



Spatio-temporal analysis of the relationship between landscape structure and the olive fruit fly *Bactrocera oleae* (Diptera: Tephritidae)

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- Abstract**
- 1 Landscape ecology studies on pest control have focused mainly on annual crops and natural enemies, whereas more studies measuring pest pressure on perennial crops are needed.
 - 2 The relationships between the abundance and damage by *Bactrocera oleae* (Rossi) and different landscape indices were analyzed using data gathered by a regional network during 2009, 2010 and 2011 in Jaén, Spain. Eleven indices of landscape composition and configuration calculated at six different spatial scales (radii of 500, 600, 750, 1000, 1500 and 2000 m) were used in correlation analyses.
 - 3 Significant correlations between abundance and some indices were observed primarily during Julian days 236–264 (24 August to 21 September) 2010. These correlations were negative with edge density, the Shannon landscape diversity index and the number of patches, and were positive with patch size standard deviation and mean patch size.
 - 4 Linear mixed-effects models were used to identify the indices most strongly related to the abundance of olive flies. These indices were mean patch size, edge density at 500–750 m and the Shannon landscape diversity index, as well as the number of patches at 1000–2000 m.
 - 5 These results suggest that greater landscape complexity may contribute to reduced numbers of *B. oleae*. More studies are needed to establish how to reduce olive fruit fly damage.

Keywords *Bactrocera oleae*, edge density, landscape ecology, olive fruit fly, patch size, pest populations, Shannon diversity.

Introduction

Agricultural intensification has resulted in landscape simplification, with losses of noncultivated areas and biodiversity (Bianchi *et al.*, 2006). Chemical pest control is an aspect of this agricultural intensification that has additional negative environmental consequences. Environmentally friendly control measures need to be found, and an increasing number of elements present in the ecosystem need to be identified to achieve natural pest control. Conservation biological control is defined as the practice of increasing the efficacy of natural enemies by

modifying the environment or the pest control measures in use (Eilenberg *et al.*, 2001). The environment includes not only the cultivated plot, but also the adjacent areas, such as edges, set aside plots or any type of natural vegetation next to the crop (Fiedler *et al.*, 2008; Thomson & Hoffmann, 2010). The introduction of the landscape in pest management (as a territorial mosaic of patches with different uses, including the crop and the adjacent natural areas) follows recent trends in sustainable pest control (Cumming & Spiesman, 2006; Goodell, 2009). Wild areas can provide natural enemies with food, refuge and alternative hosts/prey (Landis *et al.*, 2000; Bianchi & Wackers, 2008; Fiedler *et al.*, 2008; Isaacs *et al.*, 2009; Thomson & Hoffmann, 2010). In this manner, these areas favour the presence of parasitoids and predators that can disperse into the

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crop and contribute to pest control (Haenke *et al.*, 2009; Hogg & Daane, 2010; Marasas *et al.*, 2010).

In the last few years, numerous studies, including some reviews, have been published on the effect of the landscape on insects, such as pollinators, phytophagous insects and natural enemies, which are important for agriculture and their related ecosystem services (Purtauf *et al.*, 2005; Ricci *et al.*, 2009; Diekoetter *et al.*, 2010; Scheid *et al.*, 2011; Avelino *et al.*, 2012; Breitbart *et al.*, 2012; Jonsson *et al.*, 2012; Woltz *et al.*, 2012). Many of these studies have focused on natural enemies, although studies measuring the relationship of the landscape with populations of phytophagous insects and crop damage are scarcer. In addition, many studies have been performed on annual crops and in areas of northern Europe or other areas with similar environmental conditions. Only a few studies have been published regarding perennial crops, such as cherry trees, vineyards and olive groves (Boccaccio & Petacchi, 2009; Thomson *et al.*, 2010; Stutz & Entling, 2011; Tscheulin *et al.*, 2011; D'Alberto *et al.*, 2012; Scalercio *et al.*, 2012); thus, more studies on Mediterranean climate conditions and perennial crops are needed.

Unlike other agroecosystems, olive groves appear quite stable and generally have good health (Crovetti, 1996). Of the 250 potentially harmful organisms, only two to four cause actual damage to the crop (Cirio, 1997). However, the cost of sanitary measures surpasses €100 million (Haniotakis, 2005). Currently, pest control measures in Spanish olive groves focus on *Bactrocera oleae* (Rossi) (Diptera, Tephritidae), the key pest of this crop, and are based on pesticide application. The most widely used insecticide is the organophosphate dimethoate, although pyrethroids and spinosad are also sprayed (Ruiz Torres & Montiel Bueno, 2007, 2009). Other, less-used strategies are mass trapping and kaolin and copper sprays (Belcari *et al.*, 2005; Haniotakis, 2005; Daane & Johnson, 2010; Pascual *et al.*, 2010). Insecticide application has important undesirable side effects on this ecosystem (Ruano *et al.*, 2001; Haniotakis, 2005; Pascual *et al.*, 2010; Santos *et al.*, 2010). In addition, insecticide resistance to several products, including spinosad, is problematic (Kakani *et al.*, 2010; Vontas *et al.*, 2011). Thus, pesticide use should be reduced as much as possible. In addition, the number of products available to the growers for pest management is becoming increasingly restricted because of the European directive 91/414/CEE from 15 July 1991. In Spain, the new regulation on the rational use of phytosanitary products promotes the use of environmentally friendly control measures and highlights the importance of ecological infrastructures as a source of ecosystem services (BOE, 2012).

