agronomy

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Olive Landscape Affects *Bactrocera oleae* Abundance, Movement and Infestation

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Abstract: The economic importance of *Bactrocera oleae* (Rossi) and the problems associated with insecticides make necessary new management approaches, including deeper biological knowledge and its relationship with landscape structure. Landscape complexity reduces *B. oleae* abundance in late summer–autumn in areas of high dominance of olive groves, but the effect of landscape structure in spring and in areas less dominated by olive groves has not been studied. It is also unknown whether the insect disperses from olive groves, using other land uses as a refugee in summer. This work evaluates the effect of landscape structure on olive fruit fly abundance and movement in spring and autumn, and infestation in autumn, in central Spain, an area where the olive crop does not dominate the landscape. A cost–distance analysis is used to evaluate the movement of the fly, especially trying to know whether the insects move away from olive groves in summer. The results indicate that *B. oleae* abundance is consistently lower in complex landscapes with high scrubland area (CAS), patch richness (PR) and Simpson landscape diversity index (SIEI), and low olive grove area (CAO). The cost–distance analysis shows that the fly moves mainly in spring, and amongst olive groves, but there is no evidence that land uses other than olive groves serve as a summer refuge. Olive fly infestation decreased with decreasing CAO and increasing CAS and SIEI, accordingly with the effect of landscape on abundance. Thus, mixing olive groves with other land uses, which are not a source of flies, can help improve control of this important pest.

Keywords: cost–distance; dispersal; olive fruit fly; path richness; pest control; Simpson landscape diversity index

Citation: Ortega, M.; Moreno, N.; Fernández, C.E.; Pascual, S. Olive Landscape Affects *Bactrocera oleae* Abundance, Movement and Infestation. *Agronomy* **2022**, *12*, 4. https://doi.org/10.3390/agronomy12010004

Academic Editor: Andrea Sciarretta

Received: 17 November 2021
Accepted: 16 December 2021
Published: 21 December 2021

1. Introduction

The olive fruit fly, *Bactrocera oleae*, is the key pest of olive crops in most olive growing areas worldwide [1]. Control of *B. oleae* has relied for many years mainly on synthetic insecticides, with associated problems of resistance, side effects on beneficial insects and problems to human health and the environment [2,3]. There are also alternative control measures for this important pest which are more environmentally friendly, such as kaolin, spinosad or mass trapping [4,5]. However, knowledge on the biology of *B. oleae* is also needed as a basis for its management. In particular, it is necessary to study the behaviour of spring populations and to understand better their sheltering in summer, when populations decline in olive groves, only to reappear when temperatures drop.

Pupation of *B. oleae* occurs inside olives in summer. However, in autumn most 3th instar larvae leave the olive for pupation and overwintering in the soil. Also, in areas with mild winter temperatures *B. oleae* may overwinter as a larva or an adult. The following spring adults emerge between March–May, and a number of generations between two and five are completed, depending on the environmental conditions. The biology of overwintering populations has been studied, showing the presence of a complete generation in the spring [6]. During the summer, the number of *B. oleae* adults captured by different trap devices in olive groves decreases to minimum values, and increases from late summer to autumn, when olive fruit fly damage occurs. Thus, studies on *B. oleae* abundance have been conducted mainly on autumn populations, with a need to clarify the biological aspects of spring populations [6]. It is also important to try to clarify the biology of *B. oleae* in the summer, as it is unclear whether the unfavourable effects of high temperature and low humidity cause the fruit fly to disperse to cooler sites [1].

The relationship between the structure of the landscape and the abundance of *B. oleae* has been studied in late summer–fall in a region dominated by olive groves (more than 70%), namely, the province of Jaén in southern [7,8]. In this area of simple landscape due to the dominance of olive groves, it has been shown that the abundance of *B. oleae* in late summer–autumn is lower in olive groves surrounded by a more complex landscape: that is, olive groves around which the olive grove area was smaller and the Shannon landscape diversity index was higher. This landscape effect seems to be mainly direct, as predation of *B. oleae* pupae is more related to local factors than to landscape factors [9]. Parasitism rates are also usually low [10,11], although a relationship between parasitism rates and landscape structure has been reported as well [12]. The direct landscape effect on olive fruit fly abundance responds to an increased availability of resources, as *Olea europaea* L. is the only nutritious plant for *B. oleae*. However, this direct landscape effect can work also by affecting insects' dispersal, as landscape structure can favour or hinder the movement of the insect between favourable habitat patches.

In this work, we use the cost–distance tool to make inferences about the movement of *B. oleae*. This approach assigns different weights to cover types surrounding focal fields to identify spatial arrangements that facilitate or discourage the flow of organisms, and thus it can improve our understanding of how landscape affects ecological processes [13]. Cost–distance has been applied to measure landscape connectivity mainly in ecology [14–16], with some studies also on forest pests [17,18]. However, to our knowledge, this approach has been used in the field of agricultural pest control only in a study of cotton landscapes [19].

In this context, the aim of this work is to gain knowledge on the relationship between landscape structure and *B. oleae* abundance, movement and infestation, in a landscape context with a gradient of simplification (dominance of olive groves from 6 to 70%), such as the olive growing area in central Spain. The following hypotheses were raised: (a) The landscape effect on *B. oleae* abundance occurs over the complete cropping season, including in spring populations. (b) Another landscape effect occurs, in this case on the movement of *B. oleae*, throughout the growing season. (c) This relationship translates into a reduced infestation in the olive crop in more complex compared to simpler landscapes.

2. Materials and Methods

2.1. Study Area

The study was carried out in the olive growing area of south-eastern Madrid (central Spain) (Figure 1), which covers an area of approximately 1378.13 km^2. The climate is continental Mediterranean, with long and cold winters (average minimum temperature 0–2.5 °C) and long and hot summers (average maximum temperature 27.5–35 °C) (http://www.aemet.es/es/serviciosclimaticos/datosclimatologicos/valoresclimatologicos, accessed on 15 March 2020). The dominant natural habitat is a Mediterranean scrubland with plant species adapted to dry climate and gypsiferous soils, and the main crops are olives, vineyards and cereals. Olive groves are generally rain-fed and planted in a 10 × 10 m frame. The main variety in the area is Cornicabra, followed by others such as Castellana, Manzanilla or Picual. Olive grove management is mostly integrated, with low application of phytosanitary products. The soil is normally ploughed, but also treated with herbicides for weed control. The main pest in the area is the olive fruit fly (*Bactrocera oleae* Rossi), followed by the olive moth (*Prays oleae* Bernard). Pest management is focused on olive fruit fly control, and treatments are generally only applied if there is a phytosanitary alert.

