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Prays oleae (Bernard), its potential predators and biocontrol depend on the structure of the surrounding landscape

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HIGHLIGHTS

- Biocontrol of Prays oleae depend on surrounding landscape structure of olive groves.
- Landscape complexity favours control of the olive moth, *P. oleae*.
- Lacewings are responsible for egg predation of the carpophagous generation.
- Complex landscape structure also favours lacewings.
- Effects of landscape structure on *P. oleae* damage were more significant at 750 and 1000 m radii.

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ABSTRACT

Arthropod populations from agricultural fields sometimes depend on the surrounding landscape structure, both composition and configuration, which affects multiple life-history traits of arthropods such as resources for survival, dispersion or death risk (e.g., predation or parasitism). Moreover, the effect of the landscape may vary with the distance to the crop, depending on factors such as the organism requirements and dispersion capabilities. This work addresses the effect of landscape (at five different scales from 250 to 1500 m) on the olive moth (Prays oleae Bernard, a key pest in olive orchards), some of its most relevant natural enemies, and biological control. The two-years study in 15 olive groves in southeastern Madrid, Spain shows that landscape complexity favours control of the olive moth, P. oleae. Simple landscapes favour P. oleae attack to the crop (measured as oviposition of the anthophagous generation) and that egg predation of the carpophagous generation is in some cases enhanced in complex landscapes. Lacewings (Neuroptera: Chrysopidae) are responsible for egg predation and populations increase in complex landscapes. On the other hand, the role of pirate bugs (Hemiptera: Anthocoridae) as a biological control agent of this part of the life cycle of P. oleae was not demonstrated. They respond primarily to Euphyllura olivina (Costa) (Hemiptera: Psyllidae) populations and are more abundant in simple landscapes. Most of the significant relationships of pest attack were detected at 750–1000 m radii buffers around the sampled olive groves suggesting that this is the main activity range for adults of P. oleae anthophagous generation. In sum, our results suggest complex configurations of the landscape enhance the biological control of P. oleae through favouring lacewings and egg predation of the carpophagous generation.

1. Introduction

The olive moth, Prays oleae (Bernard, 1788) (Lepidoptera: Praydidae) is one of the most important olive pests in the Mediterranean basin (Arambourg, 1986) and threatens all olive growing regions across the world, which include 42 countries (FAO, 2020). The insect has three generations: the phyllophagous, developing on leaves; the anthophagous, developing on flowers; and the carpophagous developing on fruits.

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The carpophagous generation is responsible for the most important economic damage, causing fruit drop when larvae enters, and when adults exit the fruits (Ramos et al., 1998; Sabouni et al., 2008).

Pest control relies mainly on the use of chemical insecticides and Bt products (Wiesman, 2009). However, numerous natural enemies contribute to the reduction of P. oleae populations (Alves et al., 2021; Martínez-Núñez et al., 2021; Paredes et al., 2015; Plata et al., 2019; Villa et al., 2016b), and chemical products have negative effects on them (Martínez-Núñez et al., 2021; Santos et al., 2007). Predation of P. oleae by natural enemies is a key process in the control of this pest and lacewings (Neuroptera: Chrysopidae) are recognised as one of the most important predators of P. oleae (Morris et al., 1998; Paredes et al., 2015; Villa et al., 2016a). Pirate bugs such as Anthocoris nemoralis (F.) (Hemiptera: Anthocoridae) are also associated with biocontrol of the olive moth (Paredes et al., 2019). Predation has been studied deeply during the anthophagous generation, when the pest is most vulnerable (Morris et al., 1999). However, as the carphophagous generation of P. oleae can cause more damage and an enhancement of predation in this generation may significantly reduce the production losses.

Sustainable pest control requires understanding of processes regulating populations of and damaged caused by phytophagous insects, and favouring ecosystem elements enhancing natural enemies of pests. In the olive agroecosystem several studies indicated that the landscape heterogeneity or complexity reduced important olive pests. For example, populations of the olive fruit fly Bactrocera oleae (Rossi) were reduced in landscapes with high values of Shannon landscape diversity index or edge density (Ortega and Pascual, 2014). In the case of the olive moth, adult populations were also negatively associated with higher landscape heterogeneity and complexity as well as with non-crop areas with herbaceous and woody vegetation surrounding the olive groves (Villa et al., 2021). The surrounding landscape also affects natural enemies of olive pests and biocontrol in the olive agroecosystem. The area covered by scrublands promoted predation of B. oleae pupae in autumn (Ortega et al., 2018) and landscape connectivity positively affected its parasitism rate (Boccaccio and Petacchi, 2009). Although several species of carabids showed different responses to natural areas or landscape structure (Lantero et al., 2019). Regarding natural enemies of P. oleae, abundance of A. nemoralis, was influenced by natural habitat (Paredes et al., 2019) and structural simplification negatively affected the potential of insectivorous bats to control the olive moth (Costa et al., 2020). A tritrophic mathematical model showed that under unsuitable conditions for specific natural enemies (i.e., with low population of these organisms), generalist natural enemies would be important for reducing pest populations (Pappalardo et al., 2021). The higher habitat complexity within the crop through the establishment and maintenance of ground covers positively affected the egg predation of P. oleae in June and July (Álvarez et al., 2021). However, it is recognized that the effect of landscape structure on egg predation of P. oleae needs further investigation (Álvarez et al., 2021). In the various studies dedicated to evaluate the effect of the landscape on P. oleae and/or its potential natural enemies, the characterization of the landscape has been carried out at different buffer areas, grosso modo between 500 m and 2000 m (Alves et al., 2021; Martínez-Núñez et al., 2020; Moreno et al., 2022; Villa et al., 2020) and sometimes at 200 m (Gkisakis et al., 2020). In other agroecosystems, the effect of the landscape on Anthocoridae has been studied, at radii as different as 200 m and 2000 m (Samaranayake and Costamagna 2018). However, the information to choose a specific radius for evaluating the effect of the landscape on P. oleae, its natural enemies and biological control is not sufficient. The different organisms involved in this system have different dispersion ranges; therefore, in studies aiming to analyse the effect of the landscape on the system it is necessary to characterize the landscape at different radii around the olive groves to avoid an arbitrary selection of a single radius.