The number of studies on the effect of landscape on arthropods in olive groves is small. The abundance of bees depends on various parameters of the landscape (Tscheulin *et al.*, 2011). In the case of Lepidoptera, correlations have been established between landscape attributes and ecological characteristics of lepidopteran communities in olive groves of Calabria (Italy) (Scalercio *et al.*, 2012). More important in the context of conservation biological control is a study conducted in Italy showing that different landscape features affect parasitoids of *B. oleae* (Boccaccio & Petacchi, 2009). In addition, other studies conducted in Spain indicate the

importance of the landscape surrounding olive groves regarding insect diversity (Cotes *et al.*, 2011) and parasitoid community dynamics (Rodríguez *et al.*, 2012).

In the present study, we evaluated the effect of the landscape on populations of *B. oleae* and the damage caused to olive groves by this insect during 3 years (2009–2011) using data collected by the RAIF network (Red de Alerta e Información Fitosanitaria de Andalucía). A preliminary analysis of data from one sampling date in 2008 suggested that lower populations of the olive fruit fly are associated with landscapes that are more complex (Pascual, 2011; Ortega & Pascual, 2012).

The present study aimed to investigate: (i) is there a relationship between landscape structure and *B. oleae* populations; (ii) is there a relationship between landscape structure and the damage caused by *B. oleae*; (iii) is there a temporal pattern in these relationships; and (iv) at what spatial level are these relationships found?

Materials and methods

Study area

The study area was approximately 60 km from east to west and 40 km from north to south (Fig. 1) and covered the zones 'Sierra Mágina Norte', 'Sierra Cazorla' and 'La Loma' in the Jaén province. Jaén has the largest cultivated area of olive groves (570 000 ha) in Spain (Anuario Estadístico de Andalucía, 2009). The dominant cultivars at the studied sites were Picual and Hojiblanca, with some presence of Arbequina, Cornicabra, Gordal, Lechin and Manzanillo. The soil is mainly loam or clay loam, and water was supplied at some time during the crop cycle in most of the studied groves. The climate is Mediterranean, with an annual mean temperature of 17.3 °C and rainfall of 624 mm (Spanish National Institute of Meteorology, 2001). The mean altitude in the area of study is 615 ± 210 m a.s.l.

RAIF data

Data on *B. oleae* populations and damage were kindly provided by the RAIF network (Red de Alerta e Información Fitosanitaria, Consejería de Agricultura, Pesca y Medioambiente, Junta de Andalucía) (<http://www.juntadeandalucia.es/agriculturaypesca/raif/>). This network gathers information on the densities of different phytophagous insects and damage levels, as well as information on plant diseases in different crops, for all of Andalucía. Samplings were performed weekly during the growing season by field technicians generally in accordance with the strategy defined in the Regulation of Integrated Production for olive cultivation in Andalucía (BOJA, 2008). Sampling points were chosen within homogeneous crop areas in an area not exceeding 200 ha.

Data taken from 19 sampling points in the RAIF network, selected at random and separated by at least 4 km, were used in the present study (Fig. 1). The two variables used for *B. oleae* were: the number of flies captured per trap per day on yellow sticky traps with pheromone (Captures) and the percentage of attacked olives (Attack). Weeks were identified by the Julian