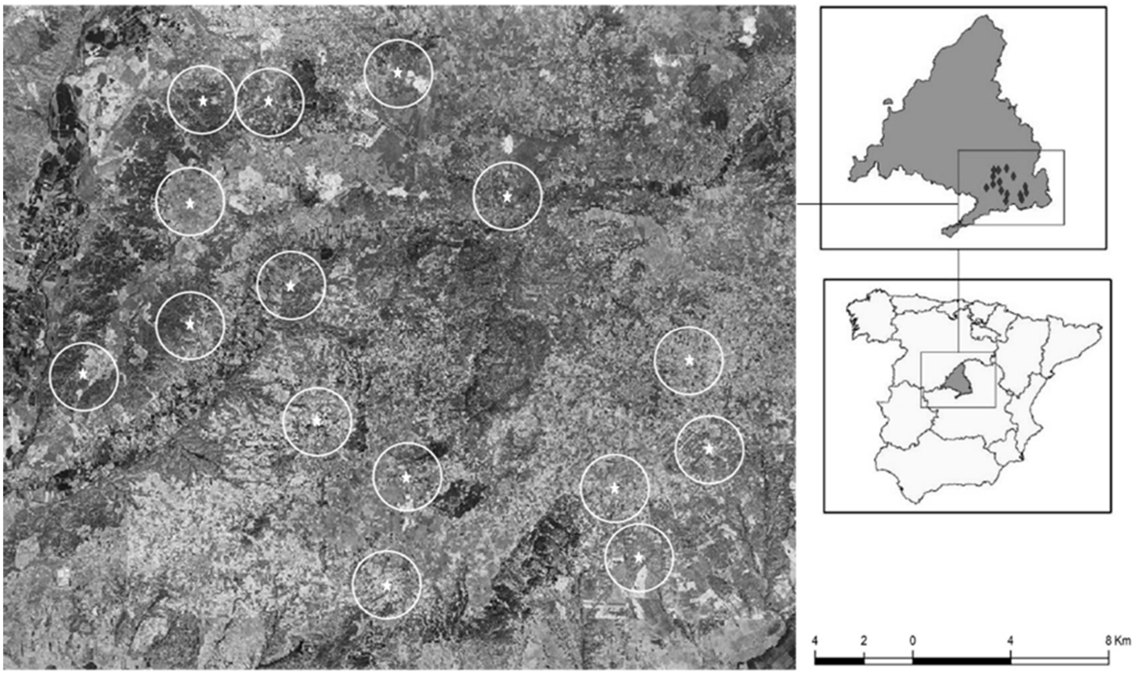

Figure 1. Location and aerial photograph of the study area. Sampled olive groves are indicated with asterisks, as well as the 1500 m radius areas around them.

Fifteen olive groves were selected in a 750 km^2 area to represent a landscape compositional gradient, according to three parameters: landscape diversity index, percentage of olive groves and percentage of natural vegetation. Details about the selection of olive groves can be found in González-Núñez et al. [11]. The olive groves were separated by at least 4 km. All of them were quite small in size, with an area ranging from 0.97 to 11 ha. The slopes were moderate, between 1 and 10%, and the altitudes ranged between 570 and 700 m a.s.l. The size and UTM coordinates of the olive groves are in Table S1. The olive groves were managed following the general procedures in the area: integrated pest management and soil management without cover crops. The dominant variety in the area, Cornicabra, was present in 13 olive groves, while the Castellana variety was present in 5 olive groves.

2.2. Estimation of Bactrocera Oleae Abundance and Infestation

Yellow sticky traps baited with sex pheromone were used to sample *Bactrocera oleae* adults. Four traps were placed in the centre of each olive grove forming a 20 × 20 m square, separated by at least 30 m from the margin of the grove. Sampling was carried out in 2015 from 22 April to 28 May and from 26 August to 7 October, and in 2016 from 21 April to 9 June and from 25 August to 5 October. The number of *B. oleae* adults were counted and removed from the traps weekly. The pheromone was replaced according to the manufacturer instructions and traps were replaced when their stickiness was reduced. The number of *B. oleae* adults was pooled in the two sampling periods each year: “spring” (22 April–28 May 2015 and 21 April–9 June 2016) and “autumn” (26 August–7 October 2015 and 25 August–5 October 2016). In “spring”, adult flies emerged from the soil and no olive fruits were available for oviposition. In “autumn” olive flies started emerging from the fruits.

Bactrocera oleae infestation was estimated by sampling olives on 22 October 2015 and 19 October 2016. On each sampling date, 100 fruits were collected from each olive grove. The total number of olives collected was 3000. Fruits were collected from trees in the area where traps were placed. Ten trees were sampled per olive grove and ten fruits from each tree were collected. Fruits were randomly picked on each of the sampled trees, with two fruits always being collected from each cardinal point and two from inside the tree canopy. The fruits were taken to the laboratory and the number of fruits with *B. oleae* oviposition stings was counted.

2.3. Landscape Metrics

Landscape indices were calculated using the software Patch Analyst for ArcGIS® 10.1 (ESRI, Redlands, CA, USA). Information from the SIOSE project (Information System on Land Occupation of Spain; http://www.siose.es, accessed on 15 June 2019) was used to calculate these indices. Verification and updating of land uses were accomplished by comparing the SIOSE information collected in 2005 with aerial photographs taken in 2015 (provided by National Aerial Orthophotography Plan; https://pnoa.ign.es/, accessed on 15 June 2019) and information provided by SIGPAC (Geographic Information System of Agricultural Plots, 2004; http://sigpac.mapa.es/fega/visor/, accessed on 15 June 2019). The patches were reclassified to obtain final number of 13 land use classes: 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), landscape mosaic (Z) and watered crop (WC). Landscape mosaic refers to artificial green areas such as parks and housing developments with vegetation that is irrigated. Buffer areas of radii 500, 750, 1000 and 1500 m were established around the selected olive groves. Figure 2 shows the mean percentages of these land uses in the buffer of 1500 m. The dominant classes were olive groves, scrublands and field crops. The following landscape structure indices were calculated for these areas: area of olive groves (CAO), area of scrublands (CAS), patch richness (PR), number of patches (NP), total edges (TE), Shannon landscape diversity index (SHEI), and Simpson landscape diversity index (SIEI).

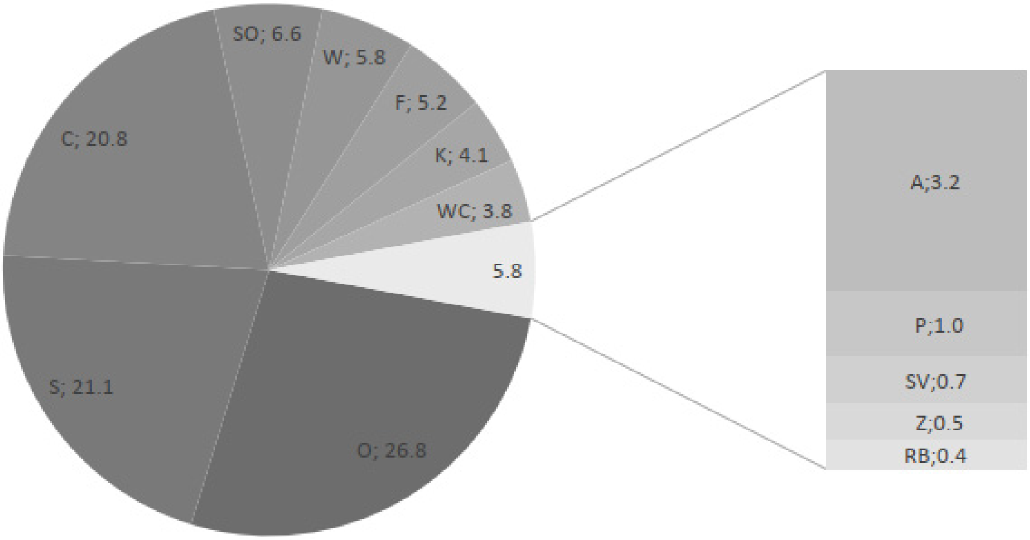

Figure 2. Average percentages of the different land uses in the 1500 m radius areas around the sampled olive groves. olive grove (O), field crop (C), scrubland (S), scrubland with oaks (SO), woody crop (W), artificial (A), pastures (P), oak forest (K), sparse vegetation (SV), pine forest (F), riverside vegetation (RB), landscape mosaic (Z) and watered crop (WC).

