



Landscape simplification increases *Bactrocera oleae* abundance in olive groves: adult population dynamics in different land uses

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Abstract

Bactrocera oleae is the main pest in olive groves, and its management requires a sustainable perspective to reduce the use of chemical products. Landscape context is being considered as an important driver of pest reduction, but results on *B. oleae* show inconsistency to date. Most of landscape-pest control studies focus on the dynamics of the pests within the focal crop, ignoring these dynamics in other land uses. Here we present a study in which we analyze the seasonal population dynamics of the olive pest *B. oleae* in the most important land uses of a typical olive landscape in Portugal. We found that *B. oleae* is present in all the land uses and the dynamics are very similar to those in the olive groves. However, the presence of these land uses in the landscape did not display any increase in *B. oleae* abundance within the olive groves. In contrast, a landscape mainly composed by olive groves increased the abundance of this pest. Importantly, more diverse landscapes surrounding olive groves reduce the abundance of the olive fly. Based on these findings, we can conclude that *B. oleae* is present in all the land uses of the studied landscape but that this presence does not imply an increase of *B. oleae* in olive groves. Indeed, other land uses can promote landscape diversification which is a driver of the reduction of *B. oleae* populations in olive groves. We thus encourage olive stakeholders to increase landscape diversification around their farms by promoting/restoring other crops/habitats.

Keywords Pest management · Land uses · Landscape diversification · Olive fly

Key message

- Pest population dynamics out of the focal crop has been poorly studied.
- *Bactrocera oleae* was found in all the land uses that compound a typical olive landscape in Portugal.
- The presence in other land uses did not lead to a rise of pest population in the olive groves.
- Landscape dominated by olive groves significantly increases the abundance of this pest.

- We encourage olive growers to promote landscape diversification to reduce the abundance of this pest.

Introduction

In the last decades, agriculture has passed through an intensification process by drastically increasing the land devoted to farming for food production (Foley et al. 2005). This process has resulted in the loss of natural habitats which in turn has provoked a loss of biodiversity and a reduction of the ecosystem services associated with it (Dirzo et al. 2014). In addition, this landscape simplification process increases the likelihood of more damaging and catastrophic pest outbreaks (Paredes et al. 2021), which has intensified farmers' dependence on insecticides. However, the resistance of pests to insecticides is augmenting, even exceeding the capacity to generate new products to combat these pests (Gould et al. 2018). Because of this, new policies are promoting the use of sustainable solutions for pest management that do not

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imply the use of this kind of products (European Commission 2020). Although most of the techniques that have been tested are orientated toward its implementation at the local level, ecologists, agronomists and farmers are increasingly recognizing the critical role that surrounding landscapes can play in determining pest damage (Thies and Tscharrntke 1999; Bianchi et al. 2006).

Simplified landscapes (i.e., expansive monocultures) can increase pest outbreaks because they promote specialized pest populations to develop and spread more easily, whereas complex landscapes (i.e., mosaics of different land uses) can be a barrier that hamper this expansion (Root 1973; O'Rourke and Petersen 2017). On the other hand, diversified landscapes can promote pest natural enemies (predators and parasitoids) by providing resources such as shelter, nectar, pollen and/or alternative prey for their optimal development, thus improving their action against pests (Landis et al. 2000; Chaplin-Kramer et al. 2011). Therefore, planting multiple crops or retaining non-crop vegetation may lower pest densities and reduce insecticide applications (Dainese et al. 2019; Paredes et al. 2021). However, pests can also use other land uses in the landscape for their development, thus increasing their presence into the crop (Tscharrntke et al. 2016). For example, in Africa, corn stemborers appeared to be promoted by grasslands (Midega et al. 2014), which aligns with another study in Australia that also showed natural grasslands as a source of pest (Parry et al. 2015). Perhaps, the most critical case is the invasive pest species *Drosophila suzukii* that seems to be positively affected by natural habitats at the landscape scale, by using alternative hosts to thrive (Santoiemma et al. 2018) and also because these habitats provide better protection against adverse weather conditions during winter and summer periods (Santoiemma et al. 2019). Thus, the inconsistency of pest responses to landscape complexity prevents researchers to emit clear conclusions about the role of landscape on pest control (Karp et al. 2018). It also highlights the importance of pest species' traits to elucidate its responses to landscape composition (Tamburini et al. 2020) as well as on how they interact with the different elements in the landscape.

