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Natural habitat increases natural pest control in olive groves: economic implications

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Abstract

Natural habitat at the landscape scale can promote biological control of crop pests, but farmers often regard natural habitat as a cost or a lost economic opportunity. Evaluating the benefits of promoting natural habitats in economic terms should make different management alternatives easier to compare. However, it is important to understand the mechanisms underlying the connection between natural habitat and natural pest control. In this study, we link measurements of natural habitat and ground cover with abundances of multiple natural enemy groups and biological control of the olive pest *Prays oleae* to describe spatial patterns in biocontrol and the economic value associated. Natural habitat increased biocontrol and crop yields by an average of 186.36 €/ha. This could be attributable to the entire community of predatory natural enemies present in the olive regardless of natural habitat. One predator species of this community, *Anthocoris nemoralis*, whose abundance was influenced by natural habitat, was strongly associated with elevated biocontrol. We hypothesize that this predator species could be the link between natural habitat and the biological control. Our results suggest that olive growers could stand to gain from conserving natural habitat. Moreover, our evidence suggests that minimizing the use of chopped pruning remains may result in increased biocontrol by bolstering the abundance of *A. nemoralis.* More generally, our study indicates that diversifying olive orchards and surrounding landscapes may improve olive yields.

Keywords *Anthocoris nemoralis* · Ecosystem services · *Euphyllura olivina* · Ground cover · Landscape · Natural enemies · *Prays oleae* · Yield

Key messages

- Natural habitat can improve pest biocontrol, but farmers often do not see the benefit of this strategy.
- Natural habitat increases crop yield by an average of 186.36 €/ha.
- *Anthocoris nemoralis* could be mediating the effect of natural habitat on biocontrol.
- Olive farmers can take advantage of promoting natural habitat for simultaneously enhancing conservation and sustainable olive production.

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Introduction

The global intensification of agriculture to meet growing demands for food is leading to more intensive farm management systems as well as an increase in the area of land devoted to farming, exacerbating an ongoing biodiversity crisis (Dirzo et al. 2014). Nevertheless, management practices such as the promotion of high crop diversity and natural habitats in agricultural landscapes can sometimes maintain both biodiversity and high yields (Letourneau et al. 2011) through the provision of biodiversity-driven ecosystem services (Cardinale et al. 2003; Ehrlich et al. 2012). Biological control—when predators and/or parasitoids suppress pest abundances—is one such service. Beyond directly reducing crop damage, enhancing biological control may also provide a viable alternative to excessive pesticide applications, which are directly responsible for human health problems (Bouchard et al. 2011; Marks et al. 2010), biodiversity declines (Hallmann et al. 2014; Kohler and Triebskorn 2013) and declines in the provision of other ecosystem services such as pollination (Whitehorn et al. 2012).

Natural habitats in agricultural landscapes are made up of a combination of natural and semi-natural habitats such as cropland boundaries, fallow land, grasslands, woodlands, wetlands and forests. Recent syntheses of the landscape ecology of natural pest control have reported more abundant and diverse communities of natural enemies in complex heterogeneous landscapes with natural habitats as compared to simple landscapes (Bianchi et al. 2006; Chaplin-Kramer et al. 2011). However, despite some showing that natural habitats can enhance natural pest control through natural enemy activity, the effectiveness of this strategy remains uncertain (Chaplin-Kramer et al. 2011; Karp et al. 2018). Indeed, natural habitat may fail to provide effective pest control because (1) natural habitats can also promote pests, (2) the amount or configuration of natural habitat may be deficient, (3) some pests may not be controlled by natural enemies, (4) crops may provide more resources for natural enemies than natural habitats and/or (5) local agriculture practices (e.g. pesticides) may counteract pest control (Tscharntke et al. 2016).

The effect of natural habitat on biocontrol has also been shown to be modulated by ground cover (Jonsson et al. 2015; Paredes et al. 2015a; Rusch et al. 2010), which can directly affect herbivore suppression, natural enemy abundance and crop damage reduction (Letourneau et al. 2011). Nevertheless, as with natural habitats, much debate continues to surround the effectiveness of ground cover in relation to natural pest control (Poveda et al. 2008). Recent studies have identified important interactions between local ground cover and natural habitat in the landscape: these habitat elements together have proven capable of increasing the abundance (Paredes et al. 2013a; Woltz et al. 2012) and diversity of natural enemies (Ditner et al. 2013) as well as the associated effect of biological control on crop yields (Jonsson et al. 2015; Tamburini et al. 2016). This highlights the importance of analysing, in an integrated manner, the impact of natural habitats at the landscape scale, local management practices, and associated natural enemy biodiversity on biocontrol (Chaplin-Kramer et al. 2011).

In practical terms, whether farmers maintain natural habitats will likely depend on a suite of trade-offs, in part associated with yields and income (Karp et al. 2013). Typically regarded as unused cropland and a source of pests, natural habitats are often seen as representing a cost or a missed economic opportunity (Tscharntke et al. 2016). Therefore, it is crucial to provide farmers with information on the economic importance of natural pest control promoted by natural habitats in order to incorporate this ecosystem service into future landscape planning (Daily et al. 2009). Relatively few studies have analysed the economic value of natural habitats for pest control. Depending on the crop involved, it can range from \$7391/ha for South Australian citrus plantations (Colloff et al. 2013) to \$37/ha for soya beans in the USA (Landis et al. 2008). Therefore, accurate estimations are crucial in order to be able to come up with realistic recommendations for different crop growers.

