Insectivorous birds are not effective pest control agents in olive groves

Carlos Martínez-Núñez[a,*], Pedro J. Rey[a,b], Antonio J. Manzaneda[a], Daniel García[c], Rubén Tarifa[d], José L. Molina[a]

[a]*Department of Biología Animal, Biología Vegetal y Ecología, Universidad de Jaén. Jaén E-23071, Spain*
[b]*Instituto Interuniversitario del Sistema Tierra de Andalucía, Universidad de Jaén, Jaén E-23071, Spain*
[c]*Departamento de Biología de Organismos y Sistemas, Universidad de Oviedo, y Unidad, Mixta de Investigación en Biodiversidad (CSIC-Uo-PA), Spain*
[d]*Estación Experimental de Zonas Áridas, Almería, Spain*

Abstract

Although avian-mediated pest control is a significant ecosystem service with important economic implications, few experimental studies have ever documented its role in Mediterranean agroforests. Specifically, information on pest control by birds is lacking in certain permanent agroecosystems of worldwide importance such as olive groves.

Here, we assess experimentally for the first time the effectiveness of insectivorous birds in controlling the two main olive-tree pests. We also explore the effects of distance to semi-natural habitat patches on avian insectivore abundance and pest control. We combined bird and pest surveys with pest damage monitoring and two field experiments (branch exclusion and plasticine models) at a regional scale.

The experiments showed that birds played a negligible role as pest controllers (measured in terms of attack rates on plasticine models and controlled pest damage) in the studied olive groves; overall, pests were abundant and pest damage was high on most farms. In addition, surveys showed that insectivorous birds were more abundant and diverse in patches of semi-natural habitat, compared to the matrix of olive groves, and that proximity to semi-natural patches was not a driver of bird-driven pest control.

This study experimentally demonstrates that insectivorous birds are not effective pest controllers in olive groves. The absence of patterns linking insectivorous birds' availability and observed pest control suggests that birds are unable to exert effective control over the main olive-tree pests. This lack of biocontrol by birds is probably due to low accessibility and/or appetence for the current insectivorous groups. Habitat improvement aimed at encouraging some under-represented forager species could improve the likelihood that birds will provide this ecosystem service.

*Corresponding author.
 E-mail address:* cmnunez@ujaen.es (C. Martínez-Núñez).

Introduction

Insectivorous birds have proven to be successful biological pest control agents in some agroecosystems (Barbaro et al., 2017; García, Miñarro & Martínez-Sastre, 2018; Karp et al., 2013). However, their effectiveness is system-dependent and there are still agroecosystems of worldwide relevance in which the effectiveness of avian-mediated pest control and the impact of habitat loss have rarely been addressed (Boesing, Nichols & Metzger, 2017).

Landscape components may benefit insectivorous bird communities and mediate their contribution to pest control. For instance, semi-natural patches commonly enhance bird communities and pest control in agroecosystems (Escobar-Ramírez, Grass, Armbrecht & Tscharntke, 2019). As well, larger natural habitat fragments often favour higher predation pressure by birds (Karp et al., 2013), although this pressure is usually mitigated by distance from the semi-natural patch (Henri et al., 2015; Jordani, Hasui & da Silva, 2015). Some studies have experimentally approached bird pest control in agroforests. Maas, Clough and Tscharntke (2013) used exclusions to demonstrate how pest biocontrol by birds and bats in agroforests increased yields in cacao plantations. By combining experimental increases in insect pests and bird exclusion, García et al. (2018) showed that insectivorous birds favoured by semi-natural woody vegetation around farms can control pest outbreaks and diminish damage in apple orchards. Similarly, Koh (2008) used exclusions to show how birds (associated with natural habitats) protect oil palms from herbivores. Other authors have used plasticine models (commonly employed to compare attack rates over gradients) to compare levels of avian predation on pests (reviewed in Bateman, Fleming & Wolfe, 2017). This method has proven useful for exploring the effects of agricultural management and semi-natural habitat on general pest control (Rusch, Delbac, Thiéry & Thi Ery, 2017) and avian pest control in vineyards (Barbaro et al., 2017). Additionally, the abundance of insectivorous birds and their predation rates on plasticine caterpillars have been positively linked to structural heterogeneity (Bereczki, Ódor, Csóka, Mag & Báldi, 2014). However, although many studies report pest control effects by insectivorous birds, it is also common to find that potential natural enemies or measures aimed at increasing their natural habitat do not increase pest control or farm production (Chaplin-Kramer, O'Rourke, Blitzer & Kremen, 2011; Pejchar, Clough, Ekroos, Nicholas, & Olsson, 2018). Several reasons including a mismatch in predator-prey life cycles, life history traits and the lack of appetence for or accessibility of prey by predators have been proposed to explain this apparent inconsistency (Tscharntke et al., 2016).