Bactrocera oleae (Rossi) is the major olive pest that induces economic losses worldwide totaling approximately 15% per year (Montiel-Bueno and Jones 2001). The effect of landscape context on this pest is not well defined. For example, a study performed in southern Spain showed a reduction of this pest in areas with more natural habitat edge density, landscape diversity and higher number of patches of natural vegetation (Ortega and Pascual 2014). However, another study carried out in Italy did not find any effect of natural habitats on *B. oleae* abundance (Picchi et al. 2016), whereas another work developed in southern Spain showed a positive effect of natural habitats on *B. oleae* abundance (Manjón-Cabeza et al. 2017). The stochasticity that pest

populations have may be behind these contrasting results (Chaplin-Kramer et al. 2013; Paredes et al. 2021). However, neither of these studies nor most of the others regarding the effect of landscape on other pests (but see Santoiemma et al. 2019) have ever explored whether the population dynamics of this pest in other land uses is different or similar from that in the olive grove.

Even more, the olive fly has a period during the year in which it disappears from the olive groves. This is called the “white period” that takes place in the months of May and June when the abundance of olive fly in the field suddenly drops, and there are no olive fruits to attack (Michelakis and Neuenschwander 1981). Before that period, there is an entire generation of flies (March–May) (Marchini et al. 2017) that can only lay eggs on the incipient olive fruits (Boccacio and Pettachi 2009). By the end of the summer, after the “white period”, a new generation begins to rise until the winter (Marchini et al. 2017). During the “white period,” the olive fly can be found within the olive fruit as larvae, but the olive fly in the adult stage can also move in the landscape looking for other resources that ultimately can reinforce its population when it starts rising in Autumn. Therefore, to understand the population dynamics of *B. oleae* in other land uses is critical to understand the importance of a landscape perspective in the management of this pest and how can we better promote natural pest control mechanisms based on landscape management (Daane and Johnson 2010).

Here we purpose a study in which we investigate the dynamics of *B. oleae* in the different land uses that compound a typical olive landscape in Portugal. We aim at answering the following questions: (1) To what extent is *Bactrocera oleae* present in the different land uses, including olive grove? (2) Which are the dynamics of *B. oleae* in these land uses? and (3) How different land uses at the landscape scale affect the abundance of *Bactrocera oleae* in olive groves?

Material and methods

Study sites and insect sampling

To achieve the objectives of this study, a total of 79 sampling points distributed among the most common land uses detected in the sampling area located in the Beira Interior region of Portugal within the municipalities of Castelo Branco and Idanha-a-Nova were selected (Fig. 1). The land uses detected in this area were shrublands, eucalyptus forests, pine forests, “montado” (Iberian oaks savannahs), grasslands, vineyards and olive groves. As it is the main land use of the study and the place where the activity of *B. oleae* takes place, of the total of 79 sampling points, 25 points were located in olive groves. The twenty-five olive groves

