



UNIVERSIDADE DE ÉVORA

ESCOLA DE CIÊNCIAS E TECNOLOGIA

DEPARTAMENTO DE BIOLOGIA

SEASONAL VARIATIONS IN THE EFFECT OF STRUCTURAL COMPLEXITY OF OLIVE PRODUCTION SYSTEMS ON BAT ACTIVITY: IMPLICATIONS FOR NATURAL PEST CONTROL SERVICES

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Orientação: Doutor José Manuel Herrera

Coorientação: Mestre Bruno Miguel Silva

Mestrado em Biologia da Conservação

Dissertação

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Seasonal variations in the effect of structural complexity of olive production systems on bat activity: implications for natural pest control services

Abstract

Agricultural landscapes have suffered drastic changes as a consequence of management intensification, leading to a decline in biodiversity, specially in Mediterranean olive farms. Among others, homogenization affects the activity levels of bats, an important component of agricultural ecosystems by acting as biocontrol agents against olive pests. To understand how seasonal variations affects bat occurrence and the biocontrol services they provide, we sampled olive groves with different structural complexities over three seasons, coinciding with the peak activity of *Prays oleae*, one of the major pests of olive production systems. We found strong differences in the response of bats to the structural complexity of olive production systems, being these species-specific and strongly season-dependent. Thus, our results suggest that habitat heterogeneity is of great importance for bat activity, implying that structurally-complex agricultural landscapes could promote higher natural pest control services provided by bats.

Keywords: biocontrol services, foraging, landscape structure, olive farming, *Prays oleae*

Variações sazonais no efeito da complexidade estrutural em olivais com diferentes sistemas de produção na atividade de morcegos: implicações para os serviços de controlo natural de pragas

Resumo

As paisagens agrícolas sofreram drásticas mudanças por consequência da intensificação da gestão, levando ao declínio da biodiversidade, especialmente em olivais mediterrânicos. Entre outros, a homogeneização afeta os níveis de atividade dos morcegos, os quais apresentam elevada importância nos ecossistemas agrícolas pela sua capacidade de controlo natural de pragas. Para compreender como as variações sazonais afetam a ocorrência destes nos olivais, amostrámos olivais com diferentes complexidades estruturais em três estações, coincidindo com o pico de atividade de *Prays oleae*, uma das principais pragas dos olivais, para investigar se morcegos poderão atuar no seu controlo. Foram encontradas diferenças nas respostas dos morcegos em relação à complexidade estrutural dos olivais, sendo estas dependentes de cada espécie e da estação. Assim, os resultados sugerem que a heterogeneidade do habitat apresenta grande importância na atividade dos morcegos, implicando que paisagens agrícolas estruturalmente complexas poderão promover serviços de controlo natural de pragas fornecidos pelos morcegos.

Palavras-chave: serviços de controlo biológico, forrageio, estrutura da paisagem, explorações de oliveiras, *Prays oleae*

Article

Seasonal variations in the effect of structural complexity of olive production systems on bat activity: implications for natural pest control services

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Abstract

Management intensification has led to an increase in the homogenization of agricultural landscapes, specially in Mediterranean olive farms. This represents one of the major causes of decline in the activity of many species over this habitat, including bats, which are an important component of agricultural ecosystems by controlling insect populations. To understand how seasonal variations affects bat occurrence in olive production systems, we sampled olive groves with different structural complexities in spring, summer and autumn in Alentejo, southern Portugal. These seasons coincide with the peak activity of *Prays oleae*, one of the major pests of olive production systems. To better understand if it is possible for bats to control populations of this pest, we surveyed bats by acoustic methods during three consecutive nights per season at each olive grove and the olive moth with Delta traps that stayed in the field for 15 days, overlapping the period in which bat monitoring was carried out. Of all recorded species, *Pipistrellus kuhlii* was, by far, the most abundant, followed by *Pipistrellus pygmaeus* and *Pipistrellus pipistrellus*. Our results indicate strong differences in the response of pipistrelle bats to the structural complexity of olive production systems. Moreover, we found that these differences were species-specific and strongly season-dependent. Both *P. kuhlii* and *P. pygmaeus* were more active in more structurally complex olive groves, specially during summer when the avoidance of lower structural olive groves is very strong. During autumn however, *P. pygmaeus* activity is quite similar regardless the structural complexity. For *P. pipistrellus*, no significant differences were found across structural complexity in any of the seasons. Our results suggest that habitat heterogeneity is of great importance for bat activity,

specially during spring and summer, implying that structurally-complex agricultural landscapes could promote higher natural pest control services provided by bats.

Keywords: biocontrol services, foraging, landscape structure, olive farming, *Prays oleae*

Introduction

Globally, nearly 40% of the land has been converted for agricultural purposes (Foley *et al.*, 2005; Park, 2015). Landscape modification is, not surprisingly, widely recognized as one of the most important environmental driver of global biodiversity loss (Kalda *et al.*, 2014; Tschardtke *et al.*, 2005; Wehling & Diekmann, 2009). Landscapes worldwide are increasingly being transformed into homogeneous single-crop production systems, which lack essential resources for biodiversity conservation, such as food and shelter (Heim *et al.*, 2015; Park, 2015). In the Euro-Mediterranean region, for example, olive (*Olea europaea* L. 1753) farming represents a significant proportion of the land surface dedicated to agriculture, being by far the most striking landscape feature throughout this wide region (Davy *et al.*, 2007; Jerez-Valle *et al.*, 2014). Indeed, with a mean annual production of 10 million tonnes per year, the Euro-Mediterranean region is currently the largest olive production region in the world, accounting for almost three quarters of global production (Azbar *et al.*, 2004; Sanz-Cortés *et al.*, 2002).

Traditionally, olive farming was practiced on upland terraces with relatively low impacts of management practices. However, over the last decades, the Common Agricultural Policy (CAP) has motivated not only the expansion of olive groves but also the intensification of management practices through the assignment of agricultural subsidies directly coupled with production levels (de Graaff & Eppink, 1999; Duarte *et al.*, 2008). Thus, far from being structurally homogeneous, olive groves typically show strong between-farm variations in their structural features ranging from traditional, structurally-complex production systems, to intensive, structurally-simple production systems (Allen *et al.*, 2005; Beaufoy, 2001; Benton *et al.*, 2003; Loumou & Giourga, 2003). Despite the expected pervasive impacts of structural simplification of olive groves on biodiversity, research literature on this topic explicitly focused on vertebrates is surprisingly scarce (but see, for example, Herrera *et al.* 2015; Rey, 2011; Wickramasinghe

et al., 2003). This being the case, the management of olive groves for biological conservation and sustainable natural resource use is far from being achieved.

Efficient pest management is recognized as one of the major challenges for fostering ecologically sustainable and economically profitable olive groves worldwide. To a large extent, this is because olive pests can cause global economic losses estimated at hundred millions of dollars per year, with additional costs related to the use of agrochemicals (Paredes *et al.*, 2013). In this context, a burgeoning research literature demonstrates that pest control services provided by naturally occurring species, such as insectivorous birds and bats, can efficiently reduce the populations of pests, thereby providing clear incentives for biodiversity conservation. Yet, the ecology of natural pest control services in agroecosystems in general and in olive groves in particular is poorly known, thus limiting our ability to plan their conservation and management (Heim *et al.*, 2016; Kahnonitch *et al.*, 2018).