Despite the fact that olive groves are one of the most important agroecosystems worldwide (http://www.fao.org/faostat) and that their major insect pests are well-known, we lack experimental information about the potential of birds as pest controllers in this agroecosystem. Most studies in olive groves have focused on natural arthropod enemies (Alvarez et al., 2019; Paredes, Cayuela, Gurr & Campos, 2015) such as ants, which seem to play an important role in olive pest control (Martínez-Núñez et al., 2021). A recent correlational study focused on bird-driven pest control in olive groves at regional scale in Andalusia (40 olive farms considered) showed generally weak effects of birds on olive pests (Martínez-Núñez et al., 2020). This could be due to a low bird preference for these species, a low pest availability for birds (e.g., mismatching of daily activity periods) or a lack of active insectivorous birds in the olive-tree matrix. Elucidating experimentally the significance of biocontrol by birds and how it is affected by landscape components (i.e. distance to semi-natural patches) is becoming necessary in light of the current progressive intensification of this agroecosystem (Infante-Amate et al., 2016) and the known importance of semi-natural patches in olive groves for conserving bird biodiversity in the Mediterranean (Rey, 2011; Rey et al., 2019).

In this study at a regional scale, we conducted field bird and pest surveys in combination with two extensive field experiments involving plasticine dummies and bird exclusion. We experimentally investigated for the first time the predation potential of insectivorous birds on the two main olive tree pest species, the olive moth *Prays oleae* (Bernard,1788) and the olive fly *Bactrocera oleae* (Rossi 1790), as well as the damage these two invertebrate pests inflict. We also tested how the distance from semi-natural habitat patches affects insectivorous bird richness and abundance (with particular attention paid to forest insectivores), pest abundance, attack rates on plasticine models, and observed crop damage. Our study was conducted exclusively in organic olive farms to avoid any confounding effects caused by pesticides. As mentioned above, a previous study has suggested that the impact of insectivorous birds on olive pests is weak (Martínez-Núñez et al., 2020), and has shown the sensitivity of insectivorous birds to the presence of semi-natural habitat patches. Therefore, we hypothesized that the richness and abundance of insectivorous birds will be higher in patches of semi-natural habitat than in the olive-tree matrix but that this will not have any effect on predation rates/damage control, which overall will be very low and similar in olive trees close to and far from semi-natural areas. On the other hand, if insectivorous birds do have an impact on pest control, predation rates/damage control will be more intense in areas nearer semi-natural habitat patches, where more avian insectivores are found. Our predictions thus are: (1) The abundance and richness of insectivorous birds (and especially forest insectivores) will be higher in patches of semi-natural habitat, compared to the olive-tree matrix; (2) Insectivorous birds will not control effectively pest damage (i.e., bird-excluded and control branches - free access to birds - will be similarly damaged by pests in olive trees); and (3) although pest availability will be high on these farms, attack rates by birds will be low and similar in trees close to and far away from the semi-natural patches the insectivorous birds originate from.
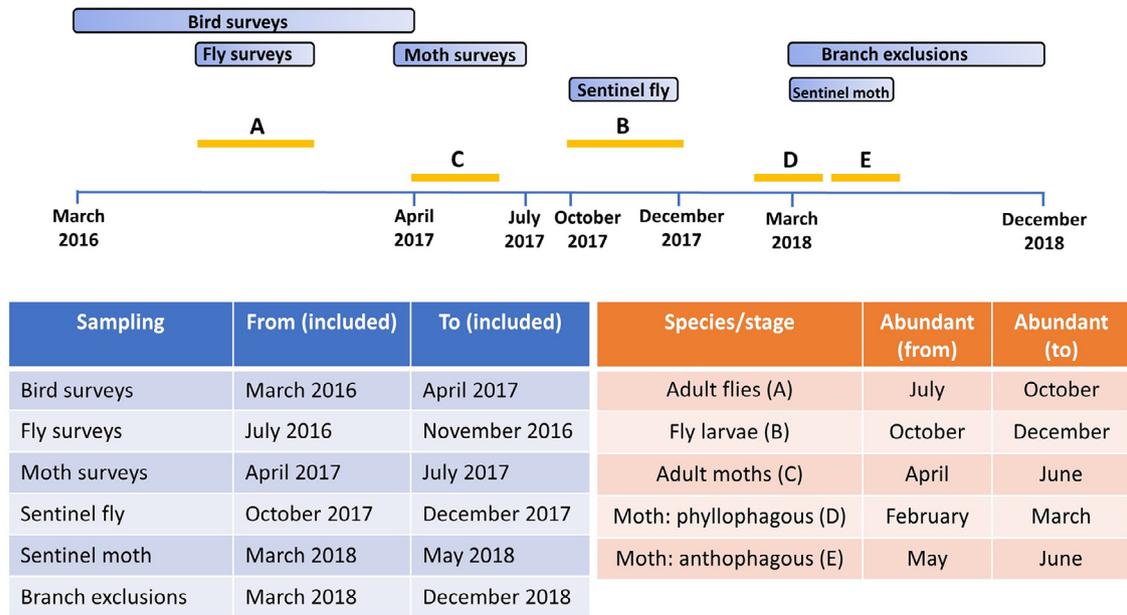
Fig. 1. Chronology of sampling and field experiments, from March 2016 to December 2018. Also, the orange table shows the months where the different stages of the pests are most abundant in our study system (i.e., peak of activity/abundance). Orange lines represent the periods when the different stages of the two pest species are more abundant. Note that the surveys and experiments match the periods of higher abundance (only years of surveys/experiments are displayed).