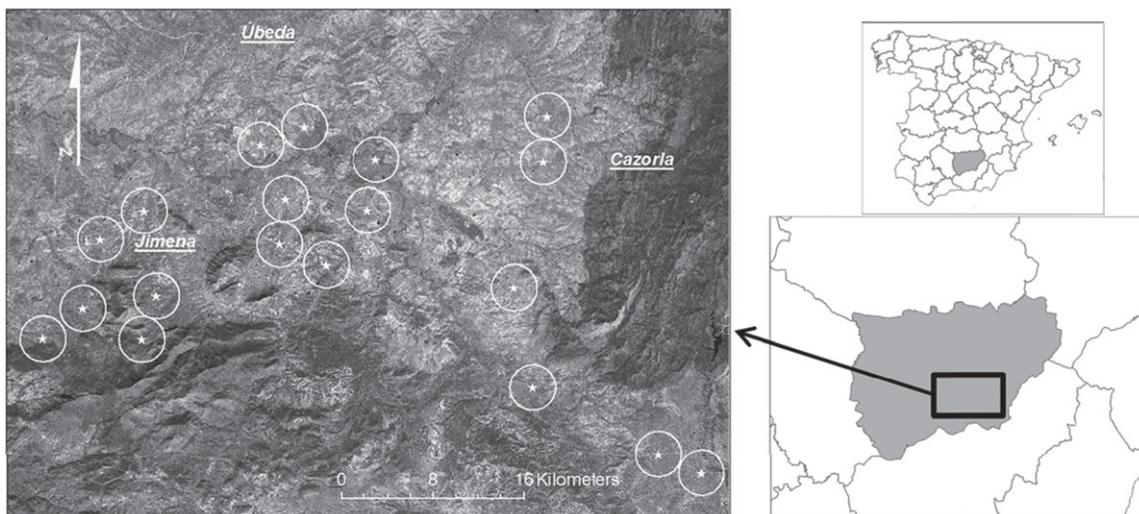


Figure 1 Location and aerial photograph of the study area. Sampling points of the RAIF network (Red de Alerta e Información Fitosanitaria de Andalucía) are indicated, as well as the 2000-m radius areas around them.

day on which the sample was obtained. Data provided by the RAIF network are the mean from at least three values per sampling point. The data used in the present study were recorded in 2009, 2010 and 2011. During these 3 years, the incidence of *B. oleae* in the Jaén province was medium in 2010 and high in 2009 and 2011. Treatments to control the olive fruit fly were applied by aerial means between the end of the summer and the beginning of autumn in a substantial part of the study area in 2009 and 2011 but were used in a negligible part in 2010 (RAIF, 2009, 2010, 2011).

Landscape metrics

Six circular areas, with radii of 500, 600, 750, 1000, 1500 and 2000 m, were nested around each sampling site. Data provided by the SIOSE project (Sistema de Información sobre Ocupación del Suelo de España; <http://www.siose.es>) were used to assess the different types of land use and their proportion (area) within each circle to determine the landscape composition and configuration. The SIOSE project includes 40 simple land cover types (23 of these types were present in our study area) and 45 predefined composed land cover types (24 of these types were present in our study area); both of these cover types have different attributes related to spatial pattern and functions. Complete information on the land cover types in the studied area is provided in the Supporting information (File S1). The minimum digitization area represented by SIOSE ranged between 0.5 and 2 ha. Reference images used to build SIOSE data were taken in 2005 and were complemented with 2004 and 2006 images. The landscape indices calculated from SIOSE data are described in Table 1. The software PATCH ANALYST for ARCGIS, version 9.3.1 (ESRI, Redlands, California) was used to calculate the landscape indices. To calculate the index of 'Percentage of Natural Area', the SIOSE simple land cover types that were considered natural were as follows: Natural Grasslands, Broadleaf Deciduous, Broadleaf Evergreen, Conifers, Scrub, Bare Soil, Ravine, Rock Outcrops and Stones,

Waterways, Reservoirs and Dehesas (Oak open fields). In the case of the SIOSE predefined composed land cover types, a patch was considered natural use if the percentage of these natural uses was higher than 50%. Aerial photographs taken in 2006 and provided by the Plan Nacional de Ortofotografía Aérea (PNOA; <http://www.ign.es/PNOA>) were consulted if needed. The areas of the patches classified as natural were summed to obtain the percentage of natural area in each radius.

Statistical analysis

The relationships between Captures and Attack and the indices of landscape structure were explored in a first step by linear correlation for each radius and week of sampling during the 3 years. The correlations of both variables, Captures and Attack, with the 11 landscape indices are shown in Table 1. In a second step, linear mixed-effects models (LMM) were applied to each radius using the data for Captures and Attack per week (in a separate analysis) as dependent variables. Sampling points were considered as random effects, repeated measures per week were considered as fixed effects, and the altitude of the sampling points and the indices of landscape structure were considered as covariates. Altitude was included because of its relationship with the *B. oleae* population (Castrignano *et al.*, 2012). The models were fitted using a restricted maximum likelihood estimation method. The best covariance structure for the repeated-measures factor was selected according to the lowest value of the Akaike and Schwarz's Bayesian information criteria fit statistics (Littell *et al.*, 1998; Wang & Goonewardene, 2004).