The olive moth, *Prays oleae* (Bernard 1788) (Lepidoptera: Praydidae), is one of the most economically relevant olive pests worldwide (Gonzalez *et al.*, 2015; Oliveira *et al.*, 2012; Villa *et al.*, 2016). In fact, crop losses due to *P. oleae* have been estimated to reach up to 8–11 kg per tree, leading to economic losses evaluated at up to 500 euros per hectare (Nave *et al.*, 2017; Pontikakos *et al.*, 2012; Ramos *et al.*, 1998). By its morphological and ecological characteristics, adults of *P. oleae* are known to be preyed by small and nocturnal flying vertebrates, such as bats (Chiroptera) (Dodd *et al.*, 2012; Jones *et al.*, 2009). In fact, bats are increasingly recognized to be key in the provisioning of natural pest control services in agroecosystems on the basis of their demonstrated impact on the population density of insect pests, particularly moths (Heim *et al.*, 2015; Kelly *et al.*, 2016; Riccucci & Lanza, 2014). In the face of an ever-increasing proportion of land surface devoted to olive farming in Mediterranean landscapes, understanding the environmental mechanisms driving pest control services provided by bats is therefore unquestionably urgent.

Previous studies show that management intensification negatively affects both species richness and activity levels of bats, with both the number of occurring species and foraging activity declining with the increase of management intensity (Herrera *et al.* 2015). However, the magnitude and sign of the impact of management intensification on

bats can show strong temporal (e.g. seasonal) variations due to, for example, fluctuations in the abundance and distribution of food resources (Lawer & Darkoh, 2016). Indeed, *P. oleae* has the singularity of developing three generations per year: antophagous, carpophagous and phyllophagous. At each generation, the adults emerge in large quantities (Mansour *et al.*, 2017), converting this insect species in the most abundant prey available for bats at local scales. Since the amount of insects is expected to be dependent of the type of production system, studies performed over more than one season are crucial, not only for establishing the impact of management intensification on bats and the potential natural pest control services they provide, but also to determine their reliability and predictability over time (Herrera and Doblas-Miranda, 2013).

In the present study, we investigated the impact that the structural complexity of olive groves has on the foraging activity of common insectivorous bats along a gradient of management intensification. The study was carried out during three consecutive seasons (that is, Spring, Summer and Autumn) in the region of Alentejo, South-Central Portugal, where olive groves belonging to a great variety of production systems co-occur throughout the regional landscape. In line with previous studies showing the negative impact of landscape homogenization on bat activity levels (Wickramasinghe *et al.*, 2003; Williams-Guillén & Perfecto, 2011), we expect an overall decrease in the activity of bats belonging to the genus *Pipistrellus* with the increase of management intensity. In addition, the demonstrated behavioral plasticity in bats' ability to adapt to changing resource availability (Heim *et al.*, 2016; Stepanian & Wainwright, 2018), seasonal variations in the impact of management intensification on bats are also expected.

Material and Methods

Study area, sampling design and sampling sites characterization

This study was carried out in the region of Alentejo, southern Portugal (Fig. 1a). The regional climate is Mediterranean characterized by mild and rainy winters and by warm and dry summers with temperatures commonly reaching up to 40°C (Rainho, 2007). The topography is flat, with altitude ranging between 100 and 400 meters a.s.l. Natural and semi-natural vegetation throughout the study region mainly occurs in the form of extensive savanna-like forests mainly composed of cork (*Quercus suber* L.) and

holm-oak (*Q. rotundifolia* L.) trees in varying densities, composing the characteristic Portuguese *montado* (for a detailed description of this system see Pinto-Correia *et al.*, 2011). The *montado*, the so-called *dehesa* in Spain, is considered a High Nature Value farming system according to the European Environmental Agency (Paracchini *et al.*, 2008). Other dominant land cover types includes orchards of tree-like crops, mainly olive (*Olea europaea* L.) and open areas allocated to cattle grazing and cereal farming. Minority land cover types include timber plantations (mainly of *Pinus pinaster* L. and *Eucalyptus* spp.) and small human settlements.

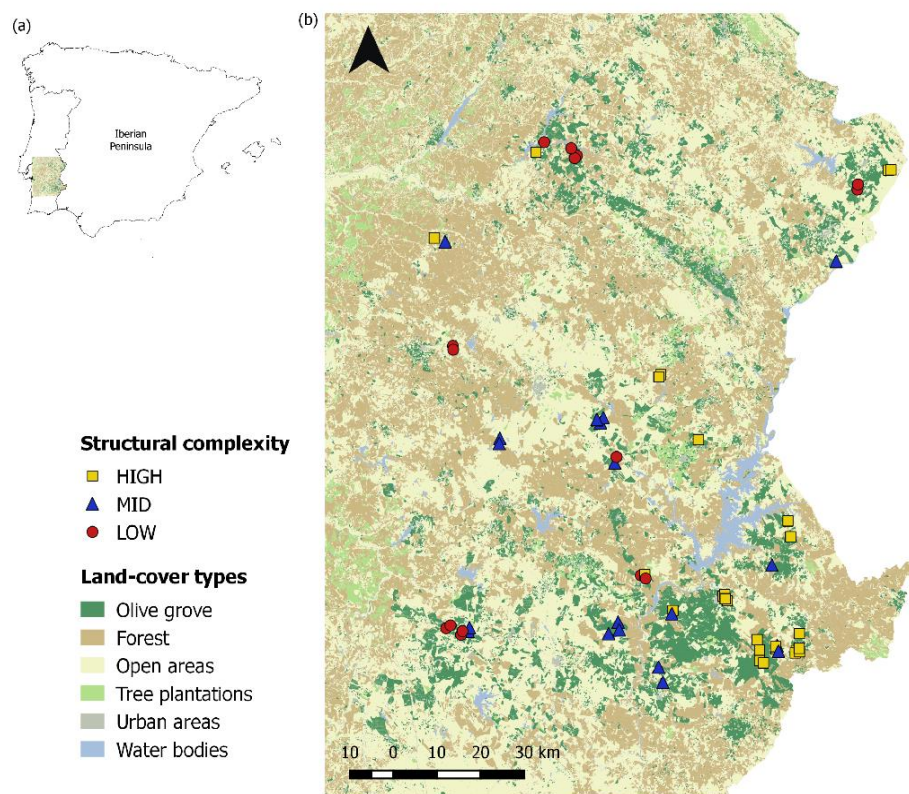


Figure 1. (a) Map of Iberian Peninsula showing the location of the study area in Southern Portugal and (b) the location of the 60 sampling points within the study area.

Throughout the study region, which comprised about 4 million hectares, we selected a total of 60 sampling points within different types of olive production systems (Fig. 1b). To determine the effects of the structural complexity of olive groves on the activity of insectivorous bats, sampling sites were selected to represent the greatest possible range of production systems. Olive groves where sampling points were located

were characterized using a set of structural features describing both planting pattern and olive tree features. Namely, we used the distance between olive trees along rows (*tree_dist*), the distance between tree rows (*row_dist*), the diameter at the breast height of olive trees (*dbh*), the standard deviation of the diameter at the breast height of olive trees (*dbh_SD*), height of the trunk (*t_height*), standard deviation of the height of the trunks (*t_height_SD*), tree canopy area (*canopy*) and standard deviation of the tree canopy area (*canopy_SD*). For each olive farm, we calculated *tree_dist*, *row_dist*, *dbh*, *t_height* *tree* and *canopy area* from at least ten replicates in order to obtain representative means and deviations (i.e., *dbh_SD*, *t_height_SD*, *canopy_SD*) (Table 1).