Materials and methods

Study area

Our study was conducted in Andalusia (S Spain), the region with the highest density of olive trees worldwide. The surveys and experiments were carried out in nine olive farms in an area measuring 311 km (from 5^0 $53'46''$W to 2^0 $64'$ $87''$W) by 190 km (from 38^0 $40'$ $05''$N to 36^0 $78'$ $36''$N). All farms were organic and so the effects of agricultural management are not considered here (see Appendix A: Fig. S1 for a map showing the sites). For additional details of the study sites, see Martínez-Núñez et al. (2019).

Study system: olive pests

In this work we focused on two pest species, *Prays oleae* (the olive moth) and *Bactrocera oleae* (the olive fruit fly). *Prays oleae* flies in three generations and has a complex life cycle that is fully adapted to the phenology of the olive tree. It is found as an adult throughout most of the year, with a peak in April−June. The phytophagous larvae (leaf generation) feed on olive tree leaves and build galleries in winter-spring and could be predated by birds in March, when they are largest and present on leaves. The anthophagous larvae (flower generation) feed on floral buttons and flowers during the flowering period of olive trees in spring (April-May). The larvae of this generation are exposed on flower bunches and are easily predated by birds. The carpophagous larvae (fruit generation) are the most harmful and cause fruit to fall

prematurely in autumn (Pelekassis, 1962). The adult moths of all generations mainly fly at night when most insectivorous bird species are not active.

The olive fruit fly is an obligate olive tree pest. The adult is present most of the year but peaks in number in July−October. Adult flies lay their eggs on the fruit, which the larvae feed on as they develop. The tunnels produced by larvae cause necrosis and fruit to fall from the tree. In autumn, the larvae pupate in the olive fruit or in the soil, where they spend the winter (Daane & Johnson, 2010). The adult flies could be vulnerable to fly-catching birds or other specialists who hunt flying insects, while their larvae are only exposed for a short period of time in October−November when they fall from the fruit and bury themselves shallowly in the ground to pupae. Our experiments/surveys matched the phenology of these pests/stages in our study area (Fig. 1).

Bird surveys

Birds were surveyed monthly from March 2016 to April 2017 (except July and August, twelve surveys) in six (in small farms, < 25 ha) or ten (in large farms, >100 ha) permanent plots per farm separated by ca. 200 m. Inside each farm, two (in small farms) or four (in large farms) of the plots were located in patches of semi-natural habitat (hereafter, non-crop plots), while the rest of the plots were inside the matrix of the olive plantation (hereafter, crop plots). This allowed us to sample communities at farm scale, thereby capturing farm heterogeneity, and also enabled us to compare plot types on the farm (habitat effects). In each of these

plots, experienced ornithologists surveyed the birds heard or seen for five minutes within a 50-m radius from the centre of the plot. Censuses were conducted during the first three hours after sunrise. For this study, only insectivorous birds were considered. Species were classified as insectivorous based on expert knowledge and validated using the functional trait database created by Storchová and Hořák (2018) and Wilman et al. (2014). Given that forest birds may have a greater impact on pests (they forage more specifically in trees where pests may be more vulnerable to birds), these same databases were also used to classify birds as either forest or open habitat species.

Pest abundance

We monitored the abundance of olive moth using funnel traps with pheromone z-7-tetradecen-1-ol, which attracts adult males, and an insecticide pellet. Monitoring was conducted in April−July 2017 (when adults are most active) by means of monthly counts of trapped moths. We also monitored the abundance of adult olive flies monthly in July−November 2016 using McPhail traps with the attractant ammonium bisulfate $((NH4) HSO4)$ diluted in water (4%). On every olive farm, we set either six or 10 traps, which were hung from olive trees throughout the whole farm in the permanent stations where bird surveys were conducted. McPhail traps were checked monthly and refilled with liquid. The olive pests were monitored to assess whether they were abundant enough to be a potential food source for birds. Although the bird surveys and field experiments (see below) were not performed in the same year, bird counts were conducted throughout the whole year and spanned the whole life-cycle of each pest. We did not attempt to relate insectivorous bird abundance and experimental results between farms. Rather, bird censuses were conducted to show that the guild of insectivorous birds is consistently richer and more abundant in semi-natural patches than in the olive-grove matrix, and to explore whether or not this is congruent with higher attack rates on dummies and lower pest damage near semi-natural patches, which theoretically will not vary between years.

Bird exclusion experiment

The aim of this experiment was to test the possible top-down control effect of birds on arthropod pest damage in olive groves. We excluded birds from some olive tree branches and the damage observed on excluded branches was compared with control branches (parallel, close by and similar to the experimental branch) from where birds were not excluded (see García et al., 2018, for a similar approach). On each farm, 10 olive trees were selected, five in the first line of trees next to a patch of semi-natural habitat and five within the olive-tree matrix ca. 100−120 m away

from the reference semi-natural patch (i.e. at some distance from a patch of semi-natural habitat). Experimental trees were arranged non-consecutively to favour data independence. Each selected tree had four excluded branches and nearby control branches. To exclude birds from branches, we used a 80-cm-long and 25-cm diameter cylinder made of $1 cm^2$ pore plastic mesh, with ends closed off with 2-mm^2 pore plastic mesh (Fig. 2). In total, at the beginning of March 2018 we excluded 360 branches on 90 trees, which remained excluded throughout the year. We conducted three checks of the damage to control and excluded branches by measuring damage to leaves, flowers and fruit. Specifically, we sampled: i) leaf damage produced by the leaf-miner larvae of the olive moth and other phytophagous insects at the end of March because damage to leaves caused by *Prays oleae* is most evident in this month; ii) leaf and flower damage by anthophagous larvae of the olive moth and other phytophagous insects in May; and iii) leaf and fruit damage by the moth, fly and other phytophagous insects at the end of October−beginning of November.