2.4. Cost–Distance Analysis

A standard component of the ArcGis software, the 'cost–distance' tool, was used to model the dispersal of a theoretical *B. oleae* individual throughout the landscape, by identifying paths that maximize the use of favourable land uses between a designated source and the destination on a map grid. In this case the source was the perimeter of the buffer areas, and the destination was the centres of the buffer areas, where *B. oleae* samples were taken. Each cell of the map grid was assigned a cost based on the land use that occupied that cell. The lowest cost (1) was assigned to those land uses that hypothetically represent preferred habitat patches; unfavourable land uses, or inhospitable matrices, were assigned higher costs (50).

Three different scenarios were hypothesized regarding the suitability of land uses for *B. oleae* and its movement. H1: The olive grove is the only land use suitable for *B. oleae*, and the flies move amongst olive groves. H2: Water sources are also suitable for *B. oleae*, acting as a summer refuge for the flies and thus as a source of infestation for olive groves. H3: Scrublands are also suitable for *B. oleae*, acting as a summer refuge for the flies and thus as a source of infestation for olive groves. H2 and H3 were raised because of the known drastic decrease in *B. oleae* abundance in olive groves in summer [20–23]. Cost values were assigned to the different land uses according to these hypotheses (Table 1). Mean cost–distance values were calculated for each olive grove at all spatial scales. H1 was tested at all radii. However, in order to have a representative gradient in cost–distance values, hypotheses H2 and H3 were tested at radii 1000 and 1500 only, because of the scarce presence of some land uses around some olive groves at the smallest radii (750 and 500). Other land uses were not tested due to their low frequency in the olive grove plots.

Table 1. Cost values assigned to land uses according to three hypotheses regarding their suitability for *Bactrocera oleae* (see text for details). O: olive grove, C: field crop, S: scrubland, SO: scrubland with oaks, W: woody crop, A: artificial, P: pastures, K: oak forest, SV: sparse vegetation, F: pine forest, RB: riverside vegetation, landscape mosaic (Z), watered crop (WC).

	Land Uses												
Hypothesis	**O**	**C**	**S**	**SO**	**W**	**A**	**P**	**K**	**SV**	**F**	**RB**	**Z**	**WC**
H1	1	50	50	50	50	50	50	50	50	50	50	50	50
H2	1	50	50	50	50	50	50	50	50	50	1	1	1
H3	1	50	1	1	50	50	50	50	50	50	50	50	50

2.5. Data Analysis

The effect of landscape structure on *B. oleae* abundance was assessed by fitting generalized linear mixed models (GLMMs) separately for every buffer radius and sampling period. The explanatory variables (landscape indices) were previously selected, allowing a minimum collinearity using the variance inflation factor (VIF) criteria (VIF < 3) (Zuur et al., 2010), and non-significant variables were dropped from the models. Olive grove was a random factor in the models. A negative binomial family was considered to account for overdispersion, and the link function was log.

GLMMs were built to assess *B. oleae* movement by comparing the effect of olive landscape structure on *B. oleae* abundance from two points of view. The first point of view was the *area* approach, in which the explanatory variable was olive grove area (CAO); the second point of view was a *dynamic* approach that studies as explanatory variables the values of cost–distance calculated for the different hypotheses (COSTH1, COSTH2 and COSTH3). GLMMs were fitted with a negative binomial distribution and log link function.

The effect of landscape structure on *B. oleae* infestation was assessed by fitting GLMMs for every buffer radius and year. The response variable was the fruits infested, with values of 1 for infestation (olive fruit with *B. oleae* oviposition sting) and 0 for non-infestation (olive fruit free of *B. oleae* oviposition sting). The explanatory variables were the landscape indices and the abundance of *B. oleae* in the autumn sampling period of the corresponding year. As in the case of *B. oleae* abundance, the explanatory variables were previously selected, allowing a minimum collinearity using the VIF < 3 criteria [24], and non-significant variables were dropped from the models. Models were fitted with a binomial distribution and logit link function.

All statistical analysis was carried out in R version 4.0.3. The glmmTMB function from the “glmmTMB” package version 1.1.2.3. was used for model building [25]. The models were validated by plotting residuals versus fitted values and covariates using the package DHARMa version 0.4.4. [26].

3. Results

3.1. Effect of Landscape Structure on B. oleae Abundance

Landscape structure affected *B. oleae* abundance in all the periods studied. All the landscape indices showed the same trend: an increase of *B. oleae* abundance in simplified landscapes. Figures 3–5 show the main effects of landscape indices calculated at 500, 1000 and 1500 m buffer areas, respectively. The effects at 750 m were similar to those found at 500 m. The complete results from the glmmTMB are in Tables S2 and S3 for 2015 and 2016, respectively. *B. oleae* abundance decreased with increasing CAS, PR and SIEI (Figures 3 and 4), and increased with CAO (Figure 5).