The objective of our study is to investigate the effect of the landscape structure on the natural biological control of P. oleae through exploring potential relationships among the different elements involved in the trophic system, i.e., moth eggs of the carpophagous generation, moth predators, alternative preys and configuration/composition landscape features. To do this, we assess the effect of the landscape structure on: (i) the egg population of the carpophagous generation of P. oleae because the fruit generation is the most damaging and because the egg is suggested for addressing the biological control of the olive moth (see Álvarez et al. (2021); (ii) the rate of egg predation; and (iii) the populations of important potential moth predators (pirate bugs and lacewings). In order to explore the predatory activity of pirate bugs and lacewings, we aim to assess the relationship between the rate of predation and the populations of these two groups of potential predators. Finally, we aim to better understand our knowledge of spatial scales when characterizing the landscape relative to our study system.

2. Materials and methods

2.1. Study area

The study was carried out in south-eastern Madrid, Spain, where olive is one of the main rain fed crops, together with cereals and vineyards. The main olive pest problem in the area is the olive fruit fly, B. oleae, P. oleae being the second most important pest. In this area, fifteen olive groves were selected representing a landscape structure gradient according to three landscape indices: the area of olive groves, the area of natural habitats and the Shannon landscape diversity index (González-Núñez et al., 2017). The size of the selected olive groves ranged between 0.97 and 11 ha and their altitudes between 570 and 700 m a.s.l. The average distance between trees was 10 m and the most abundant cultivar was Cornicabra. Pest management in these groves is focused on olive fruit fly control, and treatments on the olive fruit fly are generally only applied if there is a phytosanitary alert. Pest management is focused on olive fruit fly control, and treatments are generally only applied if there is a phytosanitary alert. Soil vegetation was removed mainly through tilling, although herbicides were applied sporadically.

2.2. Landscape analysis

Buffer areas of radii 250, 500, 750, 1000 and 1500 m for the spatial analysis of the landscape were established around the centre of the sampled olive groves to calculate landscape structure indices (Fig. 1). The calculated indices for landscape composition were: area of olive groves (CAO), area of scrublands (CAMME), Shannon Landscape Diversity Index (SDI) and Shannon's Evenness Index (SHEI). Both SDI and SHEI were calculated because they provide complementary information: a landscape less diverse (SDI) could have a more even area distribution among patch types. Moreover, the spatial analyse indicated the existence of land uses with low representation (rare) indicating the importance of using SHEI The calculated indices for landscape configuration were: number of patches (NP), total edges length (TE), mean shape index (MSI) and patch richness (PR) (McGarigal and Marks, 1995). The land use layer of the SIOSE project (Information System on Land Occupation of Spain; http://www.siose.es) was used as the source layer. SIOSE land uses assigned to the patches were revised and reclassified according to the information provided by PNOA (National Aerial Orthophotography Plan; https://pnoa.ign.es/), and SIGPAC (Geographic Information System of Agricultural Plots, 2004; http://sigpac.mapa.es/fega/visor/). Patches were reclassified to 13 land uses: olive grove (O), field crop (C), scrubland (S), scrubland with oaks (SO), woody crop (W), artificial (A), pastures (P), oak forest (K), sparse vegetation (SV), pine forest (F), riverside vegetation (RB), green urban areas (Z) and watered crop (WC). The spatial analysis program Fragstats 4.0 (McGarigal et al., 2012) was used to calculate the landscape indices.