Table 1. Full description of the variables used to characterize the structural complexity of olive groves. Mean \pm SE of olive groves classified as showing a high (HIGH; $n = 27$), medium (MID; $n = 18$) and low (LOW; $n = 15$) structural complexity are shown. Landscape context variables estimated at 1 km radius from sampling points is also shown. Units are represented between parentheses.

Variables	Description	Structural complexity			
		HIGH	MID	LOW	
In-farm	<i>tree_dist</i>	Distance between olive trees in the same row (m)	7.96 \pm 0.41	5.00 \pm 0.49	1.37 \pm 0.16
	<i>row_dist</i>	Distance between the rows of olive trees (m)	8.35 \pm 0.32	7.24 \pm 0.30	3.41 \pm 0.17
	<i>dbh</i>	Diameter at the breast height (m)	1.12 \pm 0.06	0.49 \pm 0.04	0.27 \pm 0.01
	<i>dbh_SD</i>	Standard deviation of dbh (m)	0.30 \pm 0.04	0.05 \pm 0.01	0.03 \pm 0.00
	<i>canopy</i>	Canopy area (m ²)	19.96 \pm 1.49	9.60 \pm 0.76	1.46 \pm 0.18
	<i>canopy_SD</i>	Standard deviation of canopy area (m ²)	5.40 \pm 0.68	2.01 \pm 0.18	0.00 \pm 0.00
	<i>t_height</i>	Height of the trunk (m)	0.89 \pm 0.05	0.62 \pm 0.06	0.45 \pm 0.03
<i>t_height_SD</i>	Standard deviation of trunk height (m)	0.19 \pm 0.01	0.11 \pm 0.01	0.08 \pm 0.01	
Landscape context	<i>F_cover</i>	Proportion of forest cover (%)	14.07 \pm 3.96	10.30 \pm 3.39	8.28 \pm 3.80
	<i>O_cover</i>	Proportion olive grove cover (%)	59.39 \pm 4.64	59.41 \pm 5.14	52.62 \pm 6.60

To account for any potential influence of the landscape context on bat activity, the proportions of the two dominant land cover types, that is, holm-oak (*Quercus* spp.) forests (*F_cover*) and olive groves (*O_cover*), were also measured (Table 1). Using a geographical information system (QGIS Development Team, 2016), the proportions of these two land-cover types were extracted within a circular buffer area of 1 km radius

from each sampling point. This landscape-scale radius was based on the foraging distances regularly covered by pipistrelle bats (Boughey *et al.*, 2011; Davidson-Watts & Jones, 2006).

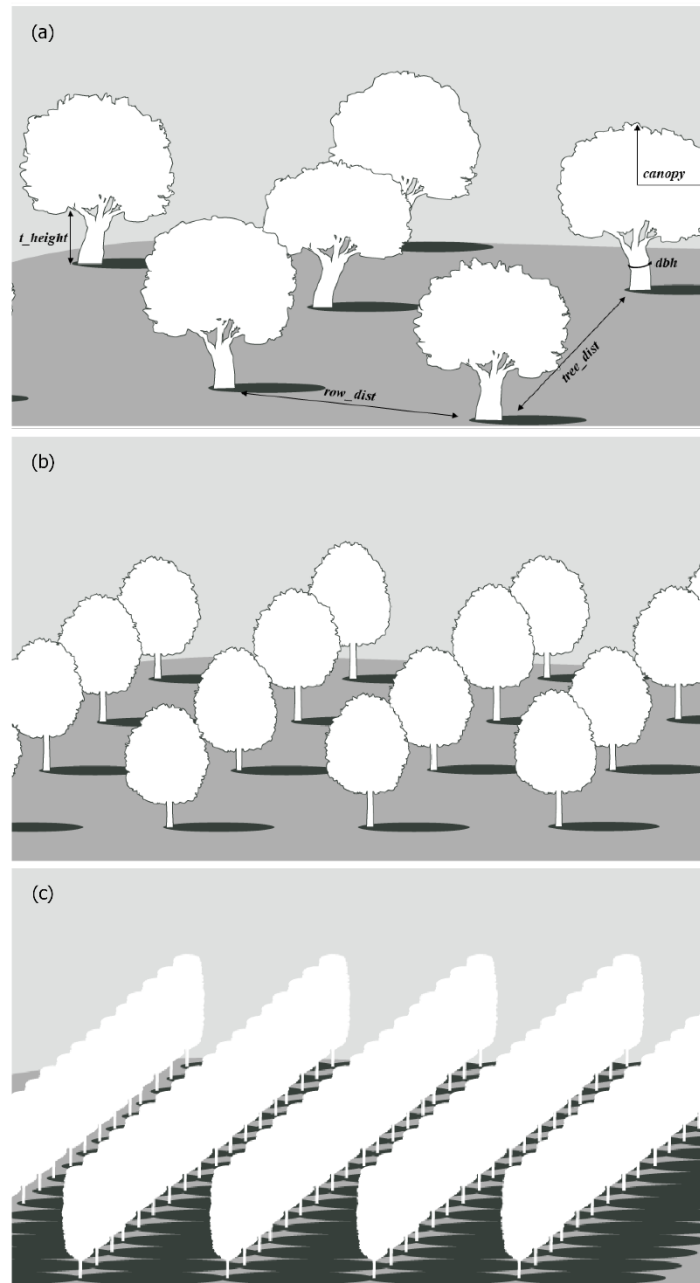


Figure 2. Conceptual diagram showing the structural complexity of the three olive production systems: **(a)** HIGH (with a representation of the variables used to characterize the structural complexity of olive groves); **(b)** MID; **(c)** LOW.

Because of the strong correlations between the structural variables, they were used to group olive production systems into categories based on their structural complexity using a multivariate clustering method, the *k*-means clustering algorithm (Herrera, *et al.*, 2018). The optimal number of clusters was obtained via the gap statistic (Tibshirani *et al.*, 2001). This approach clearly identified three clusters (Fig. S1), each belonging to a specific type of olive grove based on their structural complexity. Namely, olive groves were classified as showing a (1) high structural complexity (henceforth referred as HIGH; i.e., those exhibiting the higher averaged values and variability between all the variables), (2) mid structural complexity (MID; those exhibiting intermediate values and variability) and (3) low structural complexity (LOW; those exhibiting the lower averaged values and variability of all the variables) (Fig 2). Mean pairwise distances between sampling points classified as HIGH, MID and LOW were 69.63 ± 2.65 km (range: 0.75 - 136.25), 49.26 ± 1.55 km (range: 0.85 - 117.72) and 46.69 ± 1.51 km (range: 0.54 - 126.59), respectively.

Based on the pairwise distances between the different types of olive groves, those classified as LOW and MID were, on average, closer to each other than those classified as HIGH. This reflects the spatial distribution of these types of olive groves in the study region, particularly in the Southern region, where both these types of olive groves show their highest frequencies of occurrence (Fig. 1b).

Bat monitoring

For monitoring bats, we used acoustic recording devices (Peterson D500x; Pettersson Elektronik AB, Uppsala, Sweden) equipped with microphones with a sensitivity range of 10 to 190 kHz. Ultrasound samples were digitized at 300 kHz with a resolution of 16 bits. During all surveys, we used the same auto-recording mode setting for 3 seconds without pre-trigger. Recordings were used for species identification and determining their species-specific activity levels, using the number of passes as a surrogate of bat abundance. Bat surveys were conducted in three sampling seasons, namely in spring (mid-April), summer (mid-June) and autumn (mid-September).