Results

Pest dynamics of *B. oleae*

In 2009, the first peak of Captures was recorded in mid-August, and the maximum peak was recorded at the end of September,

Table 1 Indices used to describe landscape composition and configuration

Name	Description	Source
Shannon landscape diversity index	Evenness of land covers per sample, calculated using the Shannon formula	1
Percentage of natural area	Measured from SIOSE data as described in the text	–
Edge density	Total length of edges per sample area (m/ha)	1
Mean patch fractal dimension	Fractal dimension is twice the logarithm of patch perimeter (m) divided by the logarithm of patch area (m ²)	2
Mean patch edge	Mean amount of edge per patch (m)	2
Mean shape index	Sum of the perimeter of each patch divided by the square root of patch area (ha) for all patches, divided by the number of patches	2
Mean perimeter area ratio	Mean ratio of the patch perimeter (m) to area (m ²)	2
Mean patch size	Mean area of patches in the sample (m ²)	2
Number of patches	Number of patches present per sample	2
Patch size standard deviation	Standard deviation of patches area in the sample (m ²)	2
Largest patch index	Area of the largest patch in the sample (%)	2

Shannon landscape diversity index, number of patches and percentage of natural area are landscape composition indices and the remainder are configuration indices. Source: 1: (Eiden *et al.*, 2000); 2: (McGarigal & Marks, 1995). SIOSE, Sistema de Información sobre Ocupación del Suelo de España.

with a mean value of over 15 flies per trap per day (Fig. 2A). The maximum Attack value during this year was 10%. In 2010, the first peak of Captures was delayed until late August (Fig. 2B), and the maximum peak occurred at the end of September, with a value not exceeding 10 flies per trap per day. The maximum Attack was lower than 10%. In 2011, the pest was more severe, as shown in Fig. 2C. The first peak was reached at the end of July, and the maximum level of 20 flies per trap per day was reached in early October. The Attack value reached approximately 15%, despite pesticide treatments.

Temporal variation of the effect of indices of landscape composition and configuration on B. oleae

A correlation analysis between the variable Captures and indices of landscape composition and configuration in circular areas with radii of 500, 600, 750, 1000, 1500 and 2000 m around the sampling points showed that significant correlations were found with regularity over time (primarily in 2010) but not for all landscape indices. Only six out of the 11 indices tested showed significant correlations. Figure 3 shows the temporal variation in the correlations between the abundance of the olive fruit fly in 2010 (Captures) and landscape indices that were significant in a more or less regular manner. Most of the correlations were significant in the period between 236 and 264 Julian days (24 August to 21 September), although the significance decreased with increasing radius of the circular areas considered. During the period of peak pest population [286–314 Julian days (13 October to 10 November), approximately], some correlations were significant and only at a radius of 500 m. The indices of Shannon landscape diversity index, edge density, number of patches and percentage of natural area (Table 1) had negative correlations with the abundance of flies, whereas mean patch size and patch size standard deviation had positive correlations. The scale at which the effect of the surrounding landscape was significant differed between indices. The significant effects of the Shannon landscape diversity index and patch size standard deviation reached a

2000-m radius at some time during the year, whereas the effects of edge density and the number of patches reached 1000 m, the effect of mean patch size reached 750 m and that of the percentage of natural area did not exceed 600 m.

The correlation analysis with Attack as the dependent variable only showed significant correlations in 2010 at a radius of 500 m for two indices, patch size standard deviation and mean patch size, and only on the Julian days 236 and 257 (24 August and 14 September) [Pearson's $r = 0.57$ ($P = 0.03$) and Pearson's $r = 0.55$ ($P = 0.04$), respectively, for patch size standard deviation; Pearson's $r = 0.66$ ($P = 0.007$) and Pearson's $r = 0.57$ ($P = 0.03$), respectively, for mean patch size).

Modelling the effect of the landscape

The effects of the landscape on the variables Captures and Attack of the olive fruit fly during the entire sampling period were modelled to test the consistency of the exploratory correlation analysis by means of LMM (Table 2). The effect of the covariate altitude on Captures was not significant at any of the spatial scales (radii). However, this covariate showed significant effects on the variable Attack for all radii. On the other hand, landscape indices were significantly related to the variable Captures but not to Attack. The edge density landscape index showed significant effects ($P \leq 0.05$) for the 500 and 600 m radii and marginally significant effects ($P \leq 0.10$) at 750 m. The mean patch size showed significant effects at 500, 600 and 750 m and marginally significant effects at 1000 and 1500 m. Patch size standard deviation showed significant effects only at 500 m and marginally significant effects at 750 m. The percentage of natural area only showed marginally significant effects at 600 m. The number of patches showed marginally significant effects at 600, 750 and 2000 m, and significant effects at 1000 and 1500 m. The Shannon landscape diversity index only showed significant effects at 1500 and 2000 m.