Economic analyses of pest-suppression services are particularly lacking for olive groves. Olives are considered a strategic crop for the European Union, as four producer countries (Italy, Greece, Portugal and Spain) are responsible for ~75% of global production. More than half of global olive oil production occurs in Spain; as such, olive production constitutes a vital part of the Spanish economy (International Olive Council 2017). In Southern Spain, olive groves are mainly grown as a monoculture that slightly alternates with other crop such as cereals, almonds or vineyards and patches of remaining Mediterranean natural vegetation. In 2015, olive growers encompassed around a half a million hectares, of which 62% was non-irrigated. "Picual" variety is the most common variety (58%), followed by "Hojiblanca" (18%) and "Manzanilla" (5%). The average density of olive trees is 131 trees /ha. More than half (58%) of olive farmers do not explicitly ground cover within their orchards. Often spontaneous ground cover is allowed to grow (40% of orchards), whereas other farmers plough the ground and engage in superficial tillage (35%) (Junta de Andalucia 2016a). Approximately 25% of olive groves implement integrated pest management criteria (IPM), in which insecticides are only applied after pest populations exceed relevant economic thresholds (Junta de Andalucia 2016b).

In olive groves, *Prays oleae* (Lepidoptera: Yponomeutidae) is a major pest in the Mediterranean region. In most years, ~10% of olives are lost to the pest, but in some years, losses can increase to 50% of the harvest (Ramos et al. 1998). Each year, *P. oleae* undergoes three generations in the olive tree. The phyllophagous generation overwinters in the leaves as a larva and then feeds on leaves. The adults of this generation emerge and lay eggs on the flowers, thus beginning the anthophagous generation. The eggs develop into larvae and feed on the olive flowers. The adults then lay their eggs on the olive fruits, giving rise to the most harmful generation—carpophagous generation. The larva of this generation penetrates the fruit, feed on the stone, and cause the fruit to drop prematurely, before it can be processed into oil or table olives. Adults emerge from fallen olives, ready to lay eggs on olive leaves and complete the cycle.

Critically, natural enemies have the best potential to reduce pest infestations and olive damage during the anthophagous generation (Morris et al. 1999). Many natural enemies have been identified as potentially controlling of this pest, including predators such as *Anthocoris nemoralis* (Heteroptera: Anthocoridae), *Chrysoperla carnea* (Neuroptera: Chrysopidae), and groups such spiders, ants and mirids (Morris et al. 1999).

In this study, we discuss biocontrol strategies for olive farming based on the results of an experiment studying associations between surrounding natural habitat, ground cover, the abundance of different natural enemy groups and biological control in order to economically value biological control and analyse underlying ecological mechanisms. Specifically, we aim at answering the following questions: (1) Does natural habitat and/or ground cover have an effect on natural enemies? (2) Do natural enemies have an effect on biological control? (3) Does natural habitat or/and ground cover have an effect on biological control? And (4) if so, how does this effect translate into monetary terms?

Materials and methods

Study sites and experimental design

The experiment was carried out in the Sierra Subbética in the province of Granada in Andalusia in the south of Spain (Fig. 1). The experimental site covered a total area of 1616 km^2. We selected a total of nine olive groves with the following characteristics: Picual cultivar, rainfed irrigation, a field size of > 10 ha. Olive trees were of a single foot with a canopy of around three metres in diameter. Each grove was at least 10 km apart (Fig. 1c). Three experimental plots were delineated in each olive grove (a total of 27 plots). The three plots were located at least 300 m apart (mean ± SD = 602.44 ± 231.36 m; supplementary material 1) to exceed the dispersal threshold of natural enemies in perennial orchard (120 m) established by Miliczky and Horton (2005). Locations of plots were purposely chosen to vary in the amount of surrounding natural habitat at a landscape scale (Fig. 1d). Focal plots that were intended to be located in landscapes surrounded by natural habitat were located near edges (so that they could be near natural habitat). However, in most landscapes, olive groves are surrounding focal olive farms; thus, placing a plot near the boundary of a field could still allow it to be surrounded by more olive trees. Moreover, most of the plots with no influence of natural habitat were placed in the middle of the olive groves. Natural habitat was dominated by trees in the genus *Quercus*, as well as the following species: *Cistus albidus*, *Rubus ulmifolius*, *Dittrichia viscosa*, *Ulex parviflorus*, *Crataegus monogyna*. Each square-shaped plot comprised 7 × 7 olive trees (Fig. 2). No chemical treatments were applied during the experiment. However, an outer buffer around the experimental plot was established to ensure that no chemicals outside the plot affected the focal trees (Fig. 2). Within this