2.3. Estimation of P. oleae attack

The attack rate of the carphophagous generation of P. oleae on olive

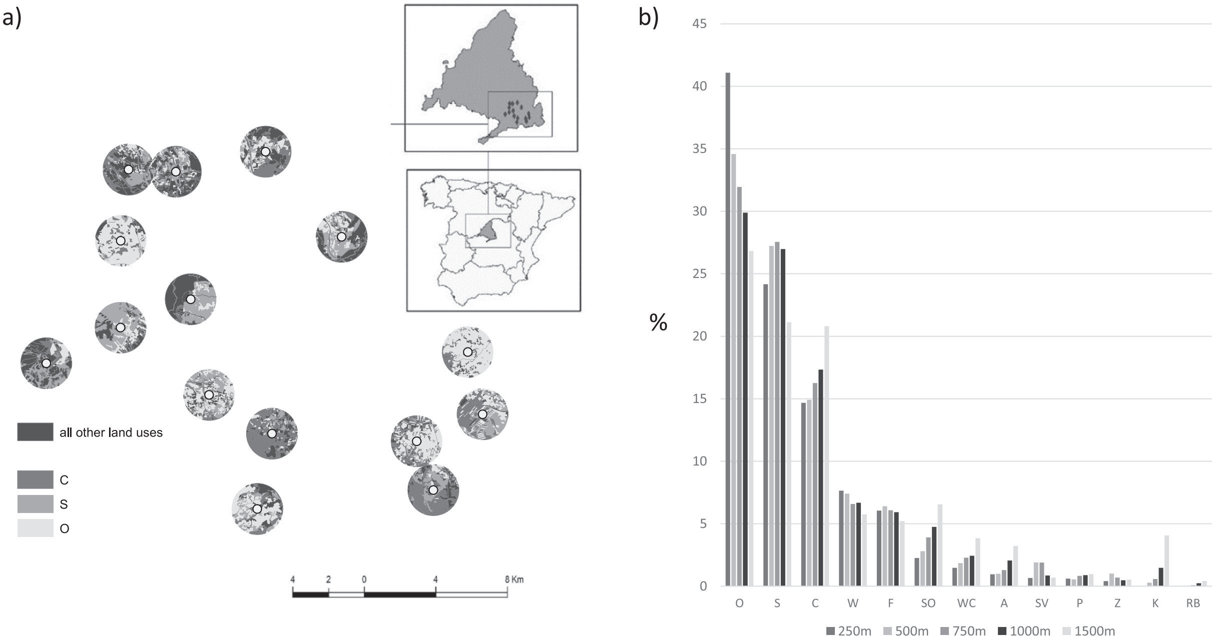

Fig. 1. Spatial analysis of the study area landscape: a) Spatial representation of the 15 analysed plots showing the areas of the three main land uses. The circles have a radius of 1500 m and within them are circles of 250 m radius. Both circles were centred on the sampling points. b) Average percentages of all land uses considered in the five analysed circle sizes. The used acronyms are: olive grove (O), field crop (C), scrubland (S), scrubland with oaks (SO), woody crop (W), artificial (A), pastures (P), oak forest (K), sparse vegetation (SV), pine forest (F), riverside vegetation (RB), green urban areas (Z) and watered crop (WC). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

fruits was estimated by assessing the presence of P. oleae eggs laid by adults of the antophagous generation on olive fruits in spring. 100 olive fruits were collected in each olive grove on 17th June 2015 and 23rd and 30th June 2016, when peak oviposition occurred. The phenological stage of the olive trees in these dates ranged between BBCH 70 and 74 (Sanz-Cortes et al., 2002). Collected fruits were carried to the laboratory, where the presence or absence of P. oleae eggs on each fruit was recorded. No parasitoids were found in any of the recorded eggs.

2.4. *Estimation of P. oleae egg predation*

The number of P. oleae eggs on each fruit was counted, and classified as predated or not predated. Predated eggs appear empty of content, keeping only the chorion. Non-predated eggs were calculated as the sum of hatched (when the entrance hole of P. oleae larvae into the fruit was observed) and unhatched eggs. The number of dead eggs by dehydration or other unknown causes were not considered in the calculations. A mean of 107 eggs were considered from each olive grove at each assessment date (17th June 2015 and 30th June 2016).

2.5. *Abundance estimation of predators (lacewings and pirate bugs) and alternative prey (olive psyllid)*

Adult populations of pirate bugs and lacewings were monitored in 2015 and 2016 by means of yellow sticky traps. Four traps were placed in four consecutive trees per each olive grove, approximately 30–40 m away from the grove edge, and were taken to the laboratory after one week in the field. Sampling dates were: 20th March, 8th and 30th April, 20th May, 10th June, 1st July, 27th August, 17th September, 8th and 27th October 2015; and 10th and 31st March, 21st April 12th May, 2nd and 23rd June, 24th August, 14th September and 6th and 27th October 2016. The number of E. olivina was also counted, as its abundance affects the abundance of pirate bugs (Plata et al., 2019). Abundance data were pooled in two sampling periods each year (based on the phenology of the anthophagous and the carpophagous generations of the olive moth in each year vary according to the year conditions): the first period, was named “spring” and comprised samples taken from March to July 2015 and from March to June 2016. The second sampling period was named “autumn” and comprised samples taken from August to October both in 2015 and 2016.

2.6. *Statistical analysis*

Ten separated generalized linear mixed models (GLMMs), one for each buffer (250, 500, 750, 1000 and 1500 m) and year (2015 and 2016), were performed to analyse the response of P. oleae attack (eggs laid by the anthophagous generation) to landscape variables. The pest attack (response variable) was measured as fruits with at least one egg, with values of 1 for success (olive fruit bearing P. oleae eggs) and 0 for failure (olive fruit free of P. oleae eggs). Similarly, ten GLMMs were performed to analyse the predation over P. oleae eggs to the abundance of predators (both lacewings and pirate bugs), as local factors, and to the landscape variables. The response variable for predation was the predated eggs, with values of 1 for success (predated egg) and 0 for failure (intact egg). In both cases (attack and predation responses), the distribution was binomial with the logit link. The orchard was used as random factor and the number of sampled fruits/eggs as offset.

Twenty separated GLMMs, one for each buffer (250, 500, 750, 1000 and 1500 m), year (2015 and 2016) and sampling period (spring and autumn) were performed to analyse the response of abundance of the predators lacewings and pirate bugs to landscape variables. Due to the role of the olive psyllid as food resource for pirate bugs, its abundance was included as explanatory variable in this predator models. For both predators, the distribution was negative binomial with the log link. The orchard was used as a random effect. Geographic latitude and longitude of the olive groves were also included as explanatory variables in all the GLMMs.