Other landscape indices, such as the mean patch edge, mean shape index, mean patch fractal dimension, mean perimeter area

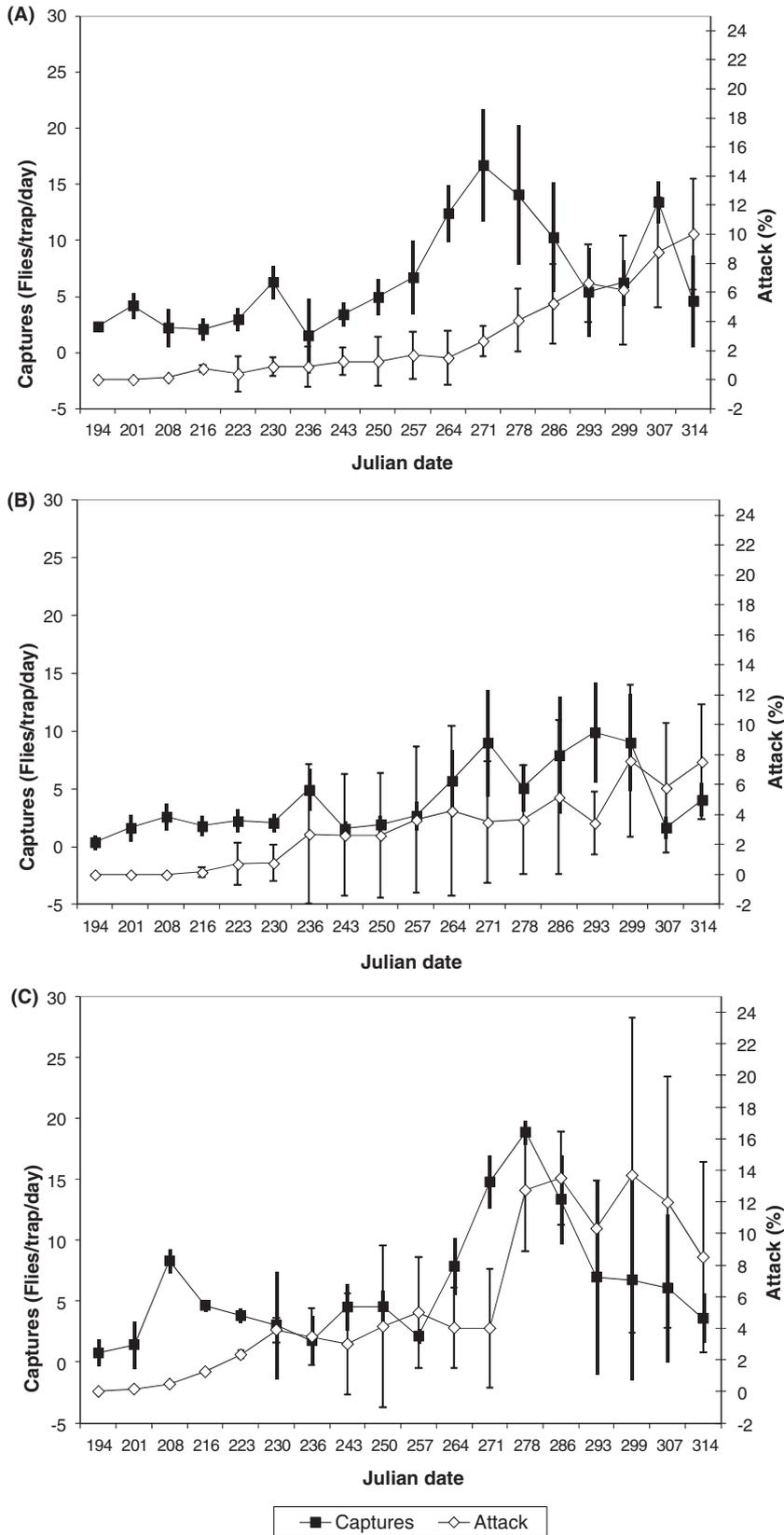


Figure 2 Phenology of the variables Captures (number of flies per trap per day) and Attack (percentage of attacked olives) in (A) 2009, (B) 2010 and (C) 2011. Mean values and 95% confidence intervals are given for the same sampling points for the 3 years (19 in 2009 and 2010; 16 in 2011). Time is represented by the corresponding Julian day.