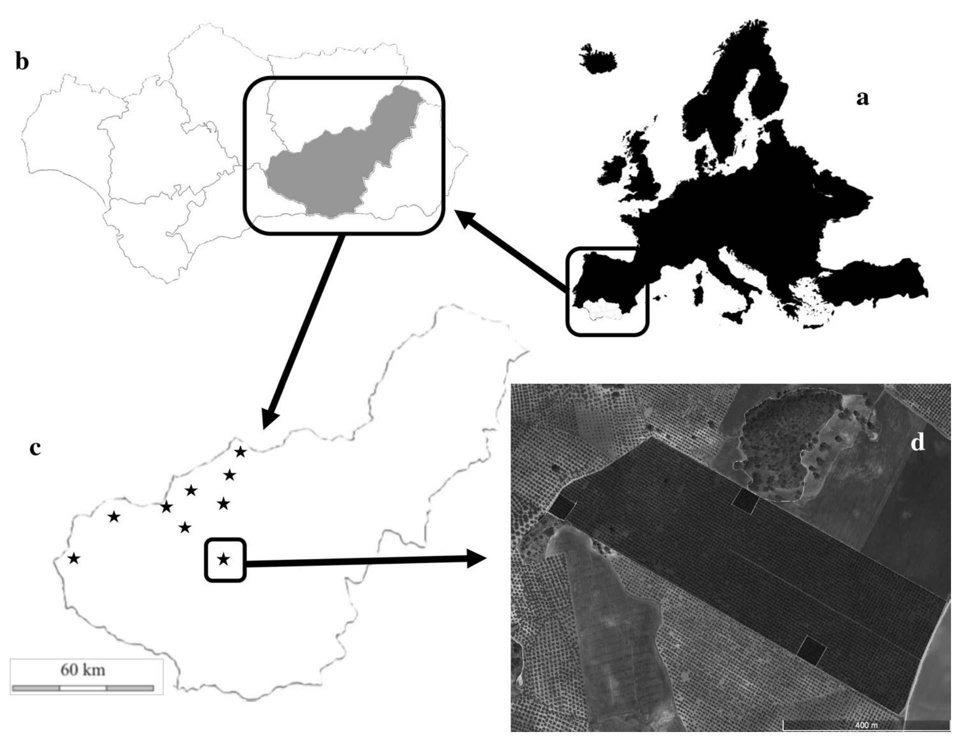

Fig. 1 **a** Andalusian region of Spain; **b** the province of Granada in Andalusia; **c** locations of experimental olive grove sites in the province of Granada; **d** photograph of an experimental olive grove site with its experimental plots and natural habitat patches

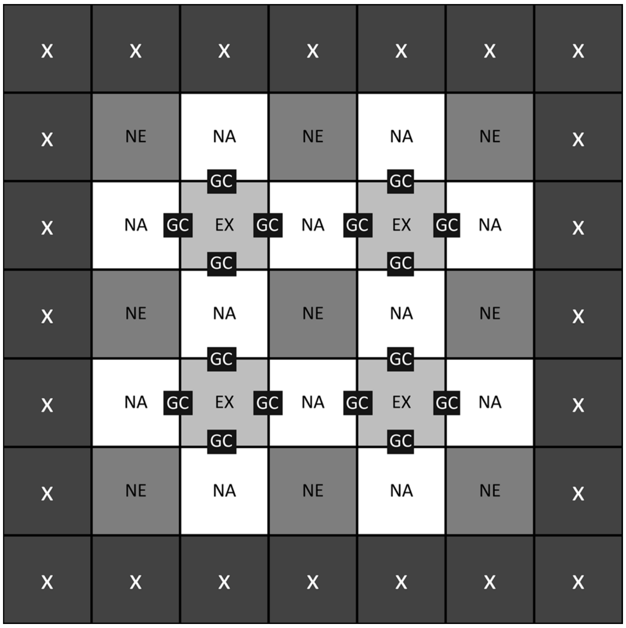

Fig. 2 Diagram of the 7×7 grid of olive trees in a square-shaped experimental plot. *X* stands for the outer buffer around olive trees, used to prevent entry of pesticide treatments, *NE* stands for natural enemy and secondary pest sampling, *EX* stands for excluded branches, *GC* stands for ground cover measurements, *NA* stands for no action taken

buffer and in the remaining square-shaped plots comprised of 5 × 5 olive trees, biocontrol, natural enemy and ground cover samples were collected as depicted in Fig. 2.

Damage calculation

We measured damage to olives from the pest *Prays oleae*. In the centre of each experimental plot, we selected four trees and conducted a natural enemy exclusion experiment on each tree (Fig. 2). Specifically, we randomly covered one branch per tree with a 0.25 mm mesh (1.50 m × 0.90 m) to exclude any natural enemies that may arrive to consume pests. Prior research in the laboratory did not yield any noticeable effects of this kind of exclusion on the development of the pest and tree. In addition, while prior experiments performed with a mesh size similar to ours did detect an effect of the exclusion cage on wind speed and solar radiation, no impacts were observed on other climate variables such as temperature or humidity (Perillo et al. 2015; Yang et al. 2018). Critically, temperature and humidity are the climate variables most directly related to the development and abiotic mortality of the different life stages of *Prays oleae* (Ramos et al. 1978, 1998). To our knowledge, there have been no studies that have focused on the dispersal capacity of *P. oleae* within an olive tree. However, there is a consensus that the distribution of a population across an olive grove is homogenous (making there no *a priori* reason that the cages should end up concentrating damage). Indeed, the cage treatments just as easily could have prevented colonization of caged fruits as it could have concentrated damage on them. Most importantly, the effect of caging was uniformly applied across the landscape gradient. Therefore, even if the cage effect was biased upwards (or downwards), the direction effect of landscape context would still be preserved.