The explanatory variables were previously selected allowing a minimum collinearity using the Variance Inflation Factor (VIF) criteria (VIF < 3) (Zuur et al., 2010). The glmmadmb function from the “glmmADMB” package (Fournier et al., 2012; Skaug et al., 2016) in R (R Core Team, 2021) was used. The stepwise backward model selection based in hypothesis testing, i.e., dropping the less significant term of the model and refitting it until p-value for all terms was < 0.1, was applied (Zuur et al., 2009). Explanatory variables were standardized. Model validation for binary dependent variables was performed using the heat map plot and heat map statistics using the heatmap.fit function from the “heatmapFit” package (Esarey et al., 2016). In the heat map plot, predicted probabilities are plotted versus within-sample empirical frequencies (obtained by nonparametric smoothing) and a heat map line is drawn. Then one-tailed p-value is obtained by comparing the original heat map line with its parametrically bootstrapped distribution (obtained by the simulation of 1000 draws of the response variable from the fitted model). If more than 20% of observations on the heat map line are $P < 0.1$, then the specification is rejected; otherwise, it is accepted (Esarey and Pierce 2017). Here, heat map statistics indicated that 0% of within-sample predictions had a bootstrapped $P < 0.1$ for all models and models were accepted. For count data, models were validated by plotting residuals versus fitted values to assess the absence of patterns in the residuals.

To assist the results interpretation, Pearson correlations among explanatory variables were calculated for each buffer and year (the values slightly varied among years because some sampled olive orchards were changed from 2015 to 2016). The function cor from corrplot package was used (Figure S1 and S2, supplementary material) (Wei and Simko 2021).

Bonferroni correction on the significance value was applied because five models (five buffers) were fitted on the same data for each response variable. Therefore, p-value = 0.01 is considered significant and p-values between 0.1 and 0.01 are considered only as weakly significant.

3. Results

3.1. *Prays oleae attack*

The percentage of fruits bearing P. oleae eggs ranged between 6 and 91 % in 2015 and between 6 and 97% in 2016. Fruits collected in the first sampling date in 2016 did not bear enough P. oleae eggs to carry out data analysis. Prays oleae attack showed a relationship with landscape indices in 2015, while in 2016 the attack rate was not related with any of the studied variables (Fig. 2, Table S1). In general, the response in 2015 indicated higher attack in structurally simple landscapes, i.e., attack was positively related with the area of olive groves (CAO) at all radii studied (at 1000 m radius CAO was excluded from model because VIF value was higher than 3). CAO was negatively correlated with all variables indicating landscape complexity (Figure S1). Patch richness (PR) indicated the same trend, as the attack rate was negatively related with this variable at 750 m, 1000 m and 1500 m radii buffers. An exception was observed to this general trend at 750 m, when attack was positively related to the Shannon’s Evenness Index (SHEI). The relationship between attack and landscape complexity was observed at all studied radii, but the highest significance levels were observed at 750–1000 m radius. Both latitude and longitude were also significantly and positively related to P. oleae attack at almost all studied radii (Fig. 2, Table S1).

3.2. *Abundance of lacewings*

A total number of 291 lacewings were captured along the study. More complex landscapes were generally related with higher abundances of lacewing in spring through (i) a negative relationship of the area of olive groves at 500 m, 750 m and 1500 m in spring 2015, although a weak significant positive relationship was detected in spring 2016 at 500 m, (ii) a positive relationship of the area of scrublands (CAMME) at 1000 m radius in spring 2015, and (iii) the mean shape index (MSI) at 500 m, 750 m and 1000 m in spring 2016. This trend was reversed in autumn, when landscape complexity was generally related with a lower lacewing abundance: negative relationships were detected between the lacewings and the number of patches (NP) at 1000 m and 1500 m in 2015 and at 500 m, 1000 m and 1500 m in 2016, and also with Shannon’s Evenness Index (SHEI) at 750 m and patch richness (PR) at 250 m, both in 2016. These general trends were not followed in all cases: a negative relationship of CAO at 250 m and 750 m in autumn

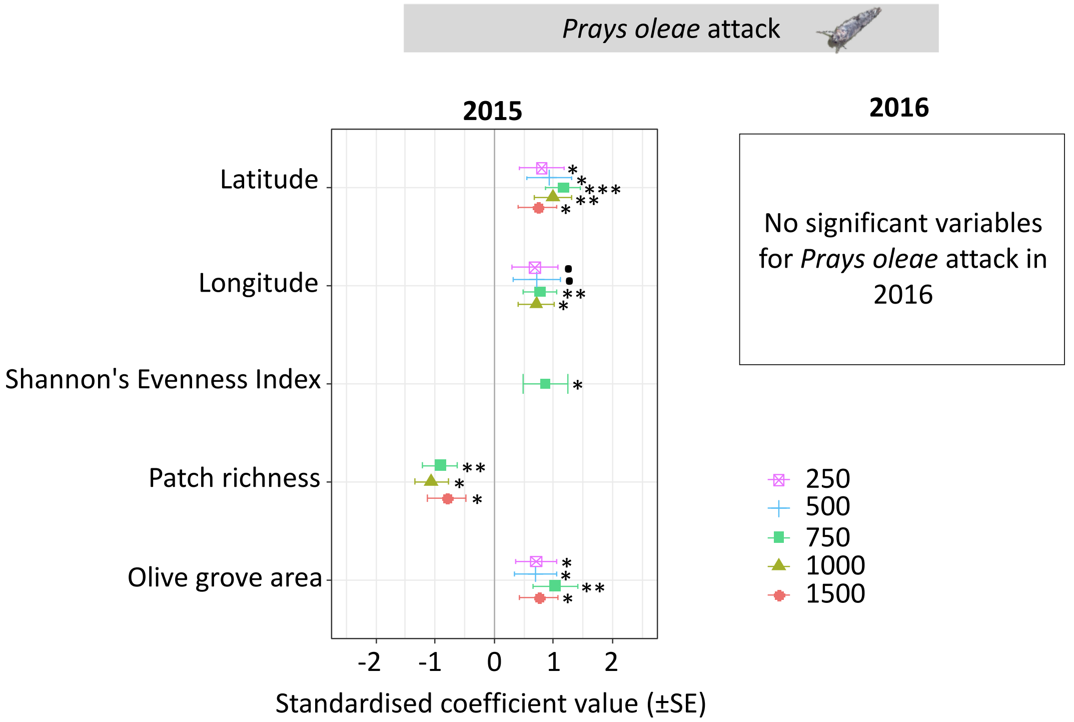

Fig. 2. Response of Prays oleae attack to landscape variables, longitude, and latitude (GLMM) in 2015 and 2016 at the different buffers (m) (***<0.001; **<0.01; *<0.05; ·<0.1).