Sentinel prey experiment

We used plasticine models to evaluate potential avian predation pressure on the two olive pest species and to determine the predation pressure as a function of the distance to patches of semi-natural habitat. Plasticine models (dummies) are commonly used in field experiments to assess and compare attack rates by certain predator guilds on specific prey items (Howe, Lövei & Nachman, 2009; Lövei & Ferrante, 2017). We mimicked the larvae of two generations of olive moth (phytophagous generation in March−April and anthophagous generation in May) and the larval stage of the olive fly (in October−December), all stages being considered as replicates of the same treatment. Plasticine models were the same size, shape and colour as the pest stage they were mimicking (see Fig. 1 for an example). In each experimental round, we set four plasticine models per tree in five trees near a patch of semi-natural vegetation and in five trees inside the olive-grove matrix. Selected olive trees were separated from the other selected trees by at least one other tree, ca. 20−30 m. Dummies were fixed to the ground, leaves or flowers depending on the pest species and the generation they were mimicking (Fig. 2). We conducted a total of six rounds per site (two rounds per pest and larval stage), and used a total of 2160 plasticine models (240 per site). We detected and counted predation marks by birds (beak marks) and by other predators (mainly ants, many small bites) on the plasticine models. All dummies were checked after 7 ± 1 days of exposure (Mäntylä et al., 2008) (with the exception of the first round in which we used 15 days ± 2 days). This method has been criticized in some systems for not being realistic (Zou et al., 2017) and so we initially also set up cameras to confirm that predation by birds on our plasticine models did take place.
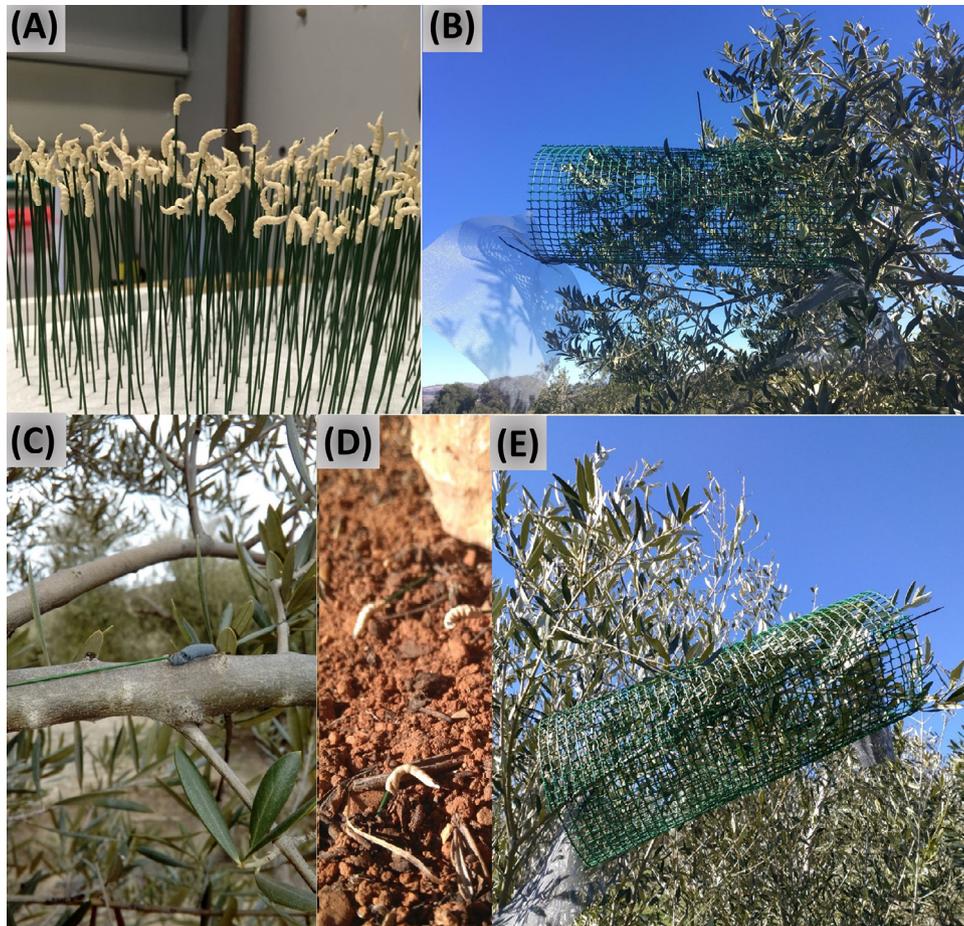
Fig. 2. Plasticine models of *Bactrocera oleae* in the laboratory (A). *P. oleae* phytophagous stage with predation marks (C) and *Bactrocera oleae* in the field; various models together used for a preliminary camera trap experiment (D). Pictures B and E show excluded olive branches (with the ends still open).