As mentioned, *Prays oleae* overwinters as a larva in the olive leaves and is already present in the olive trees at the beginning of spring; thus, it did not need to be introduced onto the olive trees for our experiments. We began excluding branches at the beginning of March 2016, before the pest finished hibernating in the leaves and before natural enemies arrived (Paredes et al. 2013a). We removed the mesh at the end of August 2016, after *P. oleae* had completed most of its life cycle. During this period, the pest completed its phyllophagous and anthophagous generations (feeding on olive leaves and flowers), and developed in carpophagous larvae (infecting the olive fruits). Our protocol followed the Warning and Information Plant Protection Network of the Andalusia Government (Red de Alerta e Información Fitosanitaria; RAIF in Spanish) (Junta de Andalucia 2016b).

At the end of exclosure experiment, we then collected 50 olives from each mesh-covered olive branch and another 50 from another branch on the same tree, from each of the four trees present within each experimental plot. Thus, we collected a total of 200 fruits per treatment and per plot. We opened the olives using pruning shears to determine whether olive moth larvae were present in the stone, this means that this olive will drop in the end of September and it will not be used to be processed into oil. We quantified the total number of positive incidences per plot. We then calculated the percentage of damage in relation to the total amount of olives collected from the excluded and non-excluded branches. When the number of olive fruits in the excluded branch was below 50, we calculated the percentage of damage out of the total number of olive fruits collected. Finally, we created a biocontrol index of damage reduction by subtracting the percentage of damage in the non-excluded branch from the percentage of damage in the excluded branch.

We used Moriana et al. (2003) to translate olive damage reductions into estimates of the economic value of biocontrol. For mature rainfed olive groves of the variety “Picual”, these authors reported an average production of 1150 L/ha across 3 years. Olive oil prices were extracted from the Observatory of Prices and Markets of the Andalusian Region (Junta de Andalucia 2018). We averaged the wholesale prices of the last 5 years, resulting in a value of 3.09 €/L of olive oil. Based on these figures, we estimated farm revenues at 3553.50 €/ha. This figure was subsequently used to calculate the economic value of biocontrol.

Natural enemies and secondary pest

Natural enemies were sampled in nine olive trees per experimental plot as shown in Fig. 2. As the *P. oleae* life cycle is synchronized with the phenological stages of the olive tree, we collected natural enemy samples four times during the growing season, according to stages at which the pest is susceptible to predation or parasitism (Morris et al. 1999). These stages were: shoot development, inflorescence emergence, flowering and fruit development; and are paired with pest stages of the phyllophagous larva, anthophagous eggs, anthophagous larva and carpophagous eggs. We used a suction sampling with a device called InsectaZooka (BioQuip Products Inc. Rancho Dominguez, CA. USA). Specifically, we sampled the entire canopy surface of each tree for 1 min and 20 s. The natural enemies collected were kept in a mesh bag fitted to the sampling device. The bags were stored on ice and transported to the laboratory for later identification and classification.

We classified the samples into groups of natural enemies characterized by high abundance (Table 1). These were the order Araneae, the family Formicidae, the family Miridae, the genus Aeolothrips, and the predator species *Anthocoris nemoralis* and *Chrysoperla carnea*. Subsequently, we combined all these groups together with all other natural enemies (included rarely detected species) a group containing all predators (Table 1). Rarely detected natural enemies belonged to the orders Dermaptera and Raphidioptera and the families Coccinelidae, Syrphidae, Coniopterygidae and Manthidae (Table 1).

Table 1 Relative abundance of each taxon in the main arthropod natural enemy groups found in the experimental olive orchard site

	Abundance	Relative abundance (%)
Total	3178	100.00
A. nemoralis	1290	40.59
Miridae	674	21.21
Aeolothrips	569	17.90
Araneae	247	7.77
C. carnea	181	5.70
Formicidae	160	5.03
Coccinelidae	20	0.63
Coniopterygidae	15	0.47
Raphidioptera	12	0.38
Dermaptera	5	0.16
Syrphidae	4	0.13
Manthidae	1	0.03

We also studied the herbivore psyllid *Euphyllura olivina*, which mainly feeds on olive flowers and overlaps with certain generations of *Prays oleae*. Although this pest can be very abundant in olive trees, it does not cause significant damage and is therefore regarded as a secondary pest. However, due to its influence on natural enemy abundance (Paredes et al. 2015b), it was included in some of our analyses. We used the same method as that for natural enemies to sample this secondary pest. Data from different dates and trees were pooled to obtain a single abundance measure per plot.

Ground cover

We used photography to monitor ground cover in the experimental plots. While collecting natural enemies, we took 16 photographs per plot and per date of the inter-row space between the four olive trees with excluded branches (Fig. 2). These photographs were framed by 50 cm × 50 cm metal squares which were later used for digital analysis. With the aid of free image-editing GIMP software (version 2.8.16), we first counted the total number of pixels within the frame. We then drew an outline of the following categories of interest: living cover, the parts of ground cover alive at the time of sampling; dry cover, composed of chopped pruning remains (used in olive orchard management); and bare soil where living cover has disappeared due to senescence. We counted the pixels in each category and then calculated the percentages. We averaged these parameters by plot and date to obtain a single measurement per plot of living, dry cover and bare soil. After investigating the correlation between these variables, we decided to only analyse living and dry ground cover (Supplementary material 3).