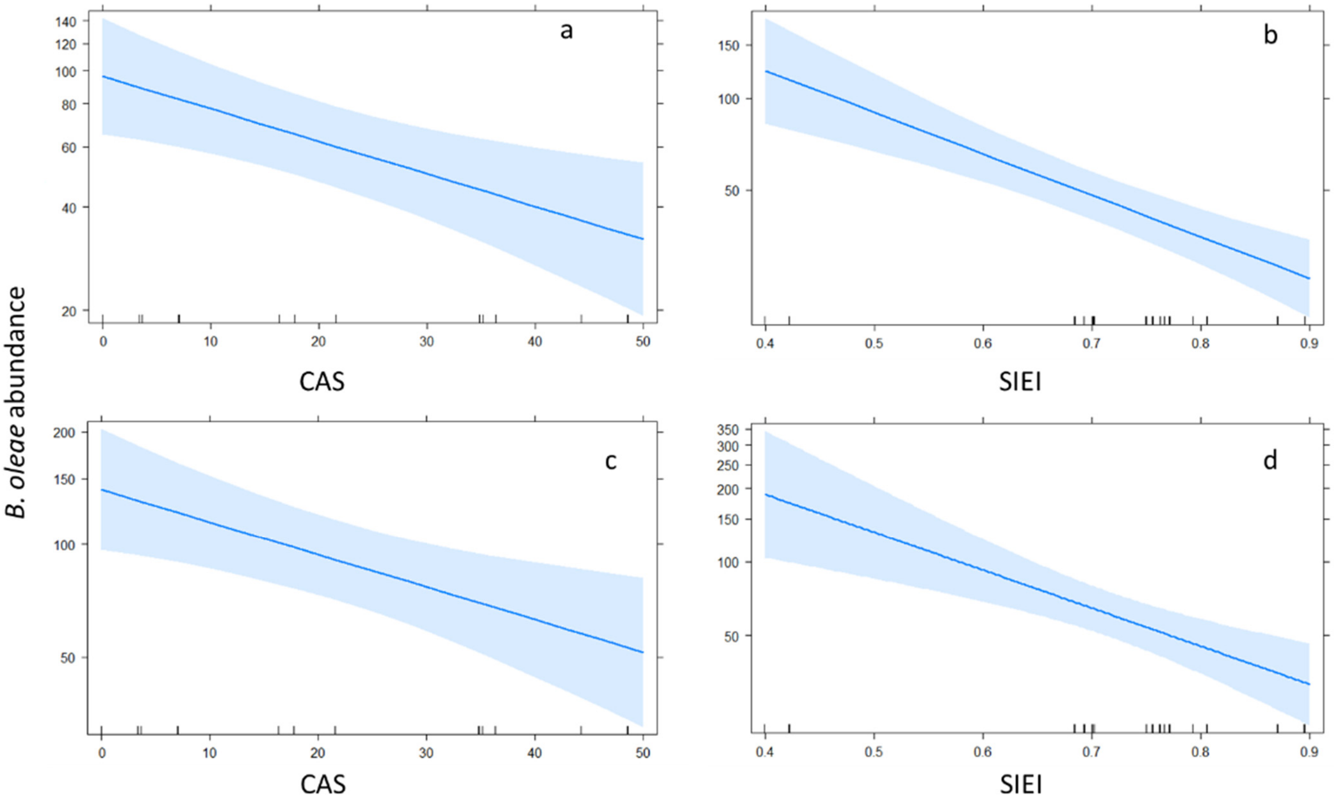

Figure 3. Effect of landscape structure on *Bactrocera oleae* abundance in spring 2015 (**a**), autumn 2015 (**b**), spring 2016 (**c**) and autumn 2016 (**d**). Landscape indices were scrubland area (CAS) and Simpson landscape diversity index (SIEI) calculated at 500 m buffer areas.

3.2. Assessment of B. oleae Movement

The models were fitted to compare the effect of landscape on *B. oleae* abundance from an *area* approach, i.e., using CAO as the landscape explanatory variable, and from a *dynamic* approach, i.e., using mean cost–distance values (COST) as explanatory variables (Tables 2 and 3).

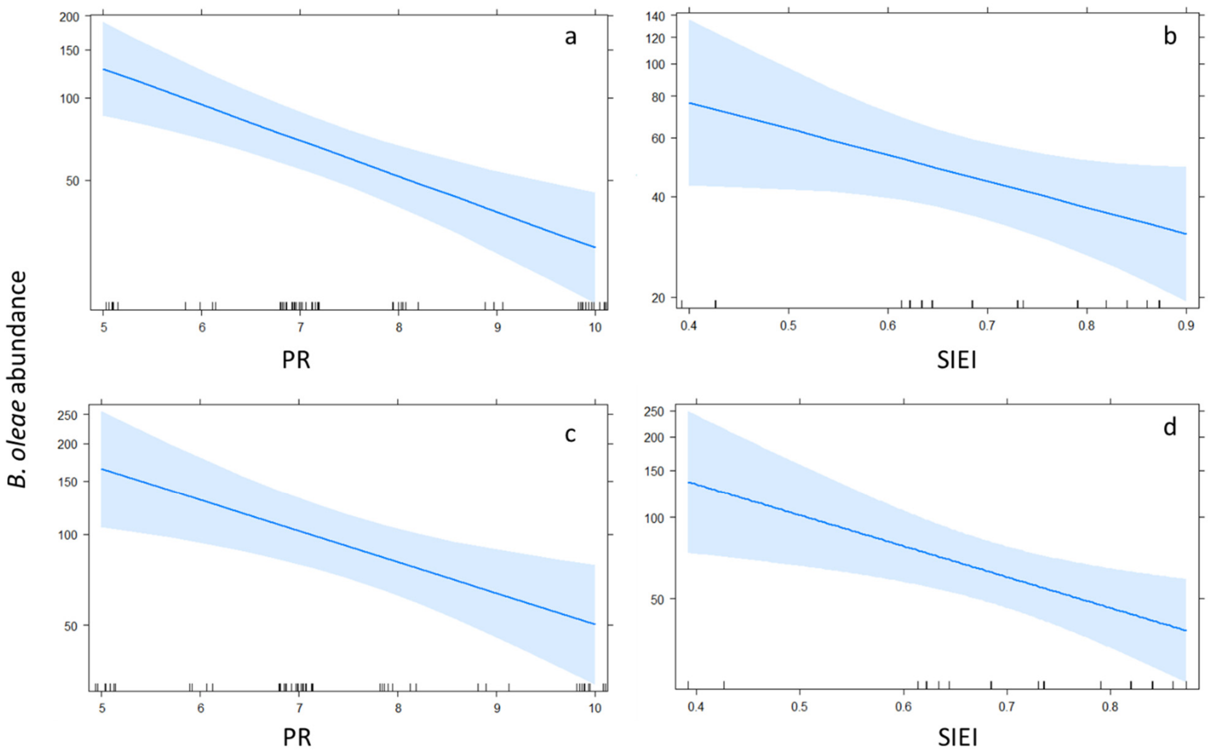

Figure 4. Effect of landscape structure on *Bactrocera oleae* abundance in spring 2015 (**a**), autumn 2015 (**b**), spring 2016 (**c**) and autumn 2016 (**d**). Landscape indices were patch richness (PR) and Simpson landscape diversity index (SIEI) calculated at 1000 m buffer areas.

