly fruit and flower damage (beta=−0.08, P = 0.035). Finally, the abundance of the moth determined the observed damage (beta = 0.15, P = 0.002).

The best model (Fig. 3B and Table 2) included bird abundance and its negative effects on pest abundance and damage, and showed that

landscape complexity (which shows a strong correlation with maximum temperature, hence engrossing part of the variability explained by climatic variables in the complete model) decreased olive moth abundance (beta=−0.45, P = 0.009) but increased olive moth damage (beta = 0.50, P = 0.005). There were negative indirect effects of management and landscape on pest abundance and pest damage, through increasing bird abundance, and decreasing pest abundance (Table S7, in Supporting information).

3.3. Model for the olive fly

The complete meta-model for the olive fly (Fig. 4A) showed that high temperatures tended to diminish the abundance of the olive fly (beta=−0.47, P = 0.085), while extensive cover management diminished the damage in olive fruits (beta=−0.14, P = 0.027). Interestingly, no effect of birds on pest abundance (t_{294} = 0.94, P = 0.348) or pest damage (t_{281}=−0.34, P = 0.734) was observed. Neither the path from olive fly abundance to damage produced by olive fly was significant (t_{283}=-0.78, P = 0.433).

The best model in this case did not include the paths of bird abundance to pest abundance and damage (Table 3 and Model in Fig. 4B), and the temperature effect on pest abundance was removed and substituted by landscape complexity (highly correlated with temperature in our dataset). In fact, landscape complexity caused an increase in olive fly abundance (likely driven by temperature, see Discussion) (beta = 0.45, P = 0.004) and an increase in observed fruit damage by olive fly (beta = 0.38, P = 0.029). There were not indirect effects of management and landscape on the olive fly abundance and damage (Table S8, in Supporting information).

4. Discussion

The set of predictions stated in this study were only partially validated. Extensive management, landscape complexity and high temperatures showed an effect on pest abundance and/or pest damage for at least one pest species. Also, the effects of landscape and management were partially mediated by their influence on the abundance of insectivorous birds. However, some effects were weak, limited to one pest species only, or the direction of the result was the opposite to the expected. Also, as predicted, extensive management and landscape complexity were associated to increments in the abundance of insectivorous birds. Nonetheless, bird's effect on pest abundance was inconsistent (only significant for the olive moth) and relatively weak. Finally, the direct effect of bird abundance on pest damage was overall negligible. This small effect of birds on pest abundance/damage is even lower after weighting bird abundance by the degree of insectivory (Fig. S1).

4.1. Management effects on birds and pests

In general, our results show that extensive management (maintenance of ground herb cover) favor bird abundance and pest control by natural enemies, although these effects were inconsistent and likely driven by different mechanisms for each pest species. Extensive management, clearly increases the abundance and richness of insectivorous birds on olive farms (see also Castro-Caro et al., 2014; Rey et al., 2019). The presence of plant cover for the most part of the year is known to favor the presence of alternative preys (Álvarez et al., 2019; Paredes et al., 2019), providing more resources to these birds. Since bird abundance effects cascade to overall pest abundance and damage (being this true at least for the olive moth but not for the olive fly), management effects on birds have an indirect effect on pest control too (see discussion below). Other studies in woody agroecosystems have evidenced the benefits of extensive management on bird diversity and ecosystem services (*e.g.* a recent meta-analysis in vineyards by Winter et al., 2018). However, extensive herb cover management in olive groves only slightly

directly diminished the overall abundance of pests (Fig. 2A), lacking this trend for each pest separately. This suggests that the benefit for pest control of herb cover extensification itself is not consistent in olive groves. These results are consistent with results previously shown by other authors (Paredes et al., 2015, 2019). Probably, a higher scale or a higher level of extensification (*e.g.* herb cover maintenance plus insecticide-free management or an increase in landscape heterogeneity) is needed to observe an effective decrease in pest abundance in olive groves (Paredes et al., 2019).