Statistical analyses

First, we searched for patterns linking the abundance and richness of insectivorous birds (by pooling information from the ten rounds in each permanent station) to habitat type (non-crop patches vs. crop patches) to elucidate whether birds use the olive-tree matrix or are mainly restricted to semi-natural patches. Because some vulnerable stages of the studied pests are terrestrial, we first only took into account insectivorous birds. However, we then reran the analyses considering only forest insectivorous birds, since this guild could have a greater impact on olive pests (they can forage in trees). We thus ran Bayesian models with insectivorous bird abundance/bird richness as response variables and the type of habitat in which they were detected as the explanatory variable. We included 'Farm ID' as a random factor in the models due to the nested sampling design. Response variables were log-transformed to run normal models. We employed multilevel mixed Bayesian models fitted through the MCMC (Markov Chain Monte Carlo) method using the *brms* package (Bürkner, 2017) in *R* (R Core Team 2019).

Results were interpreted as the posterior probability of the beta (slope) being positive/negative.

Second, we ran the same type of multilevel Bayesian mixed models using the *brms* package to search for patterns in the damage observed in excluded and control branches. The response variables − damage produced by moths, flies and other herbivores − were arcsine square-root transformed since they were proportions (observed damage in relation to number of leaves, flowers and fruits counted). The explanatory variables were treatment (excluded vs. control) and site (close to a semi-natural patch or in the olive-tree matrix, or far from the semi-natural patch). Farm and tree ID were introduced as random factors.

Finally, we tested how observed attack rates on pest dummies varied with distance to semi-natural patches (as factor: close vs. far away). Attack rates (attacked/exposed) were arcsine square-root transformed and linear mixed Bayesian models fitted. Farm ID was included as the random factor in every model.

For all the Bayesian models, we checked convergence through R^ (all equal to 1 or 1.01), the normality of the

Table 1. Results of the Bayesian hierarchical models showing the estimated effect of plot type (non-crop plot vs. crop plot) on the abundance/richness of insectivores and forest insectivorous birds. The table gives the posterior estimate, standard error, 95% credible intervals, and the probability of beta being over 0. Results are given in a log scale; in bold, estimates with a posterior probability of over 90% that the beta (slope) is negative.

Model	Fixed factors (beta/ slope)	Estimate	Standard error	95% LCI	95% UCI	Prob. $\beta > 0$
Abundance insectivorous birds	Non-crop plots (intercept)	4.28	0.11	4.06	4.50	
	Crop plots	**−0.31**	**0.07**	**−0.44**	**−0.18**	**0**
Richness insectivorous birds	Non-crop plots (intercept)	3.16	0.07	3.02	3.30	
	Crop plots	−0.00	0.03	−0.07	0.06	0.48
Abundance forest insectivorous birds	Non-crop plots (intercept)	3.91	0.10	3.70	4.11	
	Crop plots	**−0.40**	**0.09**	**−0.56**	**−0.23**	**0**
Richness forest insectivorous birds	Non-crop plots (intercept)	2.21	0.09	2.03	2.39	
	Crop plots	**−0.09**	**0.06**	**−0.21**	**0.02**	**0.05**

residuals, and the stability of results (by visual inspection of the chains). We also inspected models' goodness-of-fit via plots by contrasting observed data with posterior data generated using model simulations ($N = 200$ datasets simulated). For all models, we used uninformative diffuse priors and model specifications that rendered stable outputs (four chains and 50,000 iterations with a burn in of 10,000). All the analyses were run using R, version 3.6.1 (R Core Team 2019).

Results

During the surveys, 86 different species of insectivorous birds belonging to 62 genera and 36 families were identified; of them, 47 were forest insectivores belonging to 36 different genera (see Appendix A: Table A. 1 for the complete list of species). In all, 4966 insectivorous birds were detected during the year inside the 50-m-radius plots, of which 3349 were forest insectivores. The most abundant species were Sardinian warbler (*Sylvia melanocephala*; 15.9% of the total), Eurasian blackcap (*Sylvia atricapilla*; 11.8%), common chaffinch (*Fringilla coelebs*; 10.9%) and European robin (*Erithacus rubecula*; 10.5%). Of the bird families typically considered to be important for pest control in savannah-like agroecosystems, the Paridae (four species and 11% of total abundance), Picidae (three species and 0.2% of total abundance) and Regulidae (one species, *Regulus ignicapillus* detected outside the 50-m radius of the point censuses and so not included here) were scarce in olive groves. *Parus major* was the most frequent (8%), followed by *Cyanistes caeruleus* (3%); both *Lophophanes cristatus* and *Periparus ater* were rare and, like *Picus viridis, Dendrocopos major* and *Jynx torquilla*, only appeared in association with semi-natural and riparian forest patches. Finally, the flycatchers (two species) were also poorly represented (< 0.5%).

Insectivorous birds were strongly associated with non-crop patches (Table 1) and were less abundant in crop patches (Mean beta/slope estimated = −0.31; Probability of the slope > 0 = 0; Prob β hereafter). This pattern was stronger when only forest insectivores were taken into account, as both their abundance (Mean beta estimated = −0.40; Prob $\beta > 0 = 0$) and species richness (Mean beta estimated = −0.09; Prob $\beta > 0 = 0.05$) decreased in crop plots.