2016 was detected and PR was associated with lower lacewing abundance at 750 and 1000 m in spring 2016. Abundance of lacewings was not related with longitude, and only in 2016, a positive effect was detected for latitude, especially at 750 m (Fig. 3, Table S2).

3.3. *Abundance of pirate bugs*

A total number of 757 pirate bugs were captured along the study. Plots of residuals versus predicted values showed a pattern for the models fitted in 2016 (Figure S3). Therefore, the results of these models should be viewed with caution. In general, there was a negative effect of landscape complexity on pirate bugs abundance. The landscape indices that revealed this trend were different in the two years of study. In 2015, these indices were the area of scrublands (CAMME) at 250 m, and 1000 m in spring, with a weak effect at 500 M; the mean shape index (MSI) at 250 m has also a slight effect in autumn. In 2016, these were the Shannon’s Evenness Index (SHEI) at 500 m, at 750 m and 1000 m in spring; the number of patches (NP) at 250 m and with only a slight effect at 500 m in spring and 1500 m in autumn; and the olive grove area (CAO) at 1500 m in spring. The only opposite effect to this trend was a weak significant negative relationship between CAO and pirate bugs abundance at 1500 m in autumn 2016. The abundance of the olive psyllid positively affected pirate bugs abundance especially in spring 2016, at all studied radii. Geographic coordinates explained pirate bugs abundance only in 2016 and mainly in autumn, as both latitude and longitude negatively related to abundance of pirate bugs (higher abundances at northwest locations) (Fig. 3, Table S3).

3.4. *Predation of P. oleae eggs*

The percentage of predated P. oleae eggs ranged between 0 and 57 % in 2015, and between 0 and 50% in 2016. A relationship between predation probability of P. oleae eggs and landscape structure was detected in both years (Figs. 2 and 3, Tables S2 and S3). More complex landscapes – those with higher values of mean shape index (MSI) and a greater number of patches (NP) - were related with higher egg predation rates in 2016. The relationship with MSI was positive at 500 m, 750 m and 1000 m radii and with NP at 750 m and 1000 m radii, both in 2016. On the other hand, heterogeneous landscapes (through Shannon’s Evenness Index - SHEI) reduced egg predation rate at 500 m radius in 2015 and at