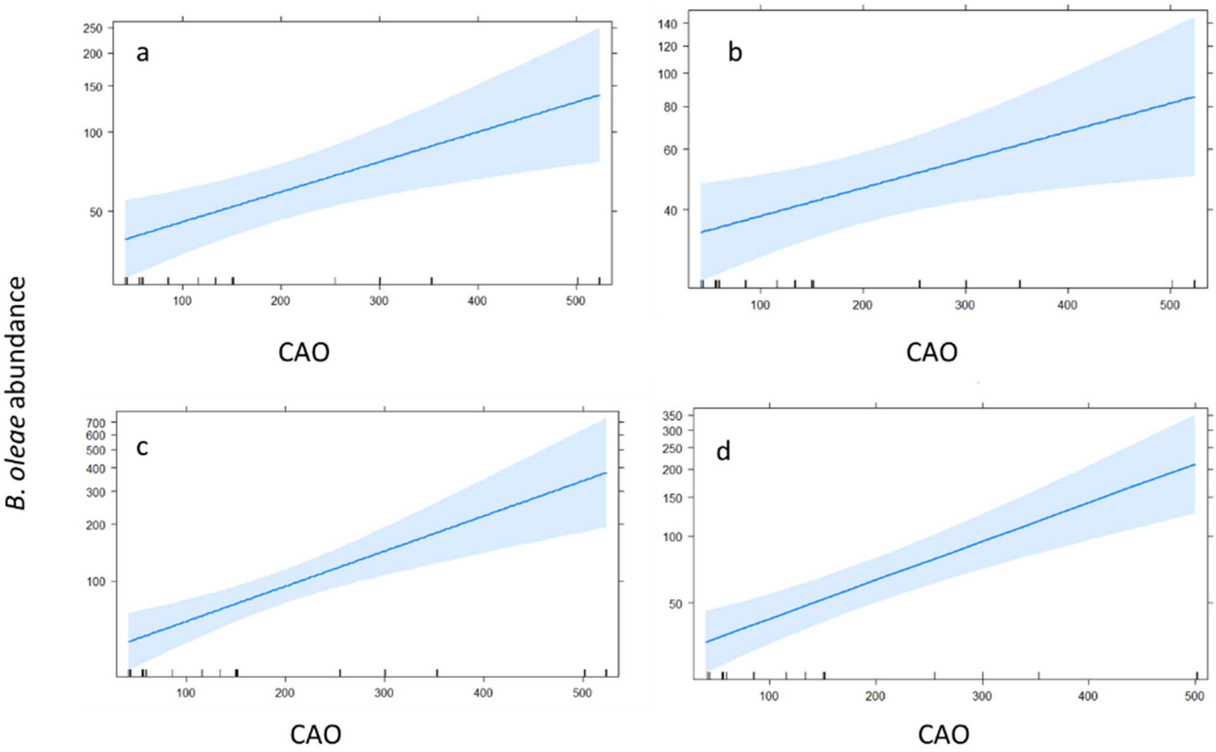

Figure 5. Effect of landscape structure on *Bactrocera oleae* abundance in spring 2015 (**a**), autumn 2015 (**b**), spring 2016 (**c**) and autumn 2016 (**d**). Landscape Index was olive grove area (CAO) calculated at 1500 m buffer areas.

Table 2. Estimated regression coefficients (EST), adjusted standard errors (SE), Z and P values from glmmTMB for the comparison of the *area* and *dynamic* approaches regarding landscape effect on *Bactrocera oleae* abundance in 2015. Abundance data were pooled in two periods. Generalized lineal mixed models were fitted with a negative binomial distribution and link function log. Olive grove area (CAO) was used as the explanatory variable for the *area* approach, and cost–distance (COST) for the dynamic approach. Both CAO and COST were calculated at four radii around the sampled olive groves (500, 750, 1000 and 1500 m). H1, H2 and H3 after COST refer to hypotheses 1, 2 and 3 respectively (see text for details). p values < 0.05 indicated in bold.

			Period							
			Spring				**Autumn**			
Radius	**Approach**	**Coefficient**	**EST**	**SE**	**Z**	**P**	**EST**	**SE**	**Z**	***P***
500	Area	Intercept	3.562	0.200	17.822	**$<2 \times 10^{-16}$**	3.391	0.171	19.788	**$<2 \times 10^{-16}$**
		CAO	0.019	0.005	3.806	**1.41×10^{-4}**	0.0154	0.005	3.356	**7.90×10^{-4}**
	Dynamic	Intercept	4.678	0.171	27.345	**$<2 \times 10^{-16}$**	4.139	0.195	21.240	**$<2 \times 10^{-16}$**
		COST H1	-1.9×10^{-4}	4.73×10^{-5}	−4.021	**5.79×10^{-5}**	-1.04×10^{-4}	4.98×10^{-5}	−2.090	**3.66×10^{-2}**
750	Area	Intercept	3.457	0.210	16.456	**$<2 \times 10^{-16}$**	3.444	0.169	20.335	**$<2 \times 10^{-16}$**
		CAO	0.010	0.003	3.673	**2.39×10^{-4}**	0.007	0.002	2.933	**3.36×10^{-3}**
	Dynamic	Intercept	4.714	0.202	23.332	**$<2 \times 10^{-16}$**	4.134	0.194	21.303	**$<2 \times 10^{-16}$**
		COST H1	-1.4×10^{-4}	3.39×10^{-5}	4.137	**3.52×10^{5}**	-6.53×10^{-5}	3.24×10^{-5}	−2.013	**4.42×10^{-2}**
1000	Area	Intercept	3.493	0.216	16.157	**$<2 \times 10^{-16}$**	3.461	0.172	20.168	**$<2 \times 10^{-16}$**
		CAO	0.006	0.002	3.371	**7.48×10^{-4}**	0.004	0.001	2.778	**5.47×10^{-3}**
	Dynamic	Intercept	4.729	0.221	21.359	**$<2 \times 10^{-16}$**	4.151	0.204	20.388	**$<2 \times 10^{-16}$**
		COST H1	-1.17×10^{-4}	3.09×10^{-5}	−3.771	**1.63×10^{-4}**	-5.59×10^{-5}	2.83×10^{-5}	−1.974	**4.84×10^{-2}**
		Intercept	4.594	0.233	19.704	**$<2 \times 10^{-16}$**	4.120	0.1942	21.220	**$<2 \times 10^{-16}$**
		COST H2	-1.05×10^{-4}	3.56×10^{-5}	−2.957	**3.11×10^{-3}**	-5.71×10^{-5}	2.96×10^{-5}	−1.932	5.34×10^{-2}
		Intercept	4.335	0.280	15.497	**$<2 \times 10^{-16}$**	4.010	2.21×10^{-1}	18.127	**$<2 \times 10^{-16}$**
		COST H3	−0.0002	0.0001	−1.177	0.239	-9.47×10^{-5}	1.01×10^{-4}	−0.942	0.346
1500	Area	Intercept	3.611	0.207	17.448	**$<2 \times 10^{-16}$**	3.458	0.186	18.634	**$<2 \times 10^{-16}$**
		CAO	0.003	0.001	3.325	**8.85×10^{-4}**	0.002	0.001	2.595	**9.46×10^{-3}**
	Dynamic	Intercept	4.801	0.209	22.935	**$<2 \times 10^{-16}$**	4.255	0.223	19.032	**$<2 \times 10^{-16}$**
		COST H1	-7.56×10^{-5}	2.02×10^{-5}	−3.747	**1.79×10^{-4}**	-4.67×10^{-5}	2.04×10^{-5}	−2.284	**2.24×10^{-2}**
		Intercept	4.593	0.236	19.467	**$<2 \times 10^{-16}$**	4.188	0.213	19.660	**$<2 \times 10^{-16}$**
		COST H2	-6.47×10^{-5}	2.59×10^{-5}	−2.496	**1.25×10^{-2}**	-4.79×10^{-5}	2.28×10^{-5}	−2.100	**3.57×10^{-2}**
		Intercept	4.422	0.235	18.860	**$<2 \times 10^{-16}$**	4.053	0.205	19.749	**$<2 \times 10^{-16}$**
		COST H3	-1.10×10^{-4}	6.22×10^{-5}	−1.774	7.60 ×10-^{2}	-7.87×10^{-5}	5.32×10^{-5}	−1.479	1.39×10^{-1}

Table 3. Estimated regression coefficients (EST), adjusted standard errors (SE), Z and P values from glmmTMB for comparison of the area and dynamic approaches regarding landscape effect on *Bactrocera oleae* abundance in 2016. Abundance data were pooled in two periods. Generalized lineal mixed models were fitted with a negative binomial distribution and link function log. Olive grove area (CAO) was used as the explanatory variable for the area approach, and cost–distance (COST) for the dynamic approach. Both CAO and COST were calculated at four radii around the sampled olive groves (500, 750, 1000 and 1500 m). H1, H2 and H3 after COST refer to the hypotheses 1, 2 and 3 respectively (see text for details). p values < 0.05 indicated in bold.