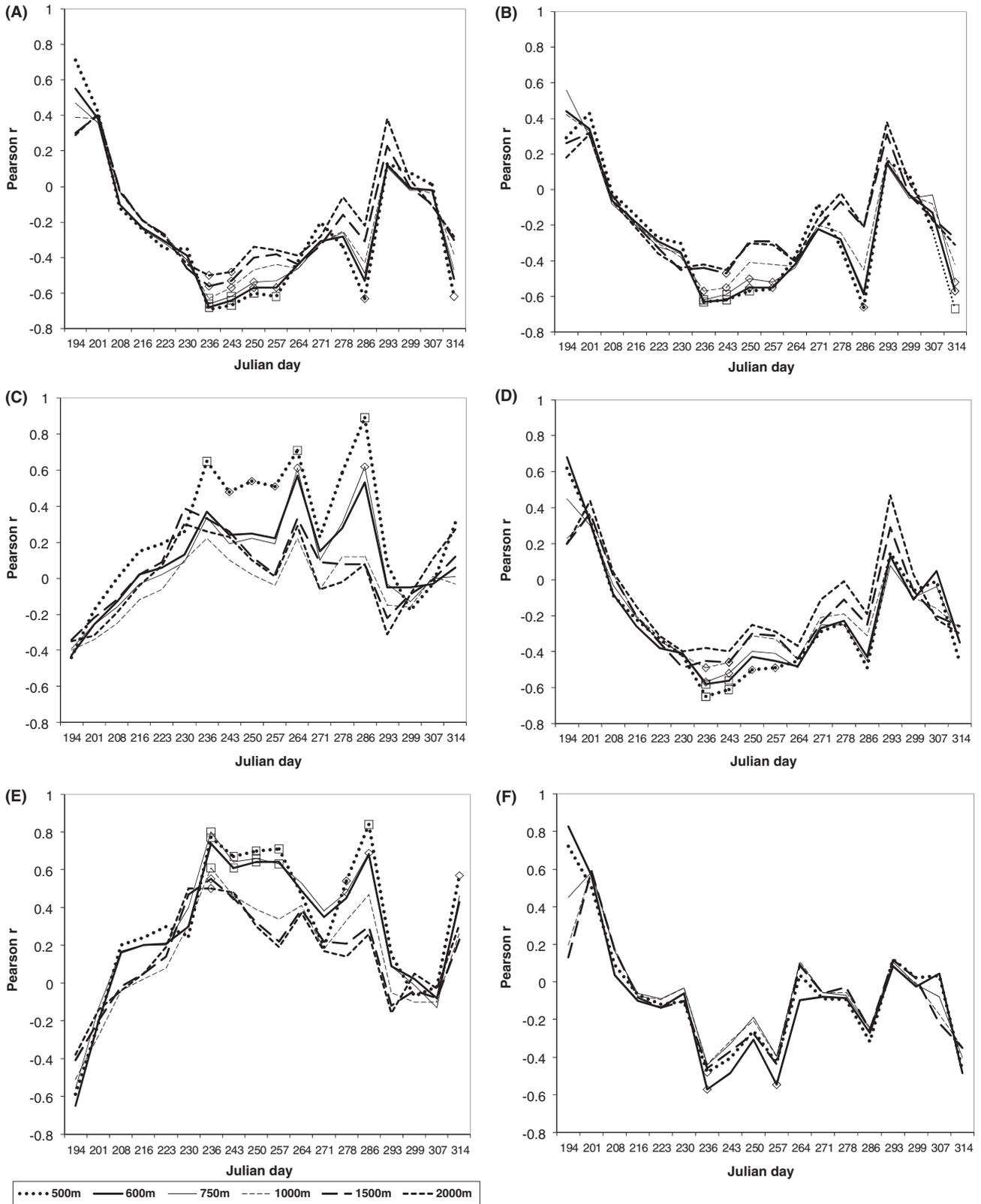


Figure 3 Correlation pattern between the variable Captures (number of flies per trap per day) in 2010 and some landscape indices for each sampling date (indicated by the Julian day). (A) Shannon landscape diversity index, (B) edge density, (C) mean patch size, (D) number of patches, (E) patch size standard deviation and (F) percentage of natural area. The line type indicates that the correlation is made at different spatial scales (radius) from the sampling point. The significance of the correlation is indicated by diamonds and squares for $P \leq 0.05$ and $P \leq 0.01$, respectively.

Table 2 Significance of linear mixed effects models showing the effect of landscape indices on Captures and Attack of *Bactrocera oleae* at different spatial scales