Bat detectors were deployed at each sampling point mounted on a tripod at about 1.5 - 2.0 meters above the ground, facing upwards at 45° and orientated towards the space between rows of olive trees in order to maximize the number and recording quality of bat

passes (Fig. 3). Detectors were placed during three consecutive nights at each sampling point per season, programmed to start the recording 30 minutes before sunset and finish 30 minutes after sunrise. Sampling was always conducted when temperature was above 15°C and wind speed below 3.5 m s⁻¹.

Recordings were identified to species level or assigned to single genus complexes using a semi-automatic classification system (Silva *et al.*, 2013, 2014) followed by a user validation, as recommended by Russo & Voigt (2016), using published data on bat calls (Rainho *et al.*, 2011). Nineteen spectral and temporal parameters of bat echolocation calls were measured through a custom-built R script and the identification was performed by comparison with a reference database using assemblages of neural networks. The database used is extensive and includes 16 000 individual calls from more than 1 400 bats belonging to 24 species captured and recorded in mainland Portugal. Only pipistrelle species, namely, *Pipistrellus kuhlii* (Kuhl, 1817), *Pipistrellus pygmaeus* (Leach, 1825) and *Pipistrellus pipistrellus* (Schreber, 1774) were considered, since they are the most abundant species in olive production systems in our study region (Herrera *et al.*, 2015).



Figure 3. Example of the placement of bat detectors in field.

Pest monitoring

We focused on the olive moth, *Prays oleae* (Bernard, 1788) (Lepidoptera: Praydidae). This lepidopteran presents three generations per year, namely, an antophagous generation (from April to June), a carpophagous generation (from July to September) and a phyllophagous generation (from October to March) (Villa *et al.*, 2016). For insect surveys, we placed a single Delta Trap (ECONEX; model TA118; 20 × 28 × 11,5 cm) baited with synthetic sex pheromone [(Z)-7-14: Ald] contained in a polyethylene capsule (Mazomenos *et al.*, 1999).

Delta traps were hanged on a tree branch at *c.* 1.5 meters aboveground and in the South-West exposition of the canopy. They were placed in the field for 15 days, overlapping with the period in which bat monitoring was carried out. This sampling procedure was performed three times, coinciding with the peaks of abundance that this insect species has along its life cycle ($n = 180$). At the end of each season, every glued specimen was counted and the total number per trap was used as a surrogate of food-resource availability for bats. This is because the particularly high abundance of *P. oleae* in olive groves is expected to exert a strong influence on the activity of opportunistic generalist species (Aizpurua *et al.*, 2017; Lawer & Darkoh, 2016), such as pipistrelle bats.

Data analyses

All statistical analysis were performed within “R” software environment, version 2.15.1 (<http://www.r-project.org>). To investigate potential between-season variations in the impact of the structural complexity of olive groves on bat activity, we used generalized linear mixed models (GLMMs) with Gaussian distribution. The type of olive grove (i.e., HIGH, MID and LOW), the amount of *P. oleae* adults caught at each sampling point as well as the amount of forest cover and olive grove cover were included as fixed effects. The identity of each olive farm was included as a random effect to account for any potential constraint related to their spatial distribution (function `lmer`; R-package “`lme4`”; Bates *et al.*, 2013). Post-hoc pairwise comparisons based on Tukey’s tests were applied to compare results from MID and LOW categories (function `glht`; R-package “`multcomp`”; Hothorn *et al.*, 2008). The fit of the GLMMs was evaluated by calculating conditional (regarding fixed effects plus random effects) and marginal (regarding only fixed effects) Pseudo R^2 values (function `r.squared` GLMM; R package “`MuMIn`”;

Barton, 2013). Visual inspections of residuals (qqplots and residual vs fitted plots) were performed to evaluate the assumptions of linearity and distributions of the models and to detect potential outliers. Spatial independence of bat activity (i.e. spatial autocorrelation) was assessed through the mantel test on the model residuals (function `mantel.rtest`; R package “`ade4`”; Dray & Dufour, 2007). For statistical analysis purpose, bat activity was log transformed to reduce skewness and the influence of extreme values.

Results

We recorded a total of 3 022 calls identified as pipistrelle bats belonging to three species, namely the Kuhl’s pipistrelle (*Pipistrellus kuhlii*), the soprano pipistrelle (*P. pygmaeus*) and the common pipistrelle (*P. pipistrellus*). The most frequently recorded species was *P. kuhlii* ($n = 2049$; 67.8%), followed by *P. pygmaeus* ($n = 625$; 20.7%) and *P. pipistrellus* ($n = 348$; 11.5%), respectively. Indeed, *P. kuhlii* was by far the most frequently recorded species across the different types of olive production systems and seasons (Table 2).

No spatial autocorrelation was found in the activity levels of *P. kuhlii* and *P. pygmaeus*. Only a significant, although weak, spatial trend was found for *P. pipistrellus* during the spring season, thereby ensuring a suitable spatial framework to test our hypotheses (Table S1).

While the activity of bats exhibited an overall trend to decrease with the simplification of the structural characteristics of olive groves, the effect of the structural complexity of the different production systems on bat activity was species-specific and season-dependent (Table 4). Thus, in the case of *P. kuhlii*, despite strong differences between the three types of olive production systems found during summer (with the activity levels decreasing as structural complexity of the olive production systems decreases), during spring and autumn these differences were judged statistically significant only for olive groves classified as HIGH (Fig. 4). During spring, *P. pygmaeus* exhibited a similar pattern to that exhibited by *P. kuhlii* (Fig. 4). However, the statistically significant differences between olive groves classified as HIGH and MID disappeared during summer as well as those between the three types of olive groves during autumn.

Table 2. Mean \pm SE passes of the three pipistrelle species recorded per night at each sampling season. HIGH, MID and LOW correspond to olive groves showing a high, intermediate and low structural complexity, respectively.

Species	Season								
	Spring			Summer			Autumn		
	Structural complexity			Structural complexity			Structural complexity		
	HIGH	MID	LOW	HIGH	MID	LOW	HIGH	MID	LOW
<i>Pipistrellus kuhlii</i>	24.74 \pm 5.97 (668)	2.39 \pm 0.65 (43)	2.93 \pm 1.16 (44)	24.04 \pm 6.49 (649)	5.17 \pm 1.60 (93)	1.27 \pm 0.59 (19)	15.89 \pm 2.97 (429)	3.67 \pm 1.15 (66)	2.53 \pm 0.53 (38)
<i>Pipistrellus pygmaeus</i>	5.00 \pm 1.30 (135)	3.11 \pm 0.92 (56)	2.60 \pm 1.63 (39)	7.07 \pm 2.86 (191)	2.83 \pm 1.42 (51)	0.93 \pm 0.64 (14)	3.67 \pm 1.18 (99)	1.56 \pm 0.51 (28)	0.80 \pm 0.28 (12)
<i>Pipistrellus pipistrellus</i>	3.11 \pm 0.99 (84)	3.44 \pm 1.25 (62)	2.47 \pm 1.08 (37)	2.30 \pm 0.65 (62)	1.50 \pm 0.82 (27)	0.67 \pm 0.29 (10)	1.19 \pm 0.40 (32)	1.33 \pm 0.51 (24)	0.67 \pm 0.29 (10)

The numbers in parentheses indicate the total number of passes recorded for each species.

Table 3. Number of specimens of *Prays oleae* adults caught per trap (mean \pm SE) at each sampling season.