			Period							
			Spring				**Autumn**			
Radius	**Approach**	**Coefficient**	**EST**	**SE**	**Z**	**P**	**EST**	**SE**	**Z**	**P**
500	Area	Intercept	3.961	0.165	23.987	**$<2 \times 10^{-16}$**	3.361	0.171	19.707	**$<2 \times 10^{-16}$**
		CAO	0.020	0.004	4.456	**8.37×10^{-6}**	0.028	0.004	6.237	**4.47×10^{-10}**
	Dynamic	Intercept	5.113	0.141	36.340	**$<2 \times 10^{-16}$**	4.852	0.200	24.273	**$<2 \times 10^{-16}$**
		COST H1	-1.97×10^{-4}	3.78×10^{-5}	-5.21	**1.84×10^{-7}**	-2.36×10^{-4}	5.25×10^{-5}	4.486	**7.27×10^{-6}**
750	Area	Intercept	3.884	0.155	25.037	**$<2 \times 10^{-16}$**	3.294	0.161	20.507	**$<2 \times 10^{-16}$**
		CAO	0.011	0.002	5.068	**4.02×10^{-7}**	0.014	0.002	6.599	**4.13×10^{-11}**
	Dynamic	Intercept	5.169	0.140	37.090	**$<2 \times 10^{-16}$**	4.879	0.460	10.602	**$<2 \times 10^{-16}$**
		COST H1	-1.44×10^{-4}	2.35×10^{-5}	-6.140	**8.46×10^{-10}**	-1.64×10^{-4}	9.77×10^{-5}	-1.677	9.36×10^{-2}
1000	Area	Intercept	4.005	0.177	22.672	**$<2 \times 10^{-16}$**	3.372	0.170	19.781	**$<2 \times 10^{-16}$**
		CAO	0.005	0.001	3.814	**1.37×10^{-4}**	0.008	0.001	6.178	**6.49×10^{-10}**
	Dynamic	Intercept	5.129	0.165	31.006	**$<2 \times 10^{-16}$**	4.875	0.226	21.613	**$<2 \times 10^{-16}$**
		COST H1	-1.08×10^{-4}	2.41×10^{-5}	-4.466	**7.97×10^{-6}**	-1.29×10^{-4}	3.23×10^{-5}	-4.002	**6.29×10^{-5}**
		Intercept	4.978	0.191	26.126	**$<2 \times 10^{-16}$**	4.749	0.236	20.088	**$<2 \times 10^{-16}$**
		COST H2	-9.21×10^{-5}	2.99×10^{-5}	-3.087	**2.02×10^{-3}**	-1.21×10^{-4}	3.68×10^{-5}	-3.293	**9.91×10^{-4}**
		Intercept	4.795	0.185	25.978	**$<2 \times 10^{-16}$**	4.310	0.572	7.542	**4.63×10^{-14}**
		COST H3	-1.54×10^{-4}	6.94×10^{-5}	-2.212	**2.69×10^{-2}**	-9.79×10^{-5}	2.86×10^{-4}	-0.342	7.33×10^{-1}
1500	Area	Intercept	4.046	0.189	21.465	**$<2 \times 10^{-16}$**	3.402	0.183	18.586	**$<2 \times 10^{-16}$**
		CAO	0.002	0.001	3.262	**1.11×10^{-3}**	0.004	0.001	5.468	**4.54×10^{-8}**
	Dynamic	Intercept	5.246	0.177	29.670	**$<2 \times 10^{-16}$**	5.064	2.26×10^{-1}	22.415	**$<2 \times 10^{-16}$**
		COST H1	-7.90×10^{-5}	1.66×10^{-5}	-4.747	**2.07×10^{-6}**	-9.99×10^{-5}	2.11×10^{-5}	-4.749	**2.05×10^{-6}**
		Intercept	5.004	0.216	23.121	**$<2 \times 10^{-16}$**	4.910	0.2349	20.91	**$<2 \times 10^{-16}$**
		COST H2	-6.43×10^{-5}	2.33×10^{-5}	-2.758	**5.82×10^{-3}**	-1.01×10^{-4}	2.55×10^{-5}	-3.960	**7.49×10^{-5}**
		Intercept	4.833	0.216	22.424	**$<2 \times 10^{-16}$**	4.360	0.293	14.892	**$<2 \times 10^{-16}$**
		COST H3	-1.09×10^{-4}	5.62×10^{-5}	-1.946	5.16×10^{-2}	-7.83×10^{-5}	7.42×10^{-5}	-1.054	2.92×10^{-1}

In the first sampling period (spring), it is remarkable that both in 2015 (Table 2) and in 2016 (Table 3) the significance of COST H1 was consistently higher than that of CAO for all the radii studied. However, in the second sampling period (autumn) variables behaved in the opposite way, i.e., the significance of CAO was consistently higher than that of COST H1 (Tables 2 and 3).

Regarding the cost values corresponding to hypothesis 2 (COST H2), their significance was lower than that of COST H1 both in 2015 and in 2016 (Tables 2 and 3). COST H3 was only significant in spring 2016 at 1000 m radius, and its significance was lower than that of COST H1, COST H2 and CAO.

3.3. Effect of Landscape Structure on B. oleae Infestation

The olive grove area (CAO), the scrubland area (CAS) and the Simpson landscape diversity index (SIEI) affected *B. oleae* infestation in 2015 and 2016 (Table S4). Figure 6 shows the main effects found at 750 and 1500 m buffer areas. *B. oleae* infestation decreased with increasing SIEI values and increased with increasing CAO values.