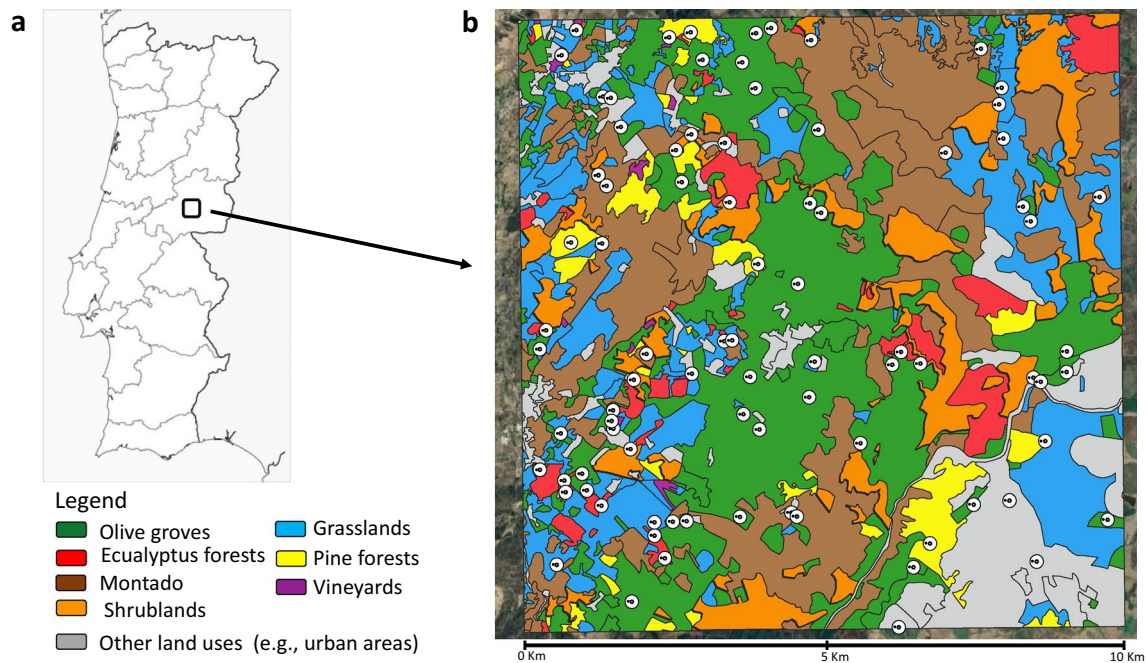


Fig. 1 Location of the study area in Portugal (a) and distribution of sampling points across the different land uses of the study area (b)

were mostly centenary of the same variety (Galega), non-irrigated, with low groundcover vegetation due to livestock presence and were cultivated at the moment of sampling. During this study, olive growers did not apply pesticides and did not use land ploughing methods. The rest of sampling points were distributed among the other land uses at the rate of nine for each one (Fig. 1).

To determine *B. oleae* abundance, a McPhail trap was placed at each one of the points selected in February 2019 (Fig. 1). Each trap was filled with a liquid content consisting of a 250 mL aqueous solution with 5% diammonium phosphate and 2% borax, which is very effective in attracting *B. oleae* adults (Porcel et al. 2009). Samples were monthly collected for one year starting in February 2019 and ending in January 2020. After collection in the field, samples were transported to the laboratory where individuals of *B. oleae* were counted.

Landscape analysis

At each of the 25 sampling points located in olive groves, a geospatial analysis of the surrounding buffer area with a radius of 500 m was performed using QGIS software (Open-Source Geospatial Foundation, Beaverton, OR, USA), a Geographic Information Systems (GIS) platform. Based on aerial photographs, we delineated polygons by representing the different patches of the different land uses found in the study area already mentioned above. The minimal digitized

polygon size was 0.8 ha, associated with a vineyard land use. To validate misalignment of the landscape elements, in addition to adding data to the elements that cannot be identified from the aerial photographs, it was necessary to perform a visual field validation to confirm the land use of each selected point. All of this geospatial information was converted to raster images and analyzed into Fragstats software (University of Massachusetts, Amherst, MA, USA). From this spatial pattern analysis, we obtained class-level landscape metrics, in which the total area of each land use within each of the landscape buffer zones was quantified as a percentage. From these values, we then obtained the Shannon's diversity index (SHDI) that we used as a proxy of landscape diversity. To estimate landscape simplification, we used the proportion of the olive land use surrounding the sampling point.

Modeling

To determine the presence of *B. oleae* in the different land uses present at the study area, we first added all the individuals counted at each sampling date to get a single value per sampling point. We then established statistically significant differences between sets of pairs of land uses by using a non-parametric Wilcoxon rank sum test with *p*-values adjusted by the Benjamini & Hochberg method (Benjamini and Hochberg 1995). Then, for better representation in a box-plot we log-transformed the data used to perform this test.