The abundance of pests captured in traps was high in all olive groves (ranging from 277 to 2216 mean captures/trap for moths and from 21 to 625 mean captures/trap for flies). Neither moth nor fly abundances were related to total insectivorous or forest insectivorous bird abundance or richness (see Appendix A: Table A.2).

There were no differences between the control and excluded branches (see Table 2 and Fig. 3) regarding damage caused by the moth (Mean beta, excluded branch = −0.01, Prob $\beta > 0 = 0.25$). Excluded branches were less damaged by flies (Mean beta, excluded branch = −0.10, Prob $\beta > 0 = 0$), phytophagous insects (Mean beta, excluded branch = −0.05, Prob $\beta > 0 = 0$) and overall pests (Mean beta, excluded branch = −0.04, Prob $\beta > 0 = 0$). Trees adjacent to semi-natural patches were less damaged than trees in the olive-grove matrix for all types of damage measured (Mean beta for matrix trees = 0.04, Prob $\beta > 0 = 1$ for moths; 0.05, Prob $\beta > 0 = 0.98$ for flies; 0.06, Prob $\beta > 0 = 1$ for phytophagous insects; and 0.05, Prob $\beta > 0 = 1$ for all types of damage pooled) (Table 2 and Fig. 3).

The observed attack rates on plasticine models were extremely low: $N = 144$ bird attacks (less than 0.8% per day; represented hereafter as d^{-1}) and $N = 344$ total attacks (by birds plus others, slightly over 1.9% d^{-1}) (Fig. 4). The models showed that there was a higher probability of attack on dummies at sites far from the semi-natural patches for *Bactrocera oleae* ($\beta = 0.03$; Prob $\beta > 0 = 0.98$) but not for *Prays oleae* ($\beta = 0.00$; Prob $\beta > 0 = 0.22$). However, differences were not substantial and the main conclusion drawn from this experiment is that attack rates by birds were generally low (on average less than 6%).

Table 2. Results of the Bayesian multilevel models showing the estimated effect of site (close vs. far from semi-natural patch) and treatment (excluded vs. control branch) on the total damage observed on olive trees. The table displays the posterior mean, standard error, 95% credible interval, and Rˆ statistic for each parameter of models with a varying intercept by locality and tree; in bold, factor levels with a β parameter higher or lower than 0 (probability of 95%).

Model	Fixed factors	Posterior intercepts and betas	Standard error	95% LCI	95% UCI	Rˆ
P. oleae damage	Intercept (Control branch and close to patch)	0.14	0.03	0.08	0.20	1.00
	Excluded branch	−0.01	0.01	−0.03	0.01	1.00
	Far from patch	**0.04**	**0.01**	**0.02**	**0.06**	**1.00**
B. oleae damage	Intercept (Control branch and close to patch)	0.34	0.07	0.20	0.48	1.01
	Excluded branch	**−0.10**	**0.03**	**−0.16**	**−0.04**	**1.00**
	Far from patch	**0.05**	**0.03**	**−0.01**	**0.12**	**1.00**
Phytophagous damage	Intercept (Control branch and close to patch)	0.60	0.09	0.43	0.78	1.01
	Excluded branch	**−0.05**	**0.02**	**−0.09**	**−0.01**	**1.00**
	Far from patch	**0.06**	**0.02**	**0.02**	**0.10**	**1.00**
Total damage	Intercept (Control branch and close to patch)	0.47	0.04	0.37	0.55	1.00
	Excluded branch	**−0.04**	**0.01**	**−0.07**	**−0.02**	**1.00**
	Far from patch	**0.05**	**0.01**	**0.03**	**0.08**	**1.00**
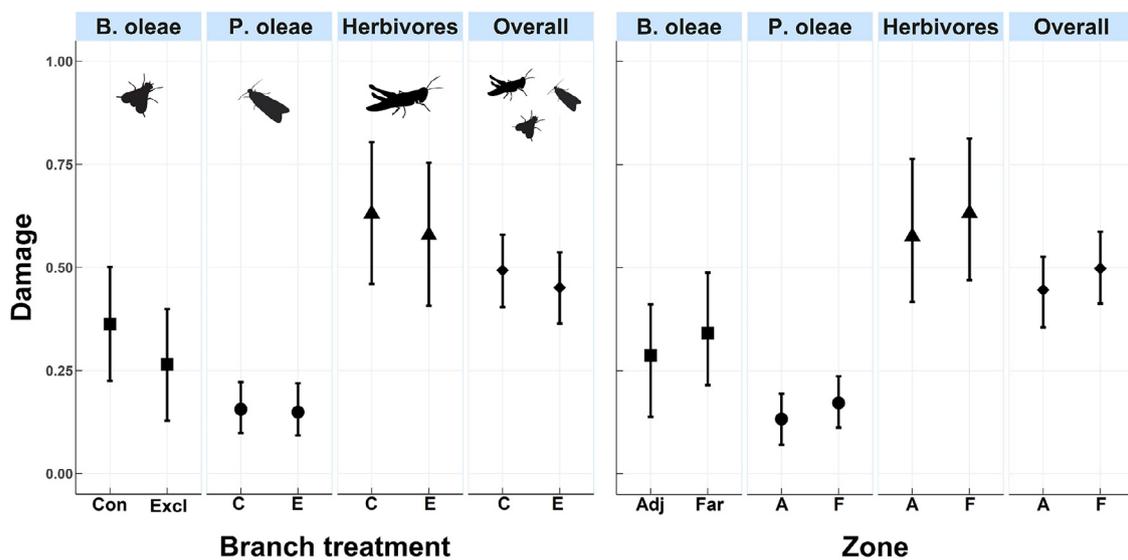
Fig. 3. Back-transformed predicted damage (proportion) by *Prays oleae*, *Bactrocera oleae*, other phytophagous insects (herbivores) and overall damage (cumulated), and its variation across treatments (Control vs. Excluded branch) and Zone (Adjacent to semi-natural patch =Adj. vs. olive orchard matrix, far from semi-natural patches= Far). Solid symbols show predicted posterior mean and whiskers 95% credible intervals.