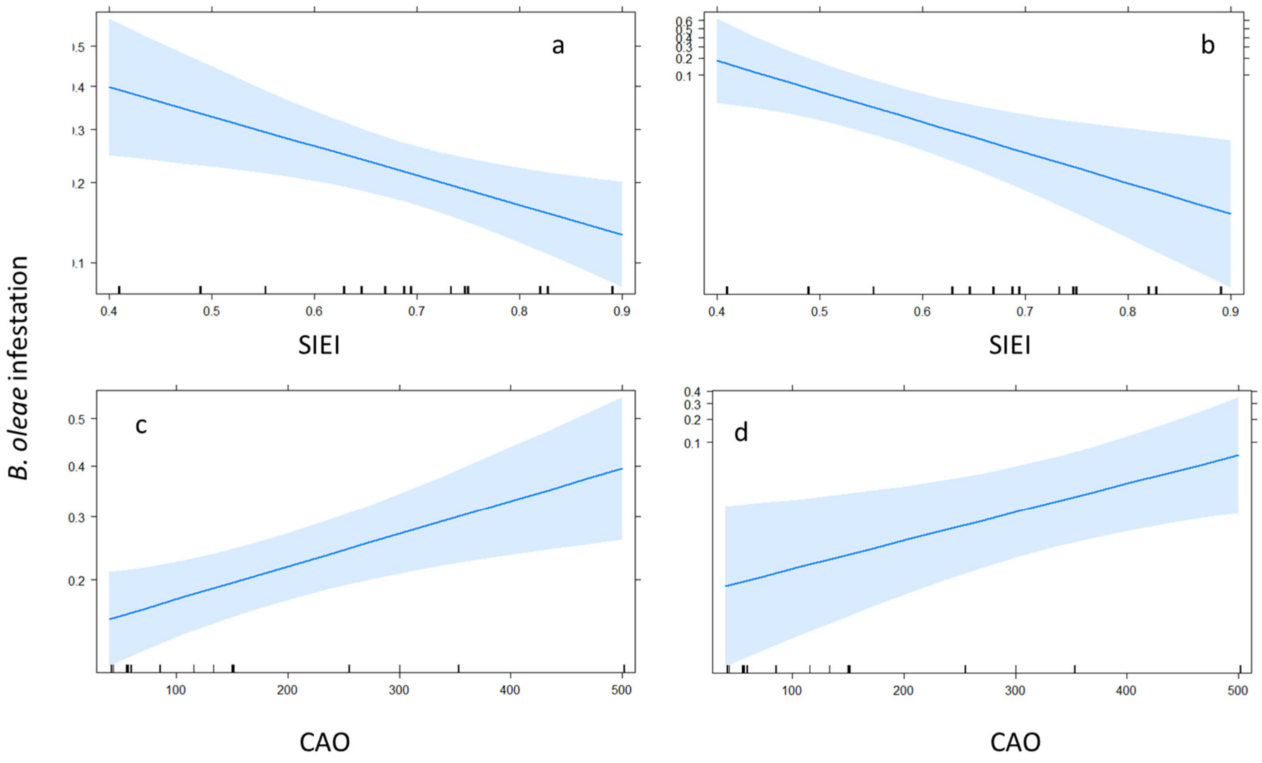

Figure 6. Effect of landscape structure on *Bactrocera oleae* infestation in 2015 (**a**,**c**) and 2016 (**b**,**d**). Landscape indices were Simpson landscape diversity index (SIEI) calculated at 750 m buffer area (**a**,**b**) and area of olive groves (CAO) calculated at a 1500 m buffer area (**c**,**d**).

4. Discussion

This work shows that landscape structure affects *B. oleae* abundance during the complete cropping season and affects *B. oleae* movement. The relationship between landscape structure and abundance of *B. oleae* translates to reduced infestation in the olive crop in more complex compared to simpler landscapes.

B. oleae abundance decreased with increasing CAS, PR and SIEI and increased with CAO. We previously reported a negative relationship between landscape diversity and autumn *B. oleae* abundance in Jaén province, southern Spain, (Ortega and Pascual, 2014, Ortega et al., 2016), an area where olive is the dominant land use. According to the Spanish Ministry of Agriculture, Fisheries and Food, the area occupied by olive groves in Jaén province is 586,921 ha, while in the Madrid province, where the present study was carried out, it is 26,585 ha (https://www.mapa.gob.es/es/estadistica/temas/estadisticas-agrarias/agricultura/superficies-producciones-anuales-cultivos/, accessed on 15 March 2020). Thus, we can conclude that landscape structure affects abundance of *B. oleae* at different levels of dominance of the olive crop. The complexity of the landscape surrounding olive groves has also been shown to be related to lower abundance of another important olive pest, the olive moth (*Prays oleae*, Bernard) [27]. In addition, several other works indicate a favourable effect of landscape complexity on different biocontrol organisms/processes [9,12,28] and the general biodiversity of arthropods [29,30]. However, other works did not detect any landscape variables explaining the distribution of olive fruit flies [31].

In this work, we used for the first time a cost-based model to make inferences about the movement of *B. oleae*. By comparing the significance of the models fitted with area metrics (*area* approach) and cost–distance metrics (*dynamic* approach) at different periods, we identified moments where movement probably occurs, if the significance of the cost–distance metrics is higher than that of area metrics. Our results suggest that *B. oleae* moves mainly amongst olive groves in spring, when olive fruits have not developed yet. Hypothesis 1 assigns a lower cost only to the land use "olive grove", and thus a high significance of COST H1 in spring means that olive groves are a source of flies that move to the sampled olive groves—i.e., that *B. oleae* moves amongst olive groves in this period. On the other hand, in autumn the significance of CAO was higher than that of COST H1. Thus, olive groves are not a source of flies then as they are in spring, i.e., *B. oleae* does not move amongst olive groves. This seems to indicate that the stimulus for movement in this period could be searching for olive groves with fruits on which to oviposit, thus leading to more active movement amongst olive groves at this time of the year when, according to (Marchini et al. [6], most of the females are fertilized. Additionally, it is possible that adult *B. oleae* flights are also due to a search for food, because while fruit fly larvae are monophagous on olive fruits, adult flies use a variety of food sources. These adults have been found on different plant species, such as fig, lemon, cypress, mulberry or orange trees, and they can use different pollens, honeydews, fruit and plant exudates, bacteria and even bird faeces [32–35]. It is likely that flies move around looking for their host plant following olfactory and visual stimuli [36–38] and that during this search, they can find food sources in other species of vegetables on which they remain, though only temporarily. Thus, although adults have been found in various plants, the abundance was always lower there than on olive groves [32]. Interestingly, Michelakis and Neuenschwander [32] found that in May–June, when there were no fruits susceptible to olive fly attack, there was an increase in the numbers of olive flies in other plant species in one of the two locations studied. They explain this difference by the olive varieties in the two locations: in the location with higher numbers outside olive groves, the variety is Tsounati, whose last fruits neglected during the harvest fall before those of the Koroneiki variety, the variety in the other site. Thus, the movement of olive flies outside olive groves to other plant species seems to be due to the lack of fruits in which to oviposit. Our findings that movement happens mainly in spring agree with this behaviour, i.e., *B. oleae* moves searching for olive fruits. In addition, Girolami et al. [39] describe that the adult behaviour corresponding to the phenological state "newly formed olives" (not suitable for oviposition) is "dispersion throughout the area".

In this first study period, other land uses apart from olive do not seem to be a source of olive fruit flies in our study. The significance of hypotheses 2 and 3, assigning lower cost to additional land uses (water sources and scrubland), is lower than that of hypothesis 1, or even not significant in the case of hypothesis 3. This means that neither land uses associated with water nor the most abundant wild land use (scrubland) are a source of *B. oleae* flies. In our study area, there are plant species susceptible to harbour *B. oleae*, such as fig and walnut trees, as described by Michelakis and Neuenschwander [32]. However, the most abundant use of wild land, scrubland, has mainly shrubby plants (*Retama sphaerocarpa* (L.) Boiss., *Teucrium pseudochamaepitys* L., *Thymus vulgaris* L.), with some interspersed oak trees (*Quercus ilex* L.), which are probably not very attractive for the flies. Thus, olive flies at this time of year are mainly in olive groves and moving amongst them.