To account for the dynamics of *B. oleae* in the different habitats during one year, we used Generalized Additive Mixed Models (GAMMs) with a predictor in the form of an interaction between the Julian day in which the traps were sampled and the land use in which they were located. Number of knots were set at five to allow for the representations of the fluctuations of the population at each land use. Finally, we added the location of the trap (sampling point) as a random factor to control for the pseudoreplication over the time as several samples were collected in the same point at different moments of the year. We first modeled this combination of factors with a Poisson error distribution for being the nature of the response variable a count but after testing for overdispersion, we finally decided to model it with a negative binomial error distribution with a log link function to account for overdispersion. To account for model stability, we performed the population dynamic models for each one of the land uses separately and obtained very similar result in terms of significant dynamics (p -value < 0.05).

To account for the effect of the different land uses on *B. oleae* abundance in olive groves, we also used the pooled dataset applied in the first analysis that contains a single value for each one of the 25 olive groves sampled. We thus decided to perform a model selection approach based on the Akaike information criteria corrected for small sample size (AICc) to choose the best model. Models with the lowest AICc and those with a difference of less than two AICc units from the lowest were chosen for further explanation. Thus, we created a set of generalized linear models each one including as predictor the percentage of a single land use

that were: olive, shrublands, “montado,” grasslands, eucalyptus forest, pine forests, vineyards and Shannon diversity index. We complete this set of models with a null model to account for non-effects. Similarly to population dynamic models, we first opted for a Poisson error distribution but after testing for overdispersion we decided to model the data with a negative binomial error distribution and log link function. All analyses were performed in R using the packages “mgcv” for GAMMs (Wood 2011), “lme4” for GLMs (Bates et al. 2015), “DHARMA” for overdispersion analysis (Hartig et al. 2018) and “ggplot2” to visualized results (Wickham 2016).

Results

A total of 10,315 *B. oleae* individuals were collected and counted during the whole experiment. They were present in all the land uses tested in this study (Fig. 2). As expected, the highest abundance was found in olive groves with a total of 8290 individuals. In the land use “montado,” a total of 794 individuals were trapped followed by eucalyptus forests in which 634 individuals were collected. For the other land uses, the total number of captured was lower, with 246 individuals in pine forest, 196 in vineyards, 114 in shrublands and only 34 in grasslands. These differences are reflected in Fig. 2 and align with the results obtained in the Wilcoxon test (Table 1). Olive groves appears as the land use having significant differences with all the rest of the land uses. “Montado” showed differences with grasslands, pine forest

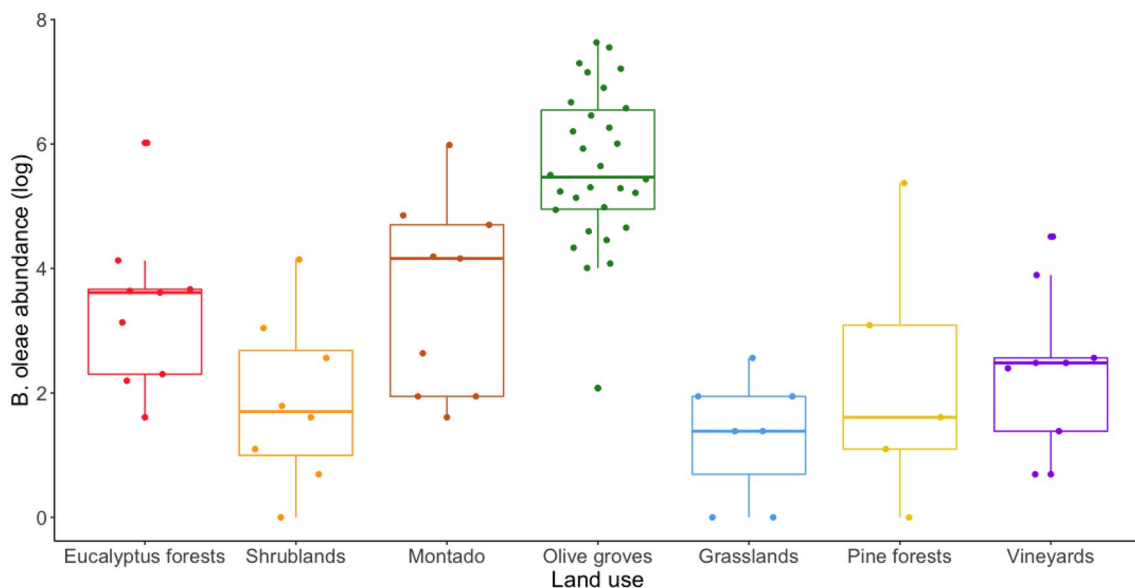


Fig. 2 Boxplot of the logarithm of the abundance of *B. oleae* for the different land uses involved in the study. The top and bottom of the box are first quartile (Q1) and third quartile (Q3), and the centerline

is median (Q2). Whiskers represent 1.5 times the IQR (Q3–Q2) in relation to the upper and lower quartiles. Points represent the log of the abundance at each sampling point