Season								
Spring			Summer			Autumn		
Structural complexity			Structural complexity			Structural complexity		
HIGH	MID	LOW	HIGH	MID	LOW	HIGH	MID	LOW
194.24 \pm 52.53 [3-972]	787.35 \pm 100.05 [32-1476]	479.47 \pm 65.13 [138-948]	295.78 \pm 50.07 [2-802]	569.39 \pm 118.61 [6-1488]	460.27 \pm 101.64 [26-1368]	101.38 \pm 15.60 [19-336]	307.39 \pm 46.40 [32-606]	170.40 \pm 31.33 [41-504]

Table 4. Summary table showing the results of the generalized linear mixed models investigating seasonal variations in the effect of structural complexity of olive production systems and landscape context on bat activity. Parameter estimates (\pm SE) and models goodness fit are presented. R^2_m (marginal R^2) includes only the goodness of fit of fixed effects and R^2_c (conditional R^2) includes also the random effects. Significant effects ($P < 0.05$) are showed in bold. Olive groves classified as HIGH were used for comparison purposes.

	Spring				Summer				Autumn			
	Estimate		R^2_m	R^2_c	Estimate		R^2_m	R^2_c	Estimate		R^2_m	R^2_c
<i>Pipistrellus kuhlii</i>												
MID	-1.720***	(± 0.350)			-1.262***	(± 0.303)			-1.205***	(± 0.278)		
LOW	-1.680***	(± 0.353)			-2.150***	(± 0.319)			-1.130***	(± 0.310)		
Forest cover	0.015	(± 0.009)	50.7	67.8	0.010	(± 0.009)	51.2	51.2	0.017**	(± 0.008)	41.5	74.1
Olive grove cover	0.010	(± 0.006)			-0.005	(± 0.006)			-0.006	(± 0.005)		
<i>Prays oleae</i>	0.000	(± 0.000)			0.000	(± 0.000)			0.001	(± 0.001)		
<i>Pipistrellus pygmaeus</i>												
MID	-0.661**	(± 0.297)			-0.156	(± 0.286)			-0.097	(± 0.254)		
LOW	-1.094***	(± 0.321)			-1.096***	(± 0.330)			-0.292	(± 0.269)		
Forest cover	-0.012	(± 0.009)	21.1	68.2	-0.010	(± 0.010)	16.9	86.3	-0.002	(± 0.008)	11.8	62.0
Olive grove cover	-0.014**	(± 0.006)			-0.014**	(± 0.006)			-0.010**	(± 0.005)		
<i>Prays oleae</i>	0.000	(± 0.000)			0.000	(± 0.000)			-0.001	(± 0.001)		
<i>Pipistrellus pipistrellus</i>												
MID	0.060	(± 0.328)			-0.260	(± 0.236)			0.022	(± 0.221)		
LOW	0.198	(± 0.365)			-0.368	(± 0.270)			-0.177	(± 0.255)		
Forest cover	0.004	(± 0.010)	1.1	66.7	-0.006	(± 0.008)	6.7	77.8	0.016**	(± 0.007)	16.3	67.3
Olive grove cover	0.004	(± 0.006)			-0.005	(± 0.005)			-0.001	(± 0.040)		
<i>Prays oleae</i>	0.000	(± 0.000)			0.000	(± 0.000)			0.000	(± 0.001)		

Signif. codes: 0 '***', 0.001 '**', 0.01 '*'

In the case of *P. pipistrellus*, no statistically significant differences were found across olive production systems at any season (Table 4).

No statistically differences between the three types of olive production systems were found in the proportion of forest cover and that of olive groves at 1 km radius surrounding the sampling points ($P > 0.05$ in all cases). The proportion of forest cover had a statistically significant and positive effect on both *P. kuhlii* and *P. pipistrellus* activities, but exclusively in the autumn season (Table 4; Fig. 5). Regarding, the proportion of olive groves, a statistically significant negative effect was found exclusively on the activity of *P. pygmaeus* at the three sampling seasons (Table 4; Fig. 6).

We found variations in the average number of specimens of *P. oleae* between the three types of olive production systems. Overall, olive groves classified as MID had consistently higher abundances of *P. oleae* (Table 3). However, statistically significant differences between the three types of olive production systems were exclusively found in spring, and no significant differences between olive groves classified as HIGH and LOW were found neither in summer nor autumn (Fig. 7). Regarding the effect of the abundance of *P. oleae* on bat activity, we found no significant influence on either pipistrelle species (Table 4).

Discussion

We investigated the effect of structural simplification of Mediterranean olive groves on the activity levels of three common insectivorous bats (i.e., *Pipistrellus kuhlii*, *P. pygmaeus* and *P. pipistrellus*) during three consecutive seasons (spring, summer and autumn). By simultaneously investigating the spatio-temporal patterns of activity of an olive pest, the olive moth (*Prays oleae*), the potential implications for the natural pest control services provided by bats were also explored. Three types of olive groves were established on the basis of their structural characteristics, that is, olive groves showing high, intermediate or low structural complexity. As expected, we found that the higher the structural complexity of olive groves, the higher the overall activity levels of insectivorous bats. Interestingly, these effects were species-specific and season-dependent. Thus, while some species strongly decreased their activity levels with increasing structural simplification, others exhibited either weak or no response.