Natural habitat

To quantify surrounding natural habitat, we drew a circle with a 1000 m radius around the olive tree in the centre of the plot (Fig. 2). Using Geographic Information Systems software (ArcMap 10.3; ESRI Inc, Redlands, CA, USA), we classified the land cover within the circle into to five categories: olive grove, natural habitat, other agriculture, anthropogenic origin and water based on images of the Spanish National Plan of air Orthophotography. We then divided the large circle into concentric rings (25 m widths) and calculated the amounts (m^2) of natural habitat within each ring. As natural habitat patches near the sampling point can have a stronger effect than patches further away, we weighted the amounts and percentages according to distance from plot. Following Karp et al. (2016), we used a weighting curve based on a Gaussian function (Eq. 1). The shape of the weighting curve can be modified by changing the decay parameter (d) of the different distances from the centre (I) to obtain the weighting for the different distances

(W). We multiplied this weighting by the amount of natural habitat in each ring at the different distances and we sum the calculation of all the rings. Then, we multiply this weighting by the total area of each ring at the different distances and we sum the calculation of all the rings. Finally, we divided the sum of the total weighted amount of natural habitat by the sum of the total weighted area thus obtaining a weighted proportion of natural habitat at three landscape scales (decay values of 250, 500 and 1000):

$$W = \exp\left(-I^2/\left(2xd^2\right)\right) \tag{1}$$

We compared the degree to which natural habitat at each landscape scale (250, 500, 1000) explained variation in each response variable. Specifically, we used likelihood ratio tests to compare null models with models containing the natural habitat variable (see next section). We found the most predictive landscape scale to be the proportion of natural habitat with a decay rate of $d=500$ (Supplementary material 2). The proportion of natural habitat less often predicted pest control and abundance variables when calculated with the other decay rates ($d=250$ and 1000) that increased the importance of areas closer or further from the study site. We subsequently utilized the proportion of natural habitat at $d=500$ in our analyses.

Modelling

Linear mixed models (LMM) were used with the two types of ground cover and natural habitat as predictor variables and the damage reduction index as the response variable. We used the nine olive groves as a random variable. Natural enemies were included as both predictors and responses depending on the model. First, we analysed the effect of natural habitat and the two types of ground cover on natural enemies, and also included the secondary pest *Euphyllura olivina* due to its possible effects on natural enemy abundance (Paredes et al. 2015b). To implement these models, we used a Gaussian error distribution with a log transformation. Then, another set of models was created to assess the effects of different groups of natural enemies, along with natural habitat and the two types of ground cover, on pest damage reduction. We also implement one model that did not contain any natural enemy group. This way, we could isolate the effect that natural habitat and/or ground cover could have on damage reduction. A Gaussian error distribution with an identity function was selected to perform all the models. Statistical significance of each predictor was evaluated via likelihood ratio tests that compared the full model to a reduced model without a given fixed effect predictor, using a threshold of $P<0.05$ (Zuur et al. 2009). We tested whether residuals of each model were normally distributed using Shapiro–Wilk tests. All analyses were carried out with the aid of the lme4 package (Bates et al. 2015) in R (R Development Core Team 2017).

Results

Overall, a total of 3178 individual natural enemies were collected during the study. The most abundant predatory species was *A. nemoralis,* which accounted for 40.6% of total natural enemies (Table 1). The Miridae family and the genus Aeolothrips were also abundant, with 21.2% and 17.9% of the total, respectively. The order Araneae, the family Formicidae and the predator *C. carnea* accounted for only 7.8, 5.0 and 5.7% of the total, respectively (Table 1).

The predator species *A. nemoralis* was significantly affected by natural habitat, ground cover and the secondary pest *E. olivine* (Table 2). *A. nemoralis* abundance increased with natural habitat and *E. olivina* abundance but declined with dry ground cover (Table 2; Fig. 3). The family Miridae declined with natural habitat (Table 2). For the total predators, there were no significant effects of natural habitat or any type of ground cover. Nevertheless, we found marginally significant positive effects of the secondary pest *E. olivina* on total predator abundance ($\chi^2=3.458$; $P=0.063$; Table 2), of natural habitat on *C. carnea* ($\chi^2=3.519$; $P=0.061$; Table 3), and of dry ground cover on Formicidae ($\chi^2=3.615$; $P=0.057$; Table 2).

As we expected, damage was generally higher (10.2%) in the excluded branches (no enemies present) compared with non-excluded branches (4.6%). When natural enemy abundance was incorporated into the damage reduction models, along with natural habitat and ground cover, total enemy abundance ($\chi^2=6.975$; $P=0.008$; Table 3), predator abundance ($\chi^2=6.327$; $P=0.012$; Table 3) and the pirate bug *A. nemoralis* ($\chi^2=5.375$; $P=0.020$; Table 3) were all positively associated with our biocontrol index, but we observed no effects of natural habitat or ground cover (Table 3). However, when no natural enemy variables were included in these models, the amount of natural habitat had a markedly positive effect on biological control ($\chi^2=4.299$; $P=0.038$; Table 3; Fig. 4). Specifically, when natural habitat increased from a proportion of 1% to a proportion of 74.8%, damage reduction also increased from 4.73 to 8.57%. In contrast, neither living nor dry ground cover was associated with biological control (Table 3). The effect size of natural enemy groups was comparable to that of natural habitat alone (Fig. 5). Based on a revenue estimation of 3553.50 €/ha (see "Material and methods" section), natural pest control resulted in an economic benefit that ranged from 168.08 to 304.53 €/ha, depending on the amount of surrounding natural habitat.