Table 1 Statistically significant differences between sets of pairs of land uses by using a nonparametric Wilcoxon rank sum test with *p*-values adjusted by the Benjamini & Hochberg method

	Eucalyptus forests	Shrublands	Montado	Olive groves	Grasslands	Pine forests
Shrublands	0.053					
Montado	0.691	0.029				
Olive groves	< 0.001	< 0.001	0.005			
Grasslands	0.006	0.442	0.009	< 0.001		
Pine forests	0.027	0.376	0.029	< 0.001	0.685	
Vineyards	0.329	0.442	0.156	< 0.001	0.074	0.137

Significant differences (*p* < 0.05) highlighted in bold

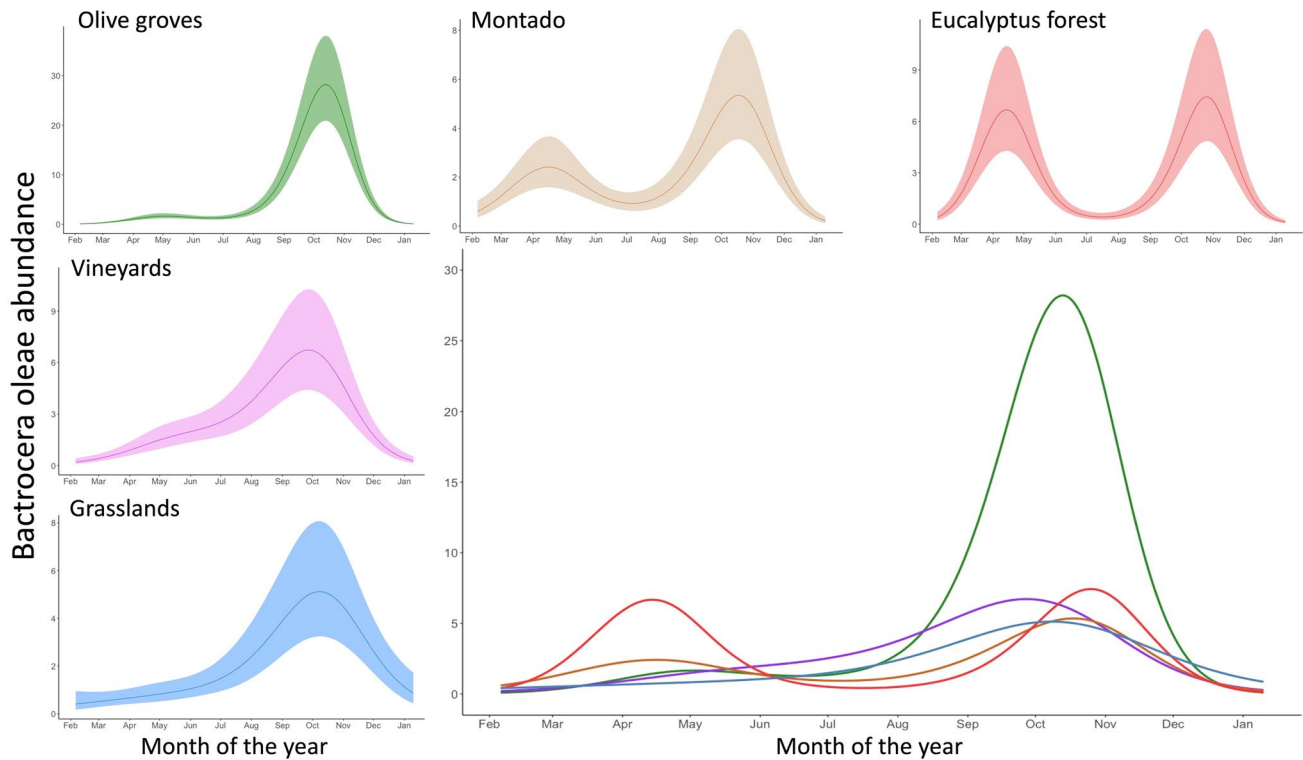


Fig. 3 *Bactrocera oleae* temporal dynamics in the different land uses that compound the study along with the representation of all the dynamics together. Blue, pink, green, brown and red lines represent