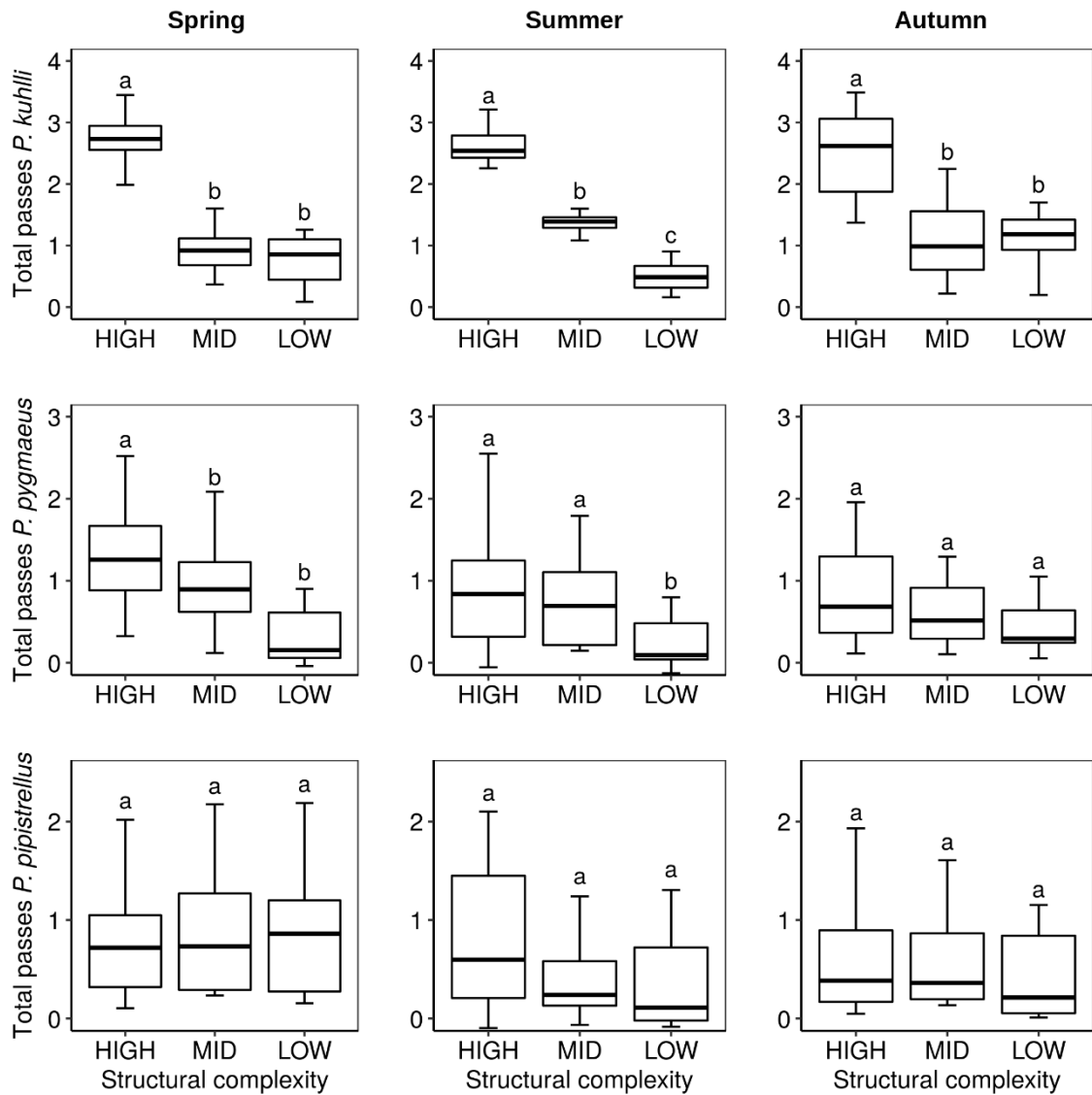


Figure 4. Boxplots showing upper whisker (maximum data point), interquartile range box (top line = 75% of the data \leq this value; middle line = median; lower line = 25% of the data \leq this value) and lower whisker (minimum data point) for the activity (total bat passes) of *P. kuhlii*, *P. pygmaeus* and *P. pipistrellus* according to each structural complexity (HIGH, MID and LOW) per season.

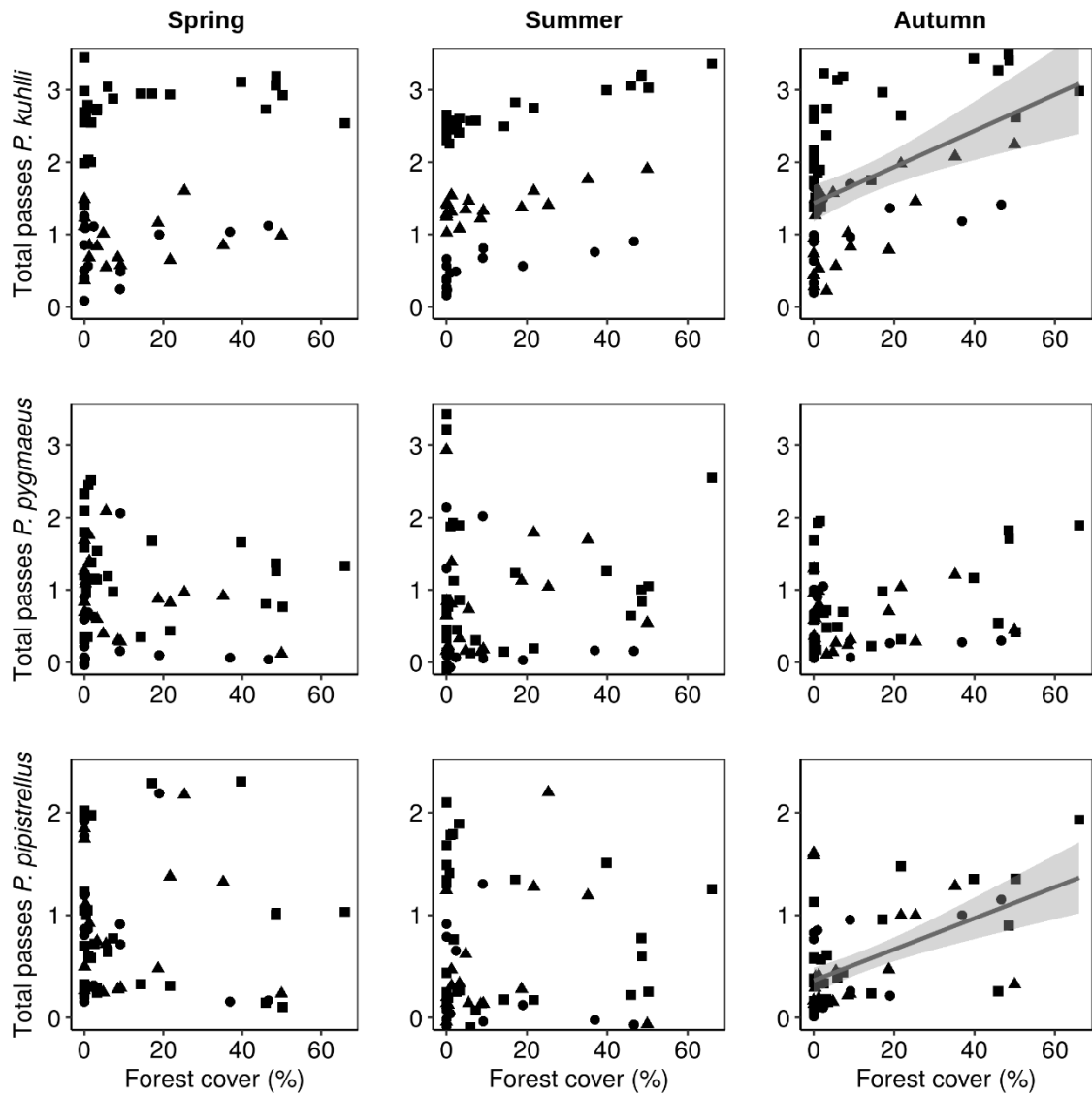


Figure 5. Scatterplots showing the correlation between the activity (total bat passes) of *P. kuhlii*., *P. pygmaeus* and *P. pipistrellus* with the percentage of forest cover in 1 km buffers per season in the three types of structural complexity: HIGH (■); MID (▲) and LOW (●).