Table 2 Generalized linear mixed models of the effect of natural habitat, ground cover type and a secondary pest (*Euphyllura olivina*) on the abundance of the different natural enemy groups

	β	χ^2	P
Predators			
Intercept			
Secondary pest		3.458	0.063
Natural habitat		0.256	0.613
Living ground		1.651	0.199
Dry ground cover		0.349	0.559
A. nemoralis			
Intercept	2.908		
Secondary pest	0.001	20.380	**< 0.001**
Natural habitat	1.456	4.364	0.037
Living ground		0.023	0.879
Dry ground cover	− 1.635	5.469	**0.019**
Miridae			
Intercept	3.471		
Secondary pest	− 0.001	9.162	**0.002**
Natural habitat		0.645	0.422
Living ground		1.027	0.311
Dry ground cover		0.224	0.636
Aeolothrips			
Intercept			
Secondary pest		2.616	0.105
Natural habitat		0.162	0.687
Living ground		1.981	0.159
Dry ground cover		0.254	0.614
Araneae			
Intercept			
Secondary pest		0.456	0.500
Natural habitat		0.297	0.586
Living ground		0.872	0.350
Dry ground cover		0.176	0.675
C. carnea			
Intercept			
Secondary pest		0.021	0.884
Natural habitat		3.519	0.061
Living ground		0.240	0.625
Dry ground cover		0.007	0.932
Formicidae			
Intercept			
Secondary pest		2.630	0.105
Natural habitat		1.174	0.278
Living ground		1.214	0.271
Dry ground cover		3.615	0.057

Significance was assessed with likelihood ratio tests (LRT), comparing models with and without predictors (see "Materials and methods" section). Following selection of a model, values for the parameters are those reported after removal of non-significant variables. When no model was selected, the values for the parameters shown are those obtained by comparing the models containing only this variable and the null model. Bolded *p*-values are significant ($P < 0.05$)

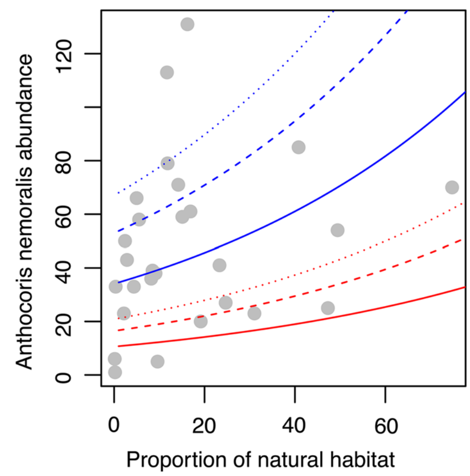

Fig. 3 Model predictions of the effects of natural habitat, secondary pest abundance and percentage of dry ground cover on the abundance of *Anthocoris nemoralis*. Blue lines represent predicted abundance of *A. nemoralis* across a natural habitat gradient when the secondary pest (*Euphyllura olivina*) was highly abundant (90% of maximum abundance reported in the study). Red lines represent predicted abundance when the secondary abundant was rare (10% of maximum abundance reported in the study). Dashed, solid and dotted lines represent estimated abundances with 95, 50 and 5% dry ground cover, respectively. Different symbols within the plot represent the olive groves sampled

Table 3 Generalized linear mixed models of the effect of natural habitat, ground cover type and natural enemy group on the biocontrol of olive pests

	Damage reduction		
	β	χ^2	P
Intercept	4.730		
No natural enemy			
Natural habitat	5.140	4.299	**0.038**
Living ground cover		0.384	0.535
Dry ground cover		0.078	0.880
Intercept	2.837		
Predator abundance	0.234	6.327	**0.012**
Natural habitat		2.379	0.123
Living ground cover		0.511	0.475
Dry ground cover		0.046	0.831
Intercept	3.953		
A. nemoralis abundance	0.034	5.375	**0.020**
Natural habitat		3.139	0.077
Living ground cover		0.666	0.415
Dry ground cover		0.020	0.889

Significance was assessed with likelihood ratio tests (LRT), comparing models with and without predictors (see "Materials and methods" section). Natural enemy groups not reported to have any effect on biocontrol (Miridae, Aeolothrips, Araneae, *C. carnea* and Formicidae) are omitted. Following selection of a model, values for the parameters are those reported after removal of non-significant variables. Bolded *p*-values are significant ($P < 0.05$)