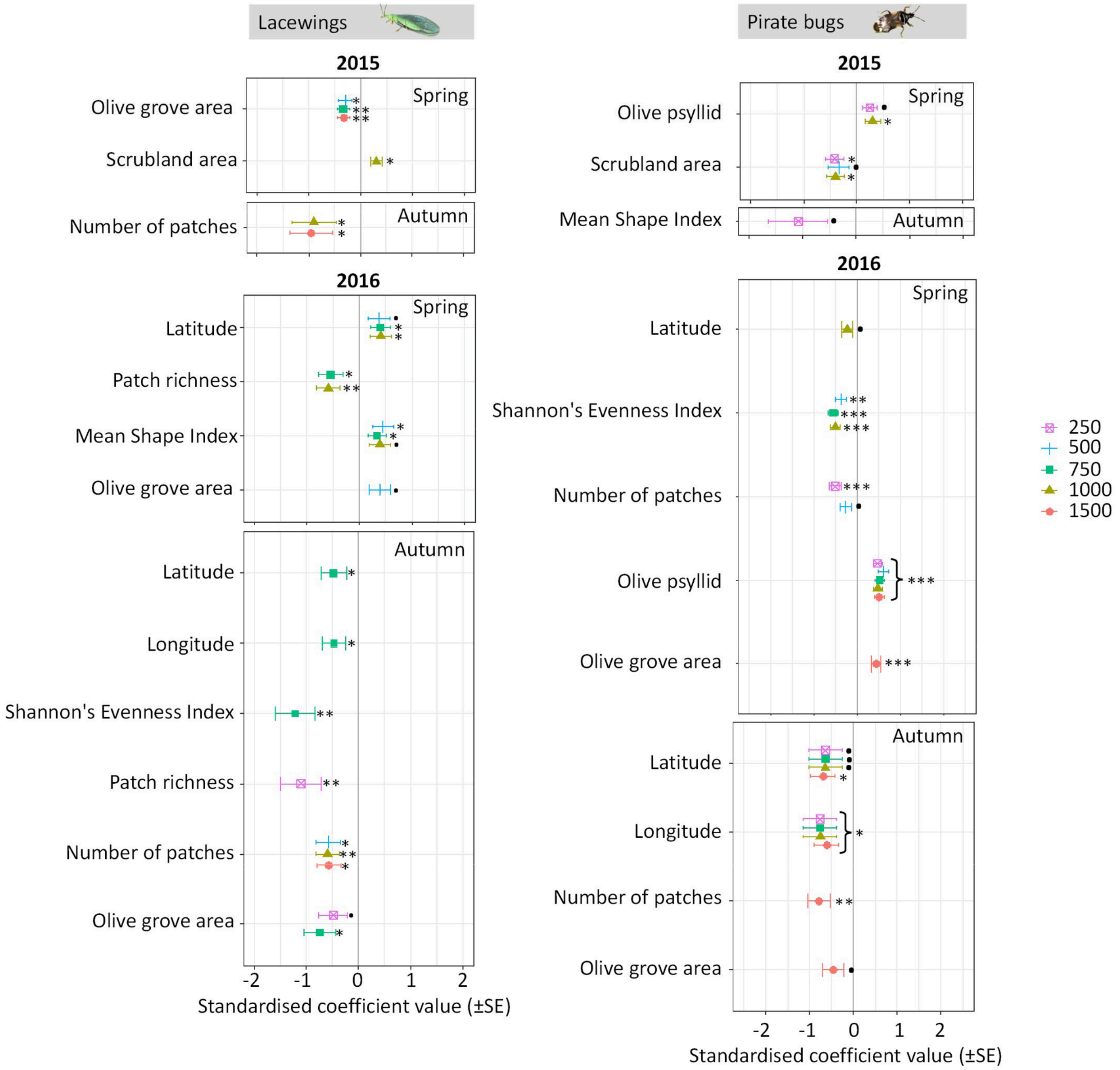

Fig. 3. Response of predators (Pirate bugs and Lacewings) to landscape variables, longitude, and latitude (GLMM) in spring and autumn 2015 and 2016 at the different buffers (m) (***<0.001; **<0.01; *<0.05; ·<0.1).

750 m and 1000 m radii in 2016. The probability of predation was explained by abundance of lacewings at 500 m in 2015 and 1000 m in 2016. The abundance of Anthocoridae was negatively related to predation rate at all radii in 2015, while no relationship was detected in 2016. Longitude (X) was negatively associated with predation, meaning higher predation at western sites, in both years of study, and in 2015 at all studied radii (Fig. 4, Table S4).

4. Discussion

4.1. *Prays oleae attack*

Our study has revealed that landscape structure affects P. oleae attack on olive fruits (carpophagous generation). Attack was higher in 2015 in simple landscapes with higher area of olive groves (CAO), and to a lesser extent, with lower patch richness (PR). This trend agrees with the reported results on the effect of landscape structure on populations of P. oleae adults along the complete cropping season (Villa et al., 2020) and with adults of the phyllophagous and anthophagous generation (Alves et al., 2021). Villa et al. (2020) showed that P. oleae abundance decreased in more complex landscape, measured by number of patches (NP) and mean shape index (MSI), and Alves et al. (2021) found higher pest abundance with the increase of surrounding olive groves. Other works have reported also that the presence of woody vegetation adjacent to olive groves or the forest cover in the surrounding landscape reduce the abundance of P. oleae adults (Costa et al., 2020; Paredes et al., 2013b). Accordingly, in one of the models (750 m) we found that P. oleae attack was higher in more even landscapes with higher Shannon's Evenness Index (SHEI), which in this study was driven by the dominance of olive groves, other crops and shrublands, but with a high significance of the spatial pattern effect (latitude and longitude). This may indicate that other spatial traits regardless the landscape structure might be involved in the observed response.

The relationship between P. oleae damage and landscape structure was more significant (i.e., higher estimate values in the models) at the intermediate studied radii (750 m and 1000 m). This is similar to the more relevant scale for the relationship detected by Villa et al. (2020) between landscape structure and P. oleae population, which suggest that this could be the range of major P. oleae activity.

4.2. *Abundance of natural enemies: Lacewings vs pirate bugs*

Our results seem to indicate that in the studied area lacewings may be more important predators of P. oleae eggs than pirate bugs. Lacewings are important oophagous predators of P. oleae (Álvarez et al., 2021; Morris et al., 1998); but also pirate bugs are reported to be important for P. oleae biocontrol (Álvarez et al., 2021; Paredes et al., 2013b; Paredes et al., 2015). For example, predator assemblages containing A. nemoralis and the green lacewing Chrysoperla carnea (Stephens) were associated with low abundance of P. oleae flower generation (Paredes et al., 2015) and A. nemoralis was strongly associated with elevated biocontrol of P. oleae (Paredes et al., 2019). In this study, we addressed the egg predation in the carpophagous generation, but pirate bugs may have a bigger importance for P. oleae reduction during the egg or larva stage of the anthophagous generation (e.g., Paredes et al., 2015). This may be because the first peak of E. olivina occurs with the first floral buttons (Pereira et al., 2007), just before the anthophagous generation of the olive moth. Additionally, it is possible that in our work the role of pirate bugs as P. oleae predators is masked by their very strong dependence on the olive psyllid, E. olivina (see below the discussion on the relationship between abundance of pirate bugs and E. olivina). Preference studies in other agroecosystems indicate that psyllids are the preferred prey for pirate bugs. For example, Anthocoris minki Dohrn showed an overall preference for psyllids over aphids (Hassanzadeh-Avval et al., 2018), and Anthocoris nemorum (L.) and A. nemoralis preferred psyllids to spider mites (Sigsgaard, 2010). Thus, it is probable that in the olive agroecosystem pirate bugs prefer E. olivina to other prey, and therefore dońt predate P. oleae eggs as long as E. olivina is available. However, specific choice experiments would be needed to confirm this behaviour. Previous work has shown that pirate bugs benefit from the presence of ground cover vegetation in olive groves (Álvarez et al., 2021; Paredes et al., 2013a), and its general absence from the groves in our study may have resulted in an insufficient number of pirate bugs feeding on eggs in the carpophagous generation of P. oleae to detect an effect.