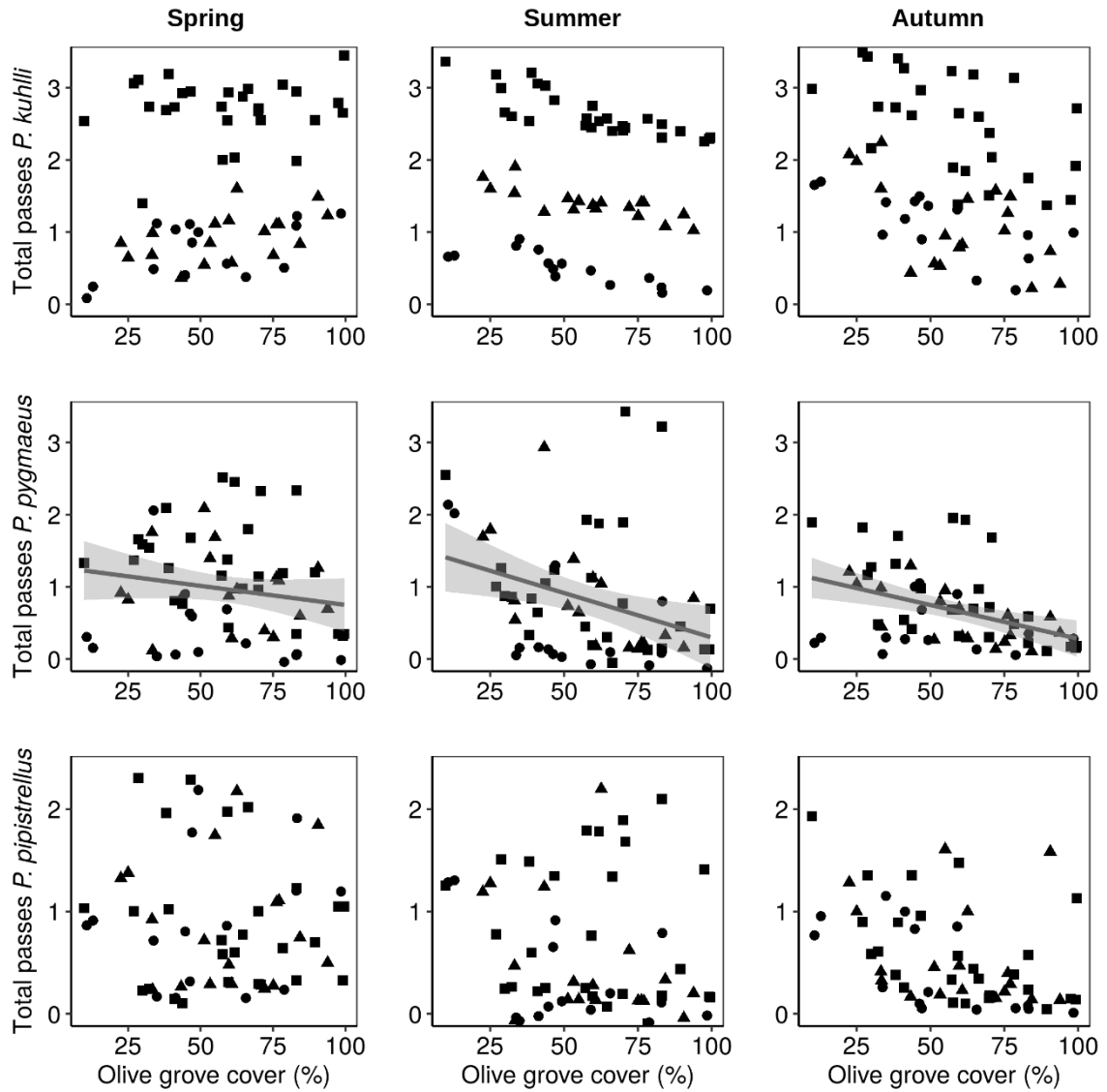


Figure 6. Scatterplots showing the correlation between the activity (total bat passes) of *P. kuhlii*., *P. pygmaeus* and *P. pipistrellus* with the percentage of olive grove cover in 1 km buffer per season in the three types of structural complexity: HIGH (■); MID (▲) and LOW (●).

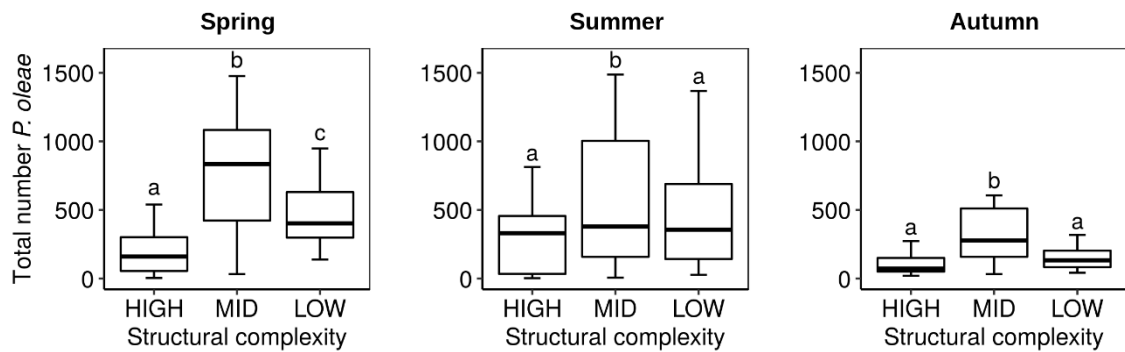


Figure 7. Boxplots showing upper whisker (maximum data point), interquartile range box (top line = 75% of the data \leq this value; middle line = median; lower line = 25% of the data \leq this value) and lower whisker (minimum data point) for the total number of *Prays oleae* according to each structural complexity (HIGH, MID and LOW) per season.

Moreover, despite strong effects of structural simplification found in some seasons, the strength of these effects either decreased or disappeared in others. The spatio-temporal activity patterns of insectivorous bats were not coupled with those of *P. oleae* neither across seasons nor across types of olive groves. Subsequently, the structural simplification of olive groves is suggested to strongly compromise the natural pest control services provided by insectivorous bats.

Our results are in line with previous studies which also have shown that activity levels of bats strongly decrease as landscape simplification increase (Wickramasinghe *et al.*, 2003). In our study region, structurally-complex olive groves were characterized by exhibiting strong variations in tree cover density and planting pattern, thereby providing a suitable spatial framework for edge-foragers like pipistrelle bats (Ducci *et al.*, 2015). Longer distances between trees and less tree cover density likely improves accessibility into olive groves and facilitates foraging activity (Erickson & West, 2003; Humes *et al.*, 1999; Loeb & Waldrop, 2008). Conversely, as tree cover become denser and spatially cluttered, flight manoeuvrability decrease and subsequently the likelihood that bats entering into olive groves decreases as well (Herrera *et al.*, 2015). This response pattern has indeed been previously observed when investigating bat activity in managed and unmanaged chestnut orchards in southern Switzerland. Managed chestnut orchards were

much less dense and cluttered, and total bat foraging (including that from pipistrelle bats) was five times higher compared to that recorded unmanaged ones (Obrist *et al.*, 2011).

Reductions in food-resource availability has also been suggested to be behind decreased bat activity with increased structural simplification of olive groves (Herrera *et al.*, 2015). We do not have data on insect availability at community-level, something that would allow to know how trophic preferences drive the species-specific foraging patterns of bats (Wickramasinghe *et al.*, 2004). Instead, we determined the abundance of the olive pest *Prays oleae* (as a surrogate of food-resource availability), which is suggested to be the most abundant insect prey locally available for bats during the three periods of adult emergence. Interestingly, we found that the abundance of *P. oleae* did not decrease as the structural complexity of olive groves increased. In fact, during at least two sampling seasons (i.e., summer and autumn) no differences were found between olive groves of higher levels of structural complexity. Thus, in close agreement with previous studies, our results strongly suggest that structural complexity rather than prey availability is a key factor affecting the foraging activity of insectivorous bats in olive groves (Erickson & West, 2003; Loeb & Waldrop, 2008; Obrist *et al.*, 2011). In other words, prey availability (here estimated by the abundance of *P. oleae*) seem to have an influence not strong enough as to counterbalance the pervasive impact of structural complexity on bat activity, particularly between extreme production systems.

Despite the strong impact of structural complexity on the activity levels of bats, we hypothesize that variations in the abundance of *P. oleae* may well explain changes in the relative strength of the effects of structural complexity on bat activity. Thus, despite both *P. kuhlii* and *P. pygmaeus* exhibited strong differences between olive groves showing high and low structural complexity, in autumn when prey abundance strongly decreased in relation to spring and summer, *P. pygmaeus* (in a similar way to *P. pipistrellus*) exhibited no differences across types of olive groves. We interpret this response pattern as *P. kuhlii* regularly use olive groves as foraging habitat, while *P. pygmaeus* seems to use olive groves only in response to peaks of abundance of insect food resources, even because this specie has a preference to forage closer to riparian habitats (Davidson-Watts *et al.*, 2006). Indeed, the consistently negative impact of the proportion of olive groves surrounding sampling points reinforce our hypothesis that

olive groves (irrespective of their structural complexity) may serve more as commuting areas than true foraging habitats for this bat species. The same can be concluded for *P. pipistrellus*, the species for which extremely reduced activity levels were found in olive groves, irrespective of their structural complexity.