Covariates	Spatial scale											
	500 m		600 m		750 m		1000 m		1500 m		2000 m	
	F	P	F	P	F	P	F	P	F	P	F	P
<i>Captures</i>												
Shannon landscape diversity index	0.2	NS	0.3	NS	0.2	NS	2.7	NS	4.5	0.034	5.7	0.019
Edge density	10.5	0.002	7.4	0.008	3.2	0.075	0.4	NS	0.2	NS	1.1	NS
Mean patch size	11.9	0.001	5.4	0.023	6.7	0.011	3.6	0.056	3.8	0.056	7.7	NS
Number of patches	0.3	NS	3.2	0.077	3.78	0.056	9.0	0.003	7.7	0.006	3.8	0.054
Patch size standard deviation	7.8	0.006	1.5	NS	3.4	0.069	0.04	NS	0.1	NS	0.4	NS
Percentage of natural area	2.1	NS	3.0	0.086	1.9	NS	0.31	NS	0.2	NS	–	–
Altitude	0.1	NS	0.0	NS	0.0	NS	0.02	NS	1.2	NS	0.1	NS
<i>Attack</i>												
Shannon landscape diversity index	1.3	NS	0.5	NS	0.2	NS	0.3	NS	0.1	NS	0.6	NS
Edge density	1.6	NS	1.1	NS	2.0	NS	1.1	NS	0.0	NS	0.1	NS
Mean patch size	1.4	NS	0.7	NS	1.1	NS	0.6	NS	1.8	NS	0.7	NS
Number of patches	0.1	NS	0.1	NS	0.0	NS	0.3	NS	0.1	NS	0.5	NS
Patch size standard deviation	0.6	NS	0.0	NS	0.0	NS	0.1	NS	1.5	NS	2.3	NS
Percentage of natural area	2.2	NS	1.2	NS	2.2	NS	1.1	NS	0.1	NS	–	–
Altitude	28.2	0.000	33.9	0.000	35.2	0.000	30.2	0.000	18.2	0.000	18.7	0.000

Sampling date along 3 years (2009, 2010 and 2011) was considered as fixed repeated measures factor. Landscape indices and altitude of sampling points were considered as covariates. The best covariance structure for the repeated-measures (date) factor was the first-order autoregressive (AR) in the case of Attack and heterogeneous AR in the case of Captures. The meanings of covariate acronyms are provided in Table 1. NS, not significant.

and largest patch index, did not show a significant relationship with Captures or Attack in the exploratory correlation analysis and were not included as covariates in the LMM.

Discussion

The results obtained in the present study indicate that population levels of the olive fruit fly *B. oleae* were correlated with some landscape parameters over a time period during the crop season, although this effect was only observed with regularity in one of the 3 years studied (2010). Modelling the effect of landscape structure during all study periods showed that landscape configuration indices, such as edge density, mean patch size and patch size standard deviation, were related to captures of *B. oleae* at short distances (500–750 m), whereas landscape composition indices, such as Shannon landscape diversity index and the number of patches, were related to captures of *B. oleae* at longer distances (1000–2000 m). Edge density measures the abundance of transition zones between different land uses (Eiden *et al.*, 2000). Both the number of species and the population densities of some species are greater in these transition zones than in the adjacent communities as a result of an edge effect (Odum, 1971). Although edges in agroecosystems may not be proper ecotones in the case of annual crops (cereal fields) (Dutoit *et al.*, 2007), the processes may be different in perennial crops. We found a negative relationship between edge density and captures of *B. oleae*, which suggests that these transition zones could host natural enemies of the olive fruit fly.

The heterogeneity of patch size is a difficult parameter to interpret without also considering mean patch size because the absolute variation is dependent on the mean patch size

(McGarigal & Marks, 1995). Data from the present study confirm a positive relationship between patch size standard deviation and mean patch size for all the studied radii. In simple landscapes, the patch size is larger, such as large areas of olive groves in the present study. A large variation in patch size indicates that very small patches appear together with these large patches, which is compatible with simple landscapes where higher numbers of olive fruit fly were found.

Some landscape composition indices have been used more frequently than edge density or patch size standard deviation in studies relating landscape structure and insect populations (Thies & Tschardtke, 1999; Steffan-Dewenter *et al.*, 2002; Eilers & Klein, 2009; Rusch *et al.*, 2011). These indices are mainly the Shannon landscape diversity index and the percentage of natural area. In the present study, we observed a significant negative relationship between the Shannon landscape diversity index and number of patches with *B. oleae* captures, whereas the percentage of natural area showed only a weak negative association. Although this index is not necessarily associated with a higher landscape complexity, this index is frequently related with other indices indicating complexity, such as the Shannon landscape diversity index (Steffan-Dewenter *et al.*, 2002; Pascual, 2011), as in the present study. The percentage of natural area is important for different insects. For example, natural area has an effect on different types of pollinators (Steffan-Dewenter *et al.*, 2002) and parasitism was shown to be facilitated by a high proportion of natural or semi-natural habitats (Thies & Tschardtke, 1999; Eilers & Klein, 2009; Rusch *et al.*, 2011). In the case of *B. oleae*, the data for captures obtained on a single date in 2008 showed a very weak negative relationship ($P = 0.0938$) with the percentage of natural area (S. Pascual, unpublished results). In the present study, significant negative correlations were observed only in 2010 in periods

of low olive fly abundance. These natural areas may include zones where the wild olive (*Olea europaea* var. *sylvestris*) grows. This tree is susceptible to *B. oleae*, which may affect the results.