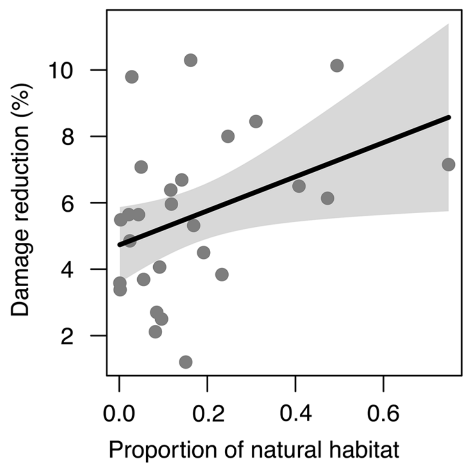

Fig. 4 Model predictions of the effect of natural habitat on the natural biological control of the olive moth. Grey shading corresponds to the 95% confident intervals

Discussion

Our study demonstrates that the natural enemy community held in olive trees substantially reduces the damage caused by the pest *Prays oleae* to Mediterranean olive orchards. Specifically, we found that olive damage was 4.7% with natural enemies present and 10.2% without them, representing a 64% reduction in olive losses. In comparison, the effectiveness of Dimetoathe in reducing pest damage has been estimated to be range from 4.43 to 24% (Albedis et al. 2004; Rosales et al. 2008). Thus, depending on the measure of Dimetoathe efficacy, natural enemies were anywhere from 2.6 to 14.4 times more effective at reducing pest density. Critically, several studies have reported detrimental effect of Dimetoathe treatments on the olive natural enemy community, calling into question excessive Dimetoathe use as an effective pest management strategy (Picchi et al. 2016; Rosales et al. 2008; Ruano et al. 2001; Santos et al. 2007).

Our study highlighted a different path forward. We found that, by promoting natural enemies, increasing natural habitat around olive orchards in this Spanish landscape can nearly double the pest control provided (from 4.7 to 8.6% damage reduction). Biocontrol was maximized when surrounding habitat reached its maximum levels, around 70% of the landscape, which is only attainable in very mountainous areas. A more realistic situation is olive orchards located in a landscape containing 0 to 20% of natural habitat, where biocontrol would be expected to increase from 4.73 to 5.76%, which would correspond to an average increase in olive oil revenues of approximately 186.38€ per hectare. This is in line with other studies emphasizing the role played by natural habitat in providing this service (Karp et al. 2013; Rusch et al. 2016). We did not find ground cover to affect biocontrol, aligning with other studies of olive farming (Paredes et al. 2013b, 2015a; Rodriguez et al. 2009). Nevertheless, ground cover can provide other ecosystem services such as

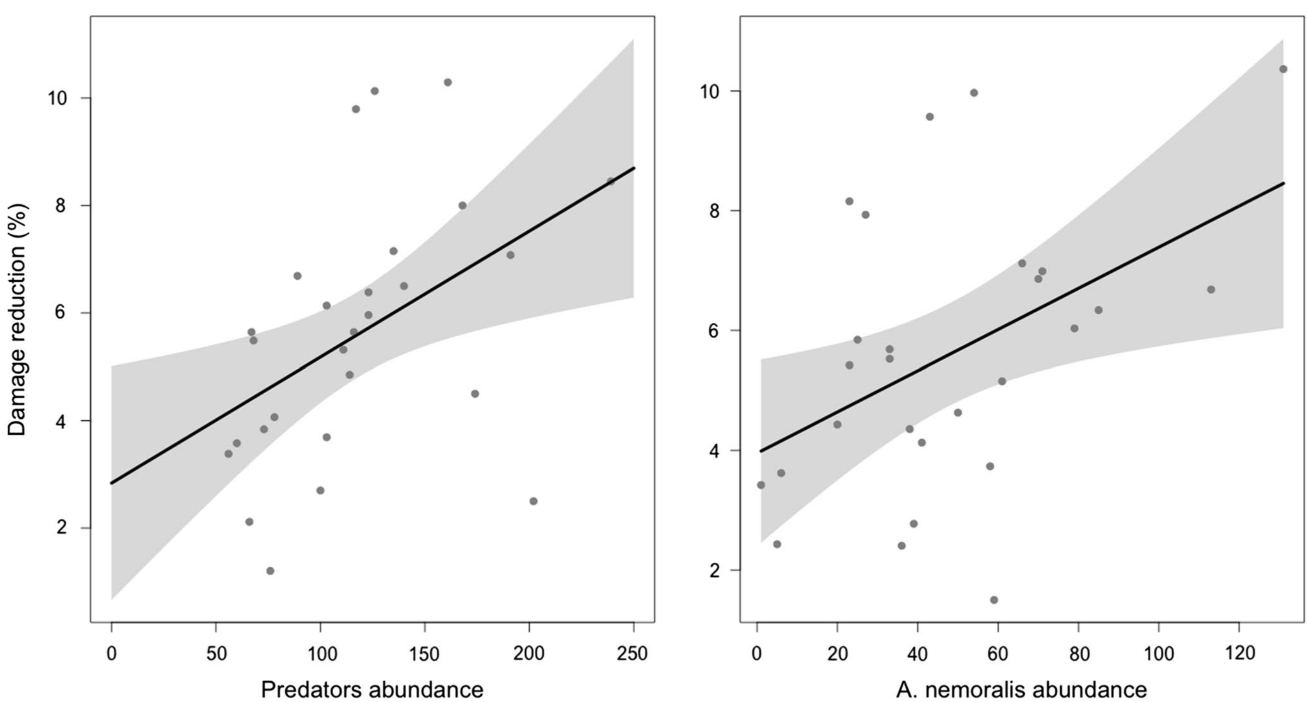

Fig. 5 Model predictions of the effect of predators and *A. nemoralis* on the biological control of the olive moth. Grey shading corresponds to the 95% confident intervals

soil erosion control (Gomez et al. 2009) and carbon sequestration (Moreno and Benitez 2016).