grasslands, vineyards, olive groves, “montado” and eucalyptus forests, respectively. Shaded areas represent the confident intervals at 95%

Table 2 Significance of values of olive fly population dynamics in the different land uses used for the Generalized Additive Model

Variable	<i>p</i> -value
Population dynamics in Eucalyptus forests	< 0.001
Population dynamics in Shrublands	0.371
Population dynamics in Montado	0.003
Population dynamics in Olive groves	< 0.001
Population dynamics in Grasslands	0.019
Population dynamics in Pine forests	0.615
Population dynamics in Vineyards	< 0.001
R2	0.204
Deviance explained	70.6%

and olive groves but not with eucalyptus forests and vineyards. Similar results were obtained for eucalyptus forests. Shrublands only showed significant differences with olive groves and “montado.” A similar situation occurred with pine forest and grasslands, but these land uses also showed significant differences with eucalyptus forests. Finally, vineyards only displayed significant differences with olive groves.

Pest dynamics were significant in five of the seven land uses tested in this study (Fig. 3). Specifically, *B. oleae* showed significant dynamics in olive groves, “montado,” eucalyptus forests, grasslands and vineyards (Table 2). *Bactrocera oleae* population in olive groves started raising in

March, reaching a peak in May. Then, it slightly decreased until mid-July when started notably spiking to find the maximum abundance in mid-October for then decrease during the winter. Grasslands and vineyards showed a very similar pattern that reflected a sustained growth from March to October and then decrease during the winter. In contrast, the dynamics of *B. oleae* in eucalyptus forests and “montado” displayed a two-hump pattern with an intense growth from February to mid-April and then a decrease finding the bottom around July and August and then experienced another growth that peaked in the beginning of November. These dynamics were very similar to the one in olive groves, but

the intensity of the first increase was higher than in olive groves, especially for eucalyptus forests (Fig. 3).

Regarding the effect of the different land uses on the abundance of *B. oleae* in olive groves, the selected models displayed a positive effect surrounding olive groves (Estimate = 0.015; p -value = 0.019) and a negative effect of the Shannon diversity index on *B. oleae* abundance (Estimate = -0.734; p -value = 0.045) (Table 3; Fig. 4). The abundance of *B. oleae* increased more than two times from olives groves with other land uses surrounding them to places with a very simplified landscape > 90% of olive groves in the buffer area). In contrast, landscape diversification displayed a negative effect reducing the abundance of *B. oleae* two times from less diversified to more diversified landscapes. It is important to notice that the parallel effect that shows the trends for landscape simplification and landscape diversity is due to the high negative correlation among these two predictors.

Table 3 Akaike values corrected for small sample size (AICc) of the different models generated for testing the effect of the amount of a land use in the landscape on the abundance of the pest *Bactrocera oleae*

Land use	AICc
Null	345.45
Montado	363.32
Eucalyptus forests	347.87
Grasslands	345.68
Pine forests	346.20
Shrublands	347.91
Vineyards	347.81
Olive groves	341.46
Shannon diversity	342.91

Minimum AICc in bold

Discussion

This study demonstrated that *B. oleae* is present in the main land uses that comprise this typical Portuguese olive landscape. As expected, maximum abundance was found in olive groves, but also important abundances were found in