Apart from the first period evaluated, it is likely that *B. oleae* remains in olive groves during the rest of the growing season. Adults emerging in spring lay eggs on fruits from the previous year [6,32] and it is possible that a substantial number of these adults do not survive summer. Alternatively, the large drop in the numbers of *B. oleae* captured in summer could be attributed to movement to areas outside of olive groves toward different land uses. In a study carried out in Crete, marked flies were liberated in July–October, and higher dispersion was found in summer than in autumn, probably because of the high temperature and favourable winds [40]. In addition, movement of *B. oleae* outside olive groves has been assumed in other works in Italy [38,39]. These studies noted that in the summer the olive flies dispersed throughout the area probably to search for food and return to the olive trees after summer rains. It is also noted that the phenomenon is not linked to the emergence of the adults of the preceding spring generation. Our results do not agree with this assumption, since in autumn the significance of the area metrics (CAO) is higher than that of the cost–distance metrics, regardless of the cost hypothesis being tested. In our study area, summer rains are not very frequent; therefore, this and other environmental conditions could be factors explaining the disagreement. On the other hand, Michelakis and Neuenschwander [32] do not find any plants other than olives acting as a refuge for flies during summer. Thus, in our area it seems that the *B. oleae* adult population at the end of summer starts mainly from larvae developed on fruits from the previous year, although adult immigration from outside olive groves cannot be completely discarded. Our approach evaluates movement indirectly, and studies assessing movement by a direct means would be necessary to confirm this behaviour. However, the cost–distance approach to assess insect movement is a relatively easy and affordable tool compared to methods such as marking flies with fluorescent powders [40], taking into account the limited number of insects that can be marked [32]. In addition, it is important to point out the remarkable consistency of the results found in our work in the two years studied.

Regarding the different radii studied, we did not find any consistent behaviour for all the parameters and moments studied, although perhaps the most relevant is a lower effect of the landscape structure for the smaller radii studied (500–750 m). According to different studies, the olive fruit fly can perform seasonal movements of several kilometres [10,36,40]; while the radius of action that olfactory stimuli may have on *B. oleae* is not exactly known [37,38]. Our previous works in the Jaén province also found significant effects of landscape structure on *B. oleae* abundance at radii ranging between 500 and 2000 m, depending on the index studied [7,8]. Other studies in olive groves use radii ranging from 200 to 2000 m [12,27,30,31]. In some of these works one radius is selected because there is previous knowledge of the phenomenon studied [31]. Otherwise, multiple scales are examined, as it is not known a priori which ones are important according mainly to the dispersal abilities of the studied organisms. However, significant effects have been found in different studies at a 1000 m radius [7,8,12,27], and the most predictive scale of response for specialist pests in different crops is around 1000 m [41].

An important result of our work is that the effect of landscape structure on *B. oleae* abundance translates into an effect on infestation in the crop, as this infestation increased in landscapes with higher coverage of olive crops (CAO) and reduced values of CAS and SIEI. In our previous work in the Jaén province we did not observe this [7]. As explained above, the Jaén area is dominated by olive groves, therefore infestation by the olive fly is probably higher there than in central Spain. In addition, control measures against *B. oleae* in the Jaén province could mask the landscape effect.

5. Conclusions

Landscape complexity reduces abundance of *B. oleae* during the growing season in areas with a relatively low dominance of olive groves, such as central Spain.

B. oleae movement occurs mainly in spring, and no other land use apart from olive groves seems to have a significant role as a refuge for the insect during summer in the area studied.

The cost–distance approach proved to be a useful means to make inferences about insect movement.

A reduced *B. oleae* infestation was observed in olive groves surrounded by a more complex landscape.

This information should be taken into account in improving agricultural spatial planning to enhance landscape resilience to pest development.

Supplementary Materials: The following are available online at https://www.mdpi.com/article/10.3390/agronomy12010004/s1. Table S1, UTM coordinates and sizes of the sampled olive groves. Table S2, Estimated regression coefficients (EST), adjusted standard errors (SE), Z and *p* values from glmmTMB for landscape effect on Bactrocera oleae abundance in 2015. Abundance data were pooled in two periods. Generalized lineal mixed models were fitted with negative binomial distribution and link function log. Explanatory variables were: Olive grove area (CAO), Scrubland area (CAS), Patch richness (PR) and Simpson landscape diversity index (SIEI), and were calculated at four radii around the sampled olive groves (500, 750, 1000 and 1500 m). p values < 0.05 indicated in bold. Table S3, Estimated regression coefficients (EST), adjusted standard errors (SE), Z and P values from glmmTMB for landscape effect on Bactrocera oleae abundance in 2016. Abundance data were pooled in two periods. Generalized lineal mixed models were fitted with negative binomial distribution and link function log. Explanatory variables were: Olive grove area (CAO), Scrubland area (CAS), Patch richness (PR) and Simpson landscape diversity index (SIEI), and were calculated at four radii around the sampled olive groves (500, 750, 1000 and 1500 m). p values < 0.05 indicated in bold. Table S4, Estimated regression coefficients (EST), adjusted standard errors (SE), Z and P values from glmmTMB for landscape effect on Bactrocera oleae infestation in 2015 and 2016. Generalized lineal models were fitted with binomial distribution and link function logit. Explanatory variables were: Abundance of B. oleae (BO), Olive grove area (CAO), Scrubland area (CAS), Simpson landscape diversity index (SIEI), and Total edges (TE). Landscape indices (CAO, CAS, SIEI and TE) were calculated at four radii around the sampled olive groves (500, 750, 1000 and 1500 m). p values < 0.05 indicated in bold.

Author Contributions: S.P. and M.O. conceived the research and gathered the abundance data; C.E.F. and S.P. evaluated infestation; N.M. carried out the cost–distance analysis; S.P. analysed the data and wrote the manuscript; M.O. improved the manuscript. All authors have read and agreed to the published version of the manuscript.

Funding: This research was funded by [Ministerio de Economía y Competitividad of Spain and the European Regional Development Fund] grant number [RTA2013-00039-C03-03].

Data Availability Statement: The data presented in this study are available on request from the corresponding author.

Acknowledgments: We would like to thank Carmen Callejas (UCM), Manuel González Núñez (INIA), Esther Lantero (UCM), Beatriz Matallanas (UCM), Alejandro Rescia (UCM) and Ismael Sánchez Ramos (INIA) for assistance in fieldwork, and María Villa (IPB, Portugal) for statistical advice. We would also like to thank Pablo Blas (RECESPAÑA Cooperative, Villarejo de Salvanés, Madrid), Esther Alonso (UCAM-Union of Madrid Agricultural Cooperatives) and the owners of the sampled olive groves.

Conflicts of Interest: The authors have no conflict of interest.

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