Even in landscapes with little surrounding natural habitat, biocontrol levels were still relatively high (damage reduction rate of 4.73%). Olives, which are perennial crops known for their stability and long-term evolution in the Mediterranean ecosystem, may provide some natural enemies with more substantial resources than natural habitats (Tscharntke et al. 2016). This could lead to some natural enemies specializing on olive orchards, independent of the proximity or amount of surrounding non-crop habitats. Of the plant species that regularly occurred in natural habitat patches, *Rubus ulmifolius*, *Dittrichia viscosa* (Kavallieratus et al. 2002) and *Crataegus monogyna* (Novak and Achtziger 1995) likely have the greatest potential to boost natural enemy populations by providing alternative prey resources (Landis et al. 2000). Nevertheless, biocontrol was observed to increase with natural habitat, and our findings suggest that the natural enemy *A. nemoralis* may be mediating this effect. Other predator species were not responsive to local or landscape management, but still may complement the effect of *A. nemoralis* on *P. oleae* biocontrol.

Anthocoris nemoralis has been reported to have a positive effect on the biological control of *P. oleae* in other studies, paralleling our finding that *A. nemoralis* abundance correlated with biocontrol (Morris et al. 1999). We also found that *A. nemoralis* was positively associated with natural habitat, which it likely uses for overwintering (Horton and Lewis 2000; Sigsgaard et al. 2006). Thus, maintaining at least some habitat in the surrounding landscape may enhance *A. nemoralis* abundance, biocontrol and on-farm olive yields. To further increase the abundance of this predator, it may be advisable to augment populations with mass releases when *A. nemoralis* abundances are too low to guarantee effective biocontrol.

Interestingly, we also found that olive psyllids (secondary pest) were positively associated with *Anthocoris nemoralis* abundance. As reported for other crops such as pears, *A. nemoralis* is very attracted to psyllids (Scutareanu et al. 1999; Shaltiel 2005).

Within natural habitat patches, the common plant *Crataegus monogyna* likely shelters psyllid species of the genus Cacopsylla, which may act as alternative prey for *Anthocoris nemoralis* and boost its abundance (Novak and Achtziger 1995; Scutareanu et al. 1999). We hypothesize that *A. nemoralis* could be attracted from natural habitats to olive trees due to presence of the secondary pest *E. olivine*. Once in the olive tree, it may depredate both the secondary and major pest, thus exerting an effective control on the pest of interest, *P. oleae*. Thus, both natural habitat and the secondary pest seem to be important drivers of *A. nemoralis* abundance, and may play important indirect roles in *P. oleae* suppression. Farmers may find it difficult to recognize the potential advantages of promoting a secondary pest, even if it bolsters a key natural enemy. As such, further studies are needed that track *A. nemoralis* abundance, olive damage and crop yields after experimentally manipulating *E. olivina* abundance. On the other hand, the use of chopped pruning remains as ground cover reduced the abundance of *A. nemoralis*. This effect could be mediated by ants which displayed a positive marginal effect of chopped pruning remains. Indeed, some species of the family Formicidae are considered predators of species in the family Anthocoridae (Eubanks et al. 2002). Also mirids could be disrupting biocontrol exerted by *A. nemoralis*. They showed a significant negative effect of the secondary pest which could be attributed to the increase of the anthocorid in those areas with a larger abundance of the secondary prey (Paredes et al. 2015b). *A. nemoralis* could depredate on the mirids thus decreasing its control on *P. oleae* (Koss and Snyder, 2005). Nevertheless, this effect is not showed by our results since mirid abundance did not increase *P. oleae* damage.

Ultimately, more studies are needed to tease apart the complex relationships between natural habitat, ground cover, *A. nemoralis*, *Euphyllura olivina* and the biocontrol of *Prays oleae* in order to optimize the delivery of this ecosystem service. Furthermore, this study was carried out in a year with relatively normal conditions but years with severe pest outbreaks should be explored. There is not much literature regarding pest outbreaks due to rarity of experiments that coincide with these rare events. Nevertheless, Berryman (1982) theorized natural enemies would only be able to prevent pest outbreaks if pests slowly increase over time (rather than rapidly spiking in abundance and quickly satiating the predator community). Regardless of the impact of predators during severe outbreaks, our study suggests that natural enemies are critical to controlling *Prays oleae* infestations in olive orchards. Maintaining surrounding natural habitat, augmenting *A. nemoralis* abundance and mitigating dry ground cover all represent promising paths forward for simultaneously enhancing conservation and sustainable production in olive orchards.

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Authors' contribution DP, RCK, EB and MC conceived the project and designed the methodology; DP collected the data; DP and DK analysed the data; DP, RCK and DK wrote the study. All authors made critical contributions to the draft and gave final approval for publication.

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Compliance with ethical standards

Conflict of interest All authors declare that they have no conflict of interest.

Ethical approval This article does not contain any studies with human participants or animals performed by any of the authors.

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