4.2. Landscape and climatic effects on birds and pests

Olive groves cover extensive areas, causing extreme landscape simplification. Our results show that, as in many other agroecosystems, landscape heterogeneity is related to increments in the abundance of insectivorous birds, contributing to the conservation and the provision of pest control ecosystem services in olive groves dominated landscapes. Most insectivorous bird species found in olive groves depend to some extent on semi-natural habitats that provide alternative preys, nest sites, and refuge from agricultural disturbance (Rey, 1993; Rey and Valera, 1999; Castro-Caro et al., 2014; Morgado et al., 2020). Olive groves have a forest-like structure, but they are exposed to many disturbances, especially in intensively managed farms (harvest machinery, spraying of phytochemicals, etc.). In addition, many olive groves have very young trees (with smooth trunks that have no holes required to nest by some birds typically associated to forests), and are managed intensively, which diminishes considerably the heterogeneity and the provision of resources at the farm scale (Rey and Valera, 1999; Morgado et al., 2020). Therefore, small and simplified communities of insectivorous birds can live in landscapes dominated by current olive monoculture (Rey, 1993, 2011) while, as shown also for other agroecosystems (Assandri et al., 2016; Boesing et al., 2017; García et al., 2018), landscape heterogeneity promotes bird abundance and diversity. Importantly, we show here that, as expected, landscape complexity diminished the abundance of pests (overall model with both pest species) by increasing the abundance of insectivorous birds, although no effect was found through insectivorous bird diversity. Note however that our design does not allow a complete separation of the variance explained by landscape heterogeneity and maximum temperatures, because these variables are highly correlated in our dataset. Therefore, we cannot completely discard that higher temperatures contribute to reduce bird abundance, as shown in the alternative models of Figs. 2–4B. Temperature effects on total annual bird abundance in the region are not easily interpretable due to the likely occurrence of seasonal effects of opposite direction. Thus, extreme summer temperatures provoke that during late spring and summer many bird species concentrate in fresh sites (normally in highlands or mountain areas) after reproduction. In winter, the pattern in the region is opposite and numerous small-sized wintering birds concentrate in lowlands warmer sites (Herrrera, 1985; Rey, 1993; Pérez-Tris and Tellería, 2002). Thus, in terms of total annuals the pattern of bird abundance in relation to temperature is not so well defined as it is the relationship of birds and landscape heterogeneity (much more predictable).

Landscape complexity also affected directly and negatively pest abundance (overall model, including the moth and the fly). This is probably because landscape complexity increases the abundance, diversity or evenness of arthropod natural enemies and diminishes the spread success of these highly specialized pests (Ortega et al., 2016; see also Martin et al., 2016). However, we found an unexpected decoupled response of pest abundance and pest damage to landscape complexity, with olive groves within heterogeneous landscapes suffering more pest damage. Two main reasons might explain this: i) farms located in complex landscapes are also historically less intensified, with lower inputs of pesticides at the landscape and temporal scale (see next section); and ii) some of the effects found (*e.g.* increase in pest damage) are partially (in the case of olive moth; see Fig. 3A *vs.* B) or mostly (in the

case of olive fly; see Fig. 4A *vs.* B) driven by temperatures, since these two pests can be vulnerable to very high temperatures (Barranco Navero et al., 2017; Ponti et al., 2014).

4.3. Birds, pest abundance and pest damage

We observed an effect of bird abundance on olive moth abundance but not on fly abundance. This might indicate that the olive moth is a species more appealing or exposed to the potential control effect of insectivorous birds. In fact, this could be expected from their respective life cycles. Bird predation is probably more prolonged and plausible on the moth larvae because the phyllophagous and anthophagous generations develop on leaves and flowers, respectively, remaining exposed to birds for several months. In contrast, the olive fly larvae are shortly exposed since develops mostly within the fruit after egg laying. However, no effect of bird abundance on pest damages was found (or a very weak effect in the case of the olive moth). In the particular case of the olive fly, the lack of a significant link between bird abundance and pest damage suggests that insectivorous birds might not be effective for pest control in current olive groves plantations and landscapes (Rey Benayas et al., 2017; see Mangan et al., 2017, for similar results in apple groves).

Unexpectedly, we did not find a strong link between pest abundance and pest damage. This is probably due to the fact that most farmers use insecticides when they start to observe damage (or they anticipate that damage will be important), especially with the olive fly, that is considered really harmful for production and attacks once the olive fruits are grown, in late Summer/early Autumn. This might be showing that traditional practices do not impair pest populations during most months, and just focus on undermining their abundance for the limited period when they produce most economic damage. These results suggest that, in managed agroecosystems, effect on pest abundance is a preferable predictor of potential pest control than observed pest damage, because the latter is highly influenced by the use of agrochemicals.

5. Conclusions

This study shows that agricultural management and landscape complexity combined are important drivers affecting the abundance of insectivorous birds in olive groves. However, landscape (both directly and indirectly) and temperature determined to a great extent the abundance of pests found in olive farms and the damage they caused. The relevance of insectivorous birds for pest control was inconsistent across pest species. Their effects were overall weak, especially when compared with the direct effects of landscape and/or management, which much likely engage non-avian natural enemy abundance and pest control. Our results emphasize the key role of landscape complexity and extensive management for bird conservation and pest control in olive groves. They also suggest that bird's role in olive pest control is currently secondary, mainly for the olive fly, and that major olive insect pests are more effectively controlled by other natural enemies (*e.g.* Paredes et al., 2019).

Authors' contributions

PJR, AJM and CMN conceived the main ideas and sampling design of this study. TS and PJR conducted the landscape analysis. RT, JLM, JI, AJP, FMC, AJM, PJR and CMN conducted fieldwork. CMN led the analysis and wrote the first draft of the manuscript with feedback from PJR. All authors contributed significantly to the final version.

Data availability statement

Data are available in the Mendeley Data repository, following this link: https://data.mendeley.com/datasets/xwnmcs82ch/draft?a=e158 23f2-620c-4d8f-a07c-10754d1b36e7.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Appendix A. Supplementary data

Supplementary material related to this article can be found, in the online version, at doi:https://doi.org/10.1016/j.agee.2020.107145.

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