Discussion

Our results support our main predictions given that non-crop habitats hosted higher abundance and richness of insectivorous birds (above all, forest insectivores). Additionally, excluded branches were not more damaged by pests and attack rates on plasticine models were very scarce, even in trees adjacent to semi-natural patches. Together, these results suggest that, although the lack of semi-natural patches could jeopardize insectivorous bird communities,

the pest control ecosystem service provided by these bird communities in these environmentally friendly olive groves is inherently very low. The sites selected for this study were on well-conserved farms (organic farms with herbaceous cover and some located in very complex landscapes) close to the maximum potential for avian community richness in olive groves in Andalusia (as suggested by Rey et al., 2019). Yet, the experiments showed that these bird communities exert no pest control. Our findings suggest that birds' inability to control olive pests could be due to an idiosyncratic
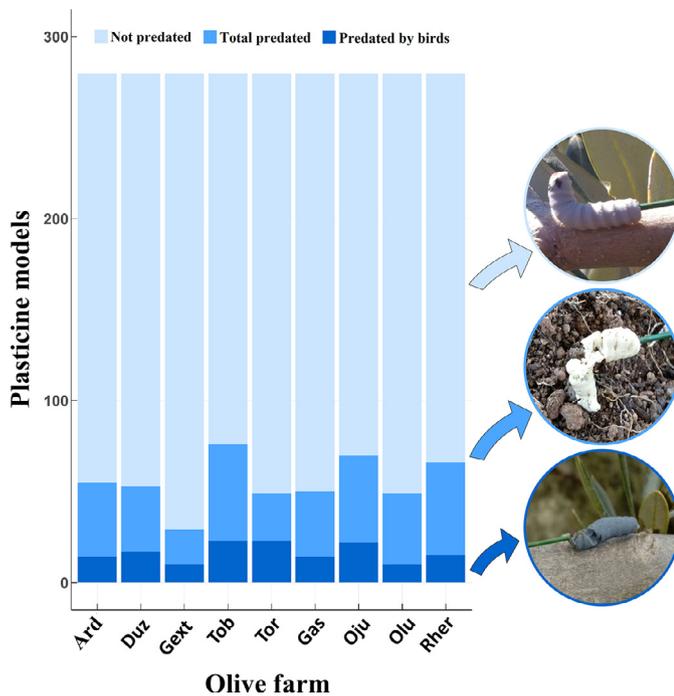
Fig. 4. Observed number of plasticine models attacked by birds (dark blue) by any predator but mainly ants (clearer blue) and not attacked (light blue).

lack of appeal to the insectivorous bird species currently inhabiting olive groves and/or the bird's difficulties in accessing these pest species.

The bird exclusion experiment showed that insectivorous birds in these olive groves do not exert effective pest control. While other studies conducted in other groves and agroforests have found more damage on the branches/trees from which birds had been excluded (García et al., 2018; Maas et al., 2013), we found similar or less damage in excluded branches compared to control branches at all our study sites. For the olive fly and other phytophagous insects, we found more damage on control branches. These results could be due to intraguild predation, with birds predating preferentially on other arthropods such as ants or spiders on control branches, thereby releasing pests from these mesopredators (Maas, Tscharntke, Saleh, Dwi Putra & Clough, 2015). In any case, birds did not reduce pest damage. Interestingly, trees close to semi-natural patches had less damage than trees located inside the olive-grove matrix. This decrease in damage was not affected by branch treatment (excluded or control), which suggests that some small arthropods associated with semi-natural patches are effective natural enemies of these two olive pests. This predation pressure might affect pest preference for trees inside groves or directly reduce pest populations in trees close to semi-natural patches. Some studies have pointed out the key role of natural arthropod enemies such as *Anthocoris nemoralis* (Fabricius) (Paredes, Karp, Chaplin-Kramer, Benítez & Campos, 2019), ants (Martínez-

Núñez et al., 2021) and other terrestrial species (Dinis et al., 2016) in olive groves. Semi-natural patches and ground cover seem to be key as they provide habitat and alternative prey items (Paredes et al., 2019). Ours results endorse the positive role of natural habitat fragments in pest control in agroecosystems, and confirm the greater predation rates observed in areas close to semi-natural patches/ecotones, as previously reported by other authors from different systems (Barbaro, Giffard, Charbonnier, van Halder & Brockerhoff, 2014; Maas et al., 2015; Milligan, Johnson, Garfinkel, Smith & Njoroge, 2016).