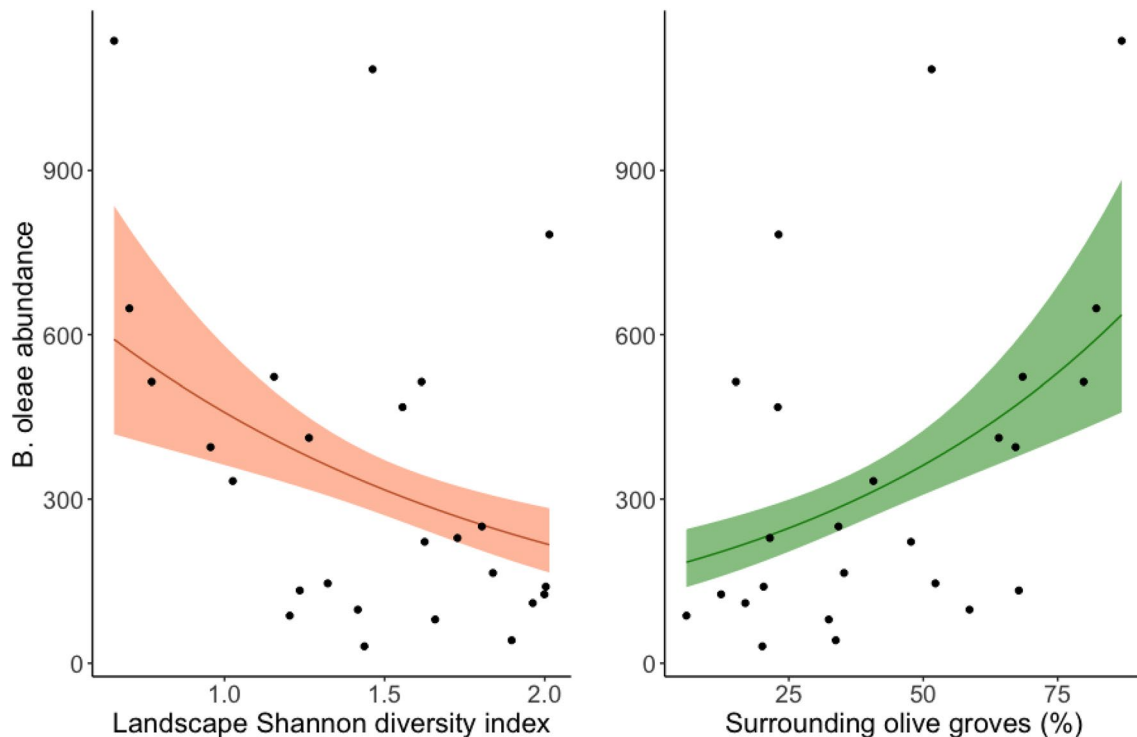


Fig. 4 Estimated effects of gradients of landscape diversity (brown line) and landscape simplification (green line) on *Bactrocera oleae* abundance. Shaded areas represent the confident intervals at 95% ($N=25$)

eucalyptus forests and “montado.” Our experimental design does not allow us to infer the reasons for the presence of *B. oleae* in the different land uses, but we can hypothesize that they are not thriving on alternative hosts due to *B. oleae* characteristics as a specialist olive pest (Daane and Johnson 2010; Clarke 2018). In contrast, the fact that this fly appears in all the land uses tested may be related to its dispersal behavior, being able to fly around 400 m per week (Fletcher and Kapatso 1981). When populations start to build, new adult flies disperse to other olive areas to develop the next generation (Kounatidis et al. 2008). During this migration, they can pass through patches of other land uses in which they rest and search for resources to survive. Consequently, it makes sense that the dynamics in other land uses has to be related to the dynamics in the olive groves as they are going to act as a source of olive flies. Nevertheless, this parallelism is not perfect in all the land uses. For example, the populations in vineyards and grassland peak at the same time as in olive groves, in the fall, but no peak is displayed in spring. Critically, however, *B. oleae* abundance in eucalyptus forest and in “montado” really encompassed olive grove dynamics with two clearly defined peaks: one in spring and the other in autumn. This fact could be explained by the similar distributional characteristics of these habitats.