Lacewings abundance indicated in some cases a positive relationship

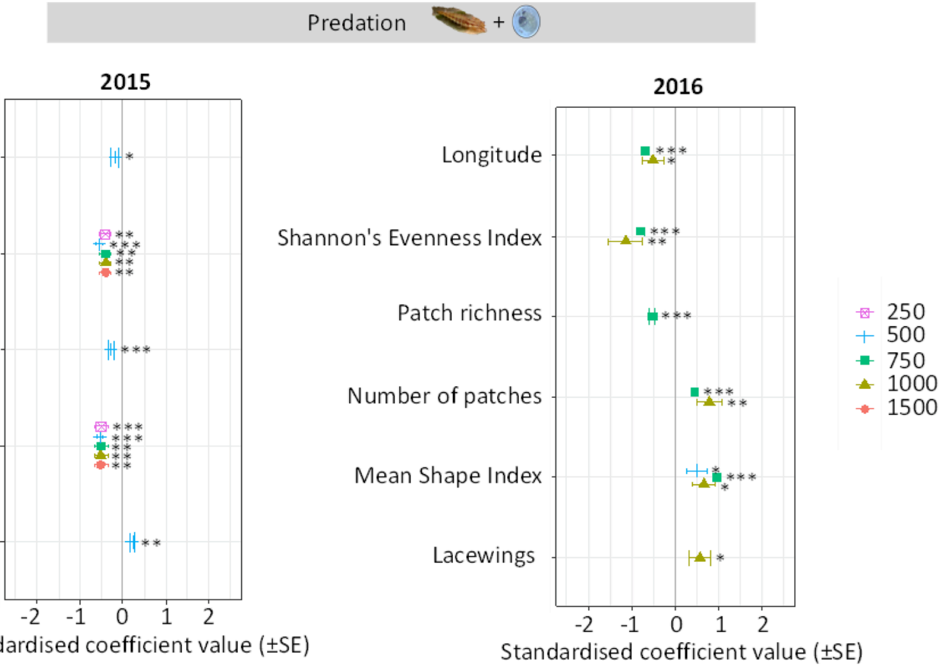

Fig. 4. Response of predation on Prays oleae eggs (carpophagous generation) to landscape variables, predator abundance (Pirate bugs and Lacewings), longitude and latitude (GLMM) in 2015 and 2016 at the different buffers (m) (***<0.001; **<0.01; *<0.05; ·<0.1).

with complex landscape structure. In spring 2015 numbers of lacewings were consistently lower in landscapes with high area of olive groves (CAO), but this was not observed in 2016. In spring, lacewings use pollen and nectar from flowering plants (Alcalá Herrera et al., 2019; Nave et al., 2016; Villa et al., 2019) that are not provided by olive groves, especially in the studied area, where soil is maintained without cover crops. Meteorological differences may account for the difference between years found in this study. May 2015 was extremely hot and dry, while May 2016 was humid and with normal temperatures (AEMET, 2021). Thus, in spite of the tilling, spontaneous vegetation growing after rains in olive groves in 2016 may have provided some of the needed floral resources, while in 2015 they may move to more favourable land uses, such as scrublands, indicated by a positive relationship with the area of scrublands in 2015. Accordingly, previous studies showed that adults of C. carnea visit scrub and herbaceous vegetation patches to fed on different pollen types (Villa et al., 2019). In 2016 a different landscape index, the mean shape index (MSI) was related with higher abundance of lacewings in spring. A high MSI value indicates a more irregular shape of the patches. This patch irregularity could suggest a more varied resources available for lacewings. This landscape index has been related to biological control agents in other ecosystems. For example, predator beetle functional diversity was greater with increasing MSI in a forest system (Kissick et al., 2018). On the other hand, lacewing abundance decreased with higher patch richness (PR) in spring 2016. PR indicate a more heterogeneous landscape, that may increase the survival resources, but also increase the landscape fragmentation and reduce the connectivity.

In autumn the abundance of lacewings was negatively related with CAO in 2016, following the general trend of higher lacewing abundance in complex landscapes. However, the most consistent relationship was a negative one with number of patches (NP), detected both in 2015 and 2016. Again, although NP may indicate a complex landscape and higher resources for natural enemies, it may also indicate a reduction of the habitat connectivity. Another potential explanation is that during this period the olive groves present insufficient resources and lacewings migrate to other more favourable patches in the landscape. Together with NP and PR, Shannon's Evenness Index (SHEI) was also negatively associated with lacewings abundance in one model in autumn 2016.

Regarding the landscape diversity in this study SDI did not show any effect on the predators. This may be because the changes in the proportions of rare land uses did not affect them. Minor land uses in the study area are (in the 1500 buffer): artificial (3.2%), pastures (1%) sparse vegetation (0.7%), landscape Mosaic (0.5%) and Riverside vegetation (0.4%) (Ortega et al., 2021). The land use diversity measured by Shannon or Simpson diversity index was found to be even negatively associated with density of ladybeetles in cotton (Zhou et al., 2014). Authors of this work suggest that analyses based on area proportions give more insight in the likely underlying processes than measures of landscape diversity that do not account for landscape functions, but merely measure diversity as such, which seems to agree with the response of the studied variables in this work where specific land uses such as scrublands or olive groves showed effects on the predators. This is also in agreement with other works, for example Seree et al. (2020) found lacewings positively associated to the proportion of seminatural areas from vineyards in most of the months during the spring (accordingly to our results at 1000 m). Contrastingly, landscape Shannon diversity index affected arthropod richness (Carpio et al., 2019) and abundance of B. oleae in olive groves (Ortega and Pascual, 2014); and landscape Simpson diversity index negatively affected abundance of P. oleae adults (Villa et al., 2020). The particularities of the different areas, translated into different ranges of values of the studied indices and differences in the specific the land uses can explain these different results. It is also worth mentioning that a very high diversity of land uses could mean for some species a fragmentation of their habitat and the connectivity of natural enemies habitats could increase or decrease with fine-grained landscapes (comprising smaller fields and habitat patches) (Haan et al., 2020).