Very few studies have analyzed the effect of landscape on olive pests or aspects related to biological control. In Spain, Cotes *et al.* (2011) found a strong negative relationship between the rate of hemerobia (describing the human influence on the landscape) and the Shannon diversity index applied to insect diversity. Very recently, Paredes *et al.* (2013) reported on the effect of vegetation adjacent to olive groves on natural enemies of insect pests. The association that we found between landscape complexity and lower numbers of olive fruit flies could be caused by the effect of landscape on natural enemies of this insect. A study conducted in Italy found that the emergence of parasitoids of the olive fruit fly was negatively affected by the splitting index of woodland (a measure of fragmentation) (Boccaccio & Petacchi, 2009). However, parasitism of the olive fruit fly in Spain is scarce. The braconid parasitoid *Psytalia concolor* was released in Jaén but was not established (Jiménez *et al.*, 1990). In addition, parasitism rates are not very high in central Spain. In Madrid, between 2005 and 2011, parasitism by *P. concolor* was only detected in the 2010–2011 season, and the level of parasitism was approximately 10% (S. Pascual, *et al.*, unpublished results). In Madrid, we have never found the other parasitoids that have been reported to attack *B. oleae* in the Mediterranean basin (*Eurytoma martellii*, *Eupelmus urozonus*, *Phygadeuon agraulis* and *Cyrtomyza latipes*) (Arambourg, 1986). Predation of *B. oleae* appears to play a more important role than parasitism in natural control of the pest. Generalist predators, such as ants, spiders or carabid and staphylinid beetles, may contribute to a decrease in the number of *B. oleae* pupae in the soil (Cavalloro & Delrio, 1976; Bigler *et al.*, 1986; Morris *et al.*, 1999; Orsini *et al.*, 2007). Nevertheless, to our knowledge, no studies on the effect of landscape on predation of *B. oleae* in Spain have been performed thus far. The relationship found here between the population of *B. oleae* and landscape indices occurs mainly during the period before the last generation of the insect and the individuals of this generation are those causing economic damage for olive cultivation. The pupal stage in the generation before this last generation does not occur in the soil but within the olive where insects are protected from ground predators. This location supports the hypothesis that generalist predators are playing a role in the relationship between landscape indices and *B. oleae* populations found in the present study.

Regarding the different spatial scales considered in the present study, we have observed that different indices are related to the *B. oleae* population at different spatial scales, as described in other studies conducted in olive groves. Cotes *et al.* (2011) found a relationship between the hemeroby index and the Shannon index applied to insect diversity at a buffer distance of 500 m, and the relationship between landscape structure and parasitism of *B. oleae* was detected at a spatial extent ranging from 1 to 2 km (Boccaccio & Petacchi, 2009). In our preliminary work with data obtained from *B. oleae* populations on a single date in 2008, we found significant effects at distances shorter than 1500 m (Ortega & Pascual,

2012). Thus, different phenomena may occur at different spatial scales that affect *B. oleae* populations; however, these scales generally do not reach 2000 m.

The damage caused by these fly populations analyzed by the variable Attack was only related to landscape at a radius of 500 m but the effect was not sufficiently consistent to be revealed in the LMM. Although a direct relationship between olive fly populations and damage to the crop should exist, damage was not related to landscape structure in the present study. Altitude may be a factor that can explain this paradox because of its relationship with temperature. Castrignano *et al.* (2012) found that areas with a high density of olive fruit flies shifted from high altitudes in summer to lower altitudes towards autumn. The LMM results indicate a lack of a relationship between Captures and the altitude for the 3 years of study, and this lack of a relationship may be the result of different effects that occur during the seasons and counteract themselves. However, the strong relationship between altitude and the damage caused by *B. oleae* suggests that the time at which the flies are at high altitude coincides with the moment in which the olives are more susceptible to fly attack.

In conclusion, we detected a relationship between a population of *B. oleae* and landscape complexity that could occur through the presence of natural enemies of the phytophagous insect in some landscape elements, such as hedgerows or field margins adjacent to land uses with natural or ruderal vegetation. This relationship was found primarily in the first part of the growing season and at relatively short distances. However, further studies are needed. In the present study, we used data from an olive fruit fly monitoring network, as in previous studies on *B. oleae* (Castrignano *et al.*, 2012). The disadvantage of this approach is that it may not detect small effects. Field trials that are specifically designed to assess which landscape variables influence olive fruit fly populations are needed, and the mechanisms through which the landscape affects *B. oleae* need to be identified. In these studies, special attention needs to be given to the role of predation and the presence of wild olives, and sampling points with similar altitudes need to be chosen. Once the mechanisms that are operating in this process are known, we will have new tools to design programmes of territorial planning for olive fruit fly control, aiming to reduce the final damage caused to the crop and therefore economic losses to the growers.

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Supporting information

Additional Supporting information may be found in the online version of this article under the DOI reference: 10.1111/afe.12030

File S1. SIOSE (Sistema de Información sobre Ocupación del Suelo de España) land cover types present in the study area.

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