The distributional characteristic of a habitat can be very important for pests to recognize new potential suitable territories to disperse (Propoki and Owens 1983; Jactel et al. 2021). This is especially relevant in herbivorous diurnal species such as tephritid flies, the group to which *B. oleae* belongs. For these insects, visual cues may play an important role in the location of host plants and essential resources, such as food, mating and oviposition sites (Propoki and Owens 1983). Indeed, some tephritid flies have been detected visually reacting to shapes and silhouettes of plant populations (Moericke et al. 1975). Therefore, size of vegetational patch, density and dispersion pattern of hosts plants within a patch, morphological differences between hosts and non-hosts, and the overall aspect of host habitats (Feeny 1976, Rauscher 1981) in space and time may all have an effect that can be really important within an agricultural context (Bach 1981; Smith 1976). Therefore, when dispersing, *B. oleae* could potentially select eucalyptus forest and, especially, “montados” as suitable habitats to look for resources during the spring, as they show dispersion patterns and densities very similar to olive groves with solitary scattered trees. Indeed, this could be the reason behind the fact that *B. oleae* population dynamic in “montados” mimic those in olive groves. However, eucalyptus forest appearance is not similar to olive groves and the reasons for repeating some temporal dynamics could be related to this habitat acting as a shelter for extreme weather conditions specially in summer when *B. oleae* is highly affected by high temperatures in the adult stage (Gutierrez et al. 2009; Wang

et al. 2009; Abd El-Salam et al. 2019). However, temporal dynamics in eucalyptus forests show a decline in the olive fly population during summer. This is not consistent with the climate shelter hypothesis, and more research should be done to elucidate why *B. oleae* feels attraction to eucalyptus forests.

Despite the fact that most of the land uses studied displayed a significant population dynamic of the pest, our results show that none act as a reservoir to boost *Bactrocera oleae* populations. This is corroborated with the null effect that any habitat had on fly abundance within the olive grove. Critically, landscape simplification (large areas just covered with olive groves in the landscape) and landscape diversification (diversity of land uses in the landscape) displayed the most notable effects. On the one hand, simplified landscapes allow *B. oleae* to easily grow as they have plenty of resources to build their population and spread easily because they have no barriers to impede its dispersion (Root 1973; O’Rourke and Petersen 2017). Importantly, the presence of *B. oleae* individuals in other land uses, as demonstrated in this study, supports the idea that these landscape elements could act as a barrier for the dispersion of this pest, which reflects its low abundance in diversified landscapes. Moreover, simplified landscapes lack natural enemies that can exert a proper top-down control of the pest population, whereas diversified landscapes can provide with resources to these natural enemies allowing the delivery of natural pest control services (Chaplin-Kramer et al. 2011; Rusch et al. 2016). Thus, the implication of increasing landscape diversity seems obvious for this pest and align with other studies that detected landscape diversification as a major driver of *B. oleae* abundance reduction (Ortega and Pascual 2014).

Management implications

As a consequence of these findings, we encourage farmers, technicians and politicians to promote landscape diversification in olive groves. Increasing areas with different land uses will likely impend the dispersion of *B. oleae*, ultimately preventing sudden population peaks, which would otherwise result in outbreaks that would necessitate insecticide applications. At the individual level, farmers could better control *B. oleae* populations by planting native vegetation around their farms. However, the increase in land use diversity will depend on the coordination between groups of neighboring farmers to redesign the arrangement of the different elements of the landscape, taking advantage of the synergies provided by the orography and changing land uses in areas where the composition is not balanced. A good way to promote coordination between different agricultural stakeholders is the financial compensation programs that governments can put in place to help increase the diversity of the landscape (Batáry et al. 2015). This type of coordination based on the

information we obtain from the landscape is an important and necessary step for obtaining collateral benefits related to the promotion of ecosystem services such as biodiversity conservation and human health.

Authors' contribution

DP, SM, JA, AAS and JPS conceived the project and designed the methods; DP, SM, JFA and JMC collected the data; DP and JPS analyzed the data; DP wrote the study. All authors made critical contributions to the draft and gave final approval for publication.

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Declarations

Conflict of interest All authors declare that they have no conflict of interest. The authors have no relevant financial or non-financial interests to disclose. The authors have no competing interests to declare that are relevant to the content of this article. All authors certify that they have no affiliations with or involvement in any organization or entity with any financial interest or non-financial interest in the subject matter or materials discussed in this manuscript. The authors have no financial or proprietary interests in any material discussed in this article.

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

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