Abundance of pirate bugs was in general negatively associated with landscape complexity. However, it is important to bear in mind that the most relevant variable affecting pirate bugs abundance was the abundance of the olive psyllid, E. olivina, and this could mask other landscape effect, as mentioned above. In addition, results from spring models should be taken with caution because of the pattern observed in the residuals plot. Other works have shown a strong association between pirate bugs and E. olivina in olive groves (Paredes et al., 2015; Plata et al., 2019), and also in other crops, such as pear, psyllids and pirate bugs are related (Scutareanu et al., 1999). Numerous works report a positive effect of landscape complexity on pirate bugs abundance, contrary to our findings. In olive groves, abundance of A. nemoralis was influenced by natural habitat (Paredes et al., 2019; Plata et al., 2019). This seems to be the response to the need of pirate bugs for natural land uses as overwintering sites. This predator overwinters in adult stage (Sigsgaard et al., 2006), particularly in natural vegetation adjacent to the orchard (Horton and Lewis, 2000; Paredes et al., 2013a). In other systems -poisson hemlock, Conium maculatum L.- the population size and spatial pattern of pirate bugs belonging to Orius genus were related to semi-natural areas (Veres et al., 2012). However, there are also works in other agroecosystems reporting a different behaviour. For example, in eggplant, the abundance of pirate bugs was higher in landscapes with a mixture of urban and agricultural areas than in landscapes dominated by a natural land use (forest) (Baba et al., 2016). This may suggest that different pirate bug species respond differently to landscape structure, as suggested by Álvarez et al. (2021), and we did not address species composition.

4.3. *Predation of P. oleae eggs*

In this study, lacewings were positively related with the predation of P. oleae eggs in some cases. In contrast the relationship between the probability of predation and the abundance of pirate bugs was negative in 2015 and absent in 2016. To our knowledge, this is the first study that investigates the relationship between landscape structure and predation of P. oleae eggs (of the carpophagous generation). Landscape structure effect on P. oleae populations (Alves et al., 2021; Costa et al., 2020; Villa et al., 2020) is composed of direct and indirect effects through affecting the pest and biological control processes respectively. In this work, we have shown different effect of landscape structure through this indirect component, as results varied depending on the assessed index. Composition indexes indicating more heterogeneous (PR) and more even (SHEI) land uses led to a reduction in predation rates while indexes indicating a more complex configuration of the landscape (NP and MSI) were related with a higher predation rates. A negative relationship between SHEI and predation rate was observed at some of the studied radii in both 2015 and 2016. This does not agree with results reported in other agroecosystems, where this index showed positive associations with predation and parasitism rates. For example, Liu et al. (2016) found enhanced parasitism of Helicoverpa armigera Hubner (Lepidoptera: Noctuidae) eggs in diverse landscapes and aphid predation was also explained by landscape complexity in soybean crop (Gardiner et al., 2009). In our case, the olive grove, crops and shrublands, were the main land uses that drive SHEI.

Concerning the configuration indices, no previous works have related predation or parasitism rates of phytophagous insects with MSI or NP. It is possible that the direct effect of landscape structure is more relevant for P. oleae than the indirect effect caused through the action of landscape on predation. This direct effect can be a consequence of the resource concentration hypothesis (Root, 1973), and indicates also a possible effect on insect movement. This deserves further investigations, and some preliminary studies show that, movement of P. oleae adults is affected by landscape structure (Moreno et al., 2022; Villa et al., 2021), as it has been shown also for B. oleae (Ortega et al., 2021). Seminatural areas previously showed relevance for enhancing P. oleae natural enemies (Álvarez et al., 2019) or reducing the pest (Paredes et al., 2013b), and this, together with our results may suggest that higher (NP) and more complex (MSI) patches of seminatural areas may reduce the pest by increasing predation.

4.4. Effect of spatial patterns

Several of the studied parameters in this work varied significantly with geographic coordinates. Despite being a relatively small area (1378.13 km^2 approximately) it seems that there are variables associated with geographic coordinates that affect attack and predation rates as well as abundances of potential predators. This deserves further investigation for two reasons: first because these effects may mask possible effects of landscape structure, and second to determine which aspects of geography specifically are driving the effect to incorporate their management into better P. oleae control.

4.5. Conclusion

This study indicates a negative effect of landscape complexity on P. oleae abundance, and biological control of the carpophagous generation could play a role in this effect. Complex landscape structure favours lacewings but not pirate bugs. This may be a masking effect by the olive psyllid, or other not addressed factors such as the vegetation ground cover. Lacewings are confirmed as predators of this generation (at least for some of the buffers), as it has been observed in other generations, however the role of pirate bugs is not clear. Taking this into account, it can be said that in general landscape complexity has a positive effect on the biological control of P. oleae in the carpophagous generation, at least for some years.

CRediT authorship contribution statement

Susana Pascual: Conceptualization, Data Curation, Formal analysis, Funding acquisition, Project administration, Writing - original draft, Writing -review & editing. **María Villa:** Data Curation, Formal analysis, Writing - original draft, Writing -review & editing. **Marta Ortega:** Data Curation, Writing -review & editing.

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.

Data availability

Data will be made available on request.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.biocontrol.2022.105092.

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