Conclusions

With this study we can better understand how landscape simplification affects bat activity within olive groves with different structural complexities. The strong decrease in the activity levels with the increase of management intensification clearly supports the results of previous studies that states the importance of habitat heterogeneity for bats. The responses of the pipistrelle bats were species-specific and season dependent, which draws attention to the importance of studies performed at more than one season, since bats can adapt their habitat selection by tracking insect fluctuations and selecting the best habitat for their energy requirements, and also to studies that focus on the species level. Lack of ecological information can be a factor that limits conservations actions (Kunz *et al.*, 2011) and the potential natural services that bats can provide.

Since olive groves consist in one the major features of the agricultural landscapes throughout the Mediterranean countries, our findings can have implications for conservation management of this group of mammals. Therefore, the decline in bat populations can affect ecosystem functions, specifically in agricultural fields. In fact, bats can act as natural pest controllers for olive pests. Thus conservation actions that increase bat biodiversity in agricultural landscapes can benefit both the wildlife community and farmers.

Implications for natural pest control services

This study can potentially have great implications for natural pest control services. Bats can, indeed, play an important role in agroecosystems, particularly in olive production systems, by controlling insect populations. We found that *Pipistrellus kuhlii* is, by far, the most abundant species in our study region, southern Portugal. If we assume that the amount of prey consumed by the three pipistrelle species is similar given the similar body characteristics, more studies and conservation actions should be focused on this species. The number of recordings identified as *P. kuhlii*, suggests that this bat can

have a great potential in olive groves with high and intermediate structural complexity by feeding on possible olive pests, having great implications for the land owners.

Besides, we also found a strong avoidance of olive groves with low structural complexity. Thus, we can conclude that, between the three types of structural complexities sampled in this study, the one with a more homogeneous landscape is not a suitable foraging habitat for generalist bats, such as the ones belonging to the genus *Pipistrellus*, confirming the importance of habitat heterogeneity in the selection of foraging habitats. Being this factor even more important than insect abundance, since we found that the abundance of *P. oleae* did not have a strong influence in bat activity, we can assume that the structural simplification of olive production systems can compromise the natural pest control services provided by insectivorous bats.

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Appendix – Supplementary Information

Table S1. Summary table showing the results of the mantel test per season for the three species of *Pipistrellus*, analyzing spatial autocorrelations of bat activity. Observed (Obs) and expected (Exp) values are presented. Significant effects ($P < 0.05$) are showed in bold.

Species	Season								
	Spring			Summer			Autumn		
	Obs	Exp	p-value	Obs	Exp	p-value	Obs	Exp	p-value
<i>P. kuhlii</i>	-0.0229	-0.0041	0.58	-0.0403	-0.0082	0.56	-0.0043	-0.0095	0.48
<i>P. pygmaeus</i>	-0.1041	0.0041	0.97	-0.0803	-0.0093	0.80	-0.0940	-0.0021	0.91
<i>P. pipistrellus</i>	0.2503	0.0077	0.02	0.0015	-0.0056	0.41	0.0833	0.0048	0.12

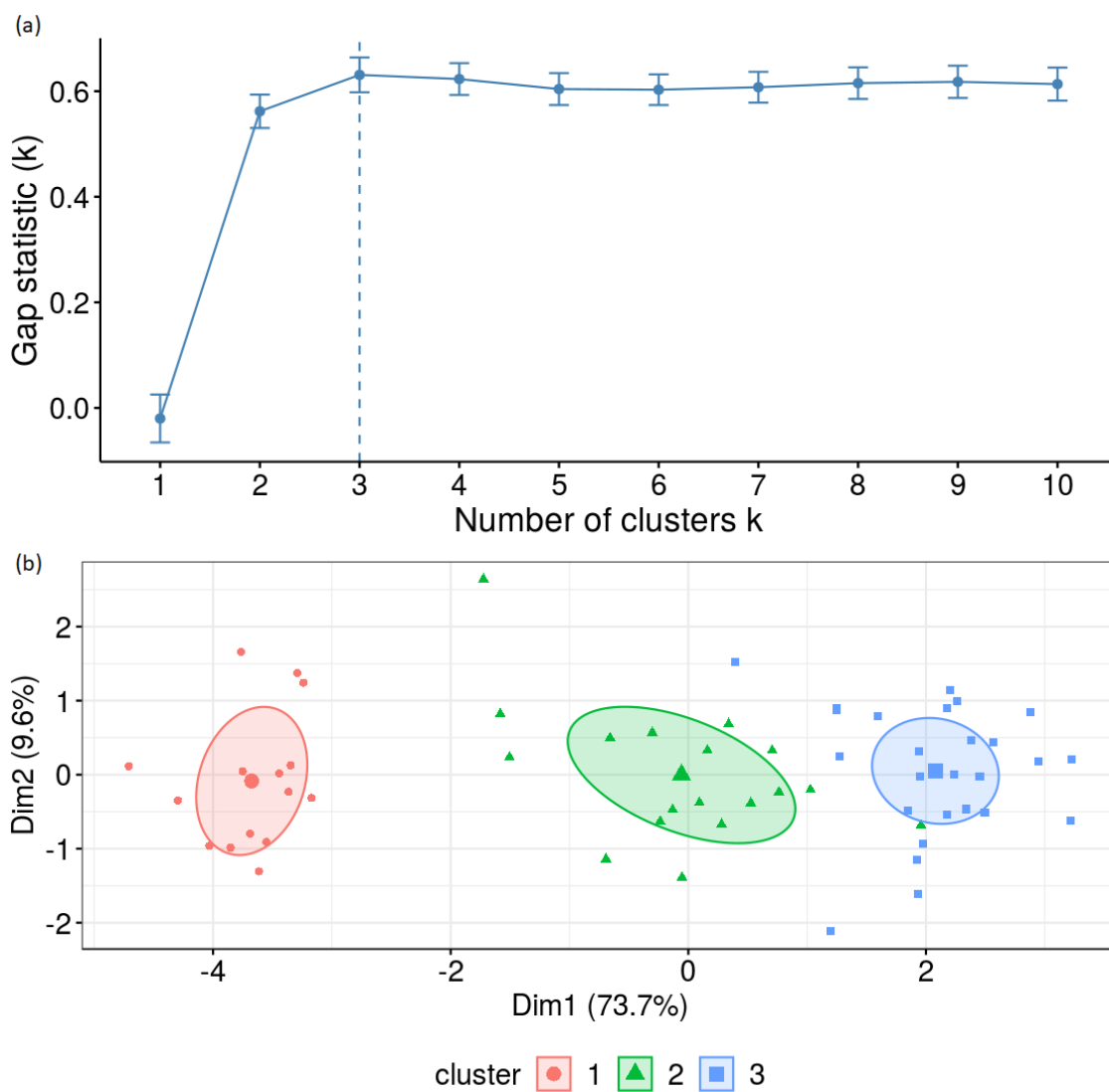


Figure S1. (a) Gap statistic plot with optimum number of clusters identified and (b) representation of the clusters obtain by the k-means analyses: 1- LOW; 2- MID; 3- HIGH.