Recorded attack rates on plasticine models were extremely low, which matches the results of the previous experiment (i.e. the branch exclusions). The *Bactrocera oleae* dummies were more easily detected in the olive-tree matrix since a subtle increase in the attack probability on this species was observed in these sites. Nonetheless, the observed numbers are well below the attack rates needed for effective pest control. Much higher attack rates on dummy prey items have been found in other agricultural systems including oil palm plantations (37% without and 53% with riparian forest fragments) (Gray & Lewis, 2014), apple orchards (63%, Martínez-Sastre et al. in press), cacao agroforest matrices (2.9% d^{-1} attack rate by birds, and 6.5% d^{-1} including all arthropods) (Maas et al., 2015) and cotton fields (ca. 4% d^{-1}) (Howe, Nachman & Lövei, 2015).

We recorded a large number of adult pests in traps (mean of 1372 per trap for olive moths and 134 per trap for olive flies, above the levels typically used as thresholds for insecticide/pheromone application by growers (https://www. mapa.gob.es/es/agricultura/temas/sanidad-vegetal), and the observed damage was also high (ca. 15% damaged by olive moths; ca. 30% by olive flies; and ca. 60% of leaves damaged by phytophagous insects). This is evidence of the high density of moths, flies and other phytophagous insects in the studied farms. However, despite this high temporal availability of pests, insectivorous birds only occasionally seem to feed in the olive groves, which suggests a generally overall limited attractiveness of the olive-tree matrix for avian insectivore groups, especially forest insectivores, and only very limited spillover from adjacent semi-natural areas (Blitzer et al., 2012; Boesing et al., 2017). This is supported by the fact that insectivorous bird assemblages were higher in non-crop patches on farms than in the olive-tree matrix, an effect that was even stronger for forest insectivores. Other studies have also shown that the abundance and richness of insectivorous-frugivorous birds drops in olive groves in relation to semi-natural wild olive scrublands and other reference woodlands (Rey 1993; 2011). Forest insectivores have also been shown to decline in olive groves during the breeding season depending on the degree of agricultural intensification and/or landscape simplification (Castro-Caro, Barrio & Tortosa, 2015; Morgado et al., 2020). This limited attractiveness of the olive-tree matrix could be related to the current suboptimal (structural and feeding) conditions of this habitat, in which management implies the regular

distribution of trees, an absence of nesting cavities in tree trunks, and small, low tree canopies.

To our knowledge, this is the first study to have ever assessed pest control by birds in olive groves and so no comparison of our results is possible. Unfortunately, there is no reference information since there is a notable lack of studies analysing the relationship between the diets of insectivorous birds in olive groves and the major pests found in these groves. As in other agroecosystems (e.g. Karp et al., 2013 in coffee plantations and Mangan, Piaggio, Hopken, Werner & Pejchar, 2018 in apple orchards), studies analysing bird diet using molecular tools (e.g. DNA analyses from faecal sampling) are needed to elucidate how frequently insectivorous birds feed on olive pests.

Further research is also needed to unravel the specific mechanisms underlying the reasons why birds barely use the olive-tree matrix as a habitat and so are not effective pest control agents against olive pests. Our results point to a lack of appetence, preference or inaccessibility to the prey implicit in the life histories (Tscharntke et al., 2016) of the current insectivorous species, and rule out overall insectivorous bird abundance as the main driver. For instance, although preliminary analyses suggest that the energetic demand of insectivorous birds throughout the season in our olive farms is well above the energetic offer potentially provided by fly abundance (Camacho 2020), there are very few flycatchers or other foragers that predate on the abundant adult flies; likewise, fly larvae are accessible to birds only on the ground (they develop within the fruit) and for only a few seconds or minutes before they bury themselves. In the case of moths, flying adults are predominantly active in the early evening (Herrera J.M. pers. com), which does not match the main activity period of insectivorous bird.

This study thus suggests that, despite the fact that insectivorous birds are jeopardized by the lack of semi-natural areas in olive groves, their communities are currently inherently unable to act as effective biological control agents against the two main olive tree pests in Andalusia (Spain). Habitat improvement for increasing abundance and spillover into the olive groves by some bird species with specific functional traits and foraging behaviour could help enhance pest control by birds in this agroecosystem. Good examples would include birds such as flycatchers, species that forage on buried insect larvae and invertebrates (e.g. *Upupa, Scolopax, Vanellus* and *Burhinus*), or twig-gleaners able to forage on insects present in hanging flower bunches (e.g. *Regulus* and *Parus* spp.), which are currently underrepresented or absent in olive groves (Boesing, Nichols, & Metzger, 2017)

Data deposition information

Data supporting the main findings of this study are freely available in this link: 10.17632/v8f6xc55td.1.

Declaration of Competing Interest

None.

Acknowledgments

Supplementary materials

Supplementary material associated with this article can be found in the online version at doi:10.1016/j.baae.2021.08.006.

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