Universidade de - Évora - Escola de Ciências e Tecnologia

Mestrado em Biologia da Conservação

Dissertação

Phenological mismatches disrupt bat-mediated biocontrol services in olive groves

Ana Isabel Peixoto Costa Carvalho

Orientador(es) José Manuel Herrera Vega
Bruno Miguel Santos Antunes Silva

Évora 2020

Esta dissertação não inclui as críticas e as sugestões feitas pelo júri

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Abstract

Management intensification is known to compromise bat-mediated biocontrol services in olive groves through spatial mismatches between bats and olive pests. However, no information exists regarding disruptions in biocontrol services driven by temporal mismatches between species.

To fit this gap of knowledge, we analyzed the distribution of *Pipistrellus kuhlii* passes throughout the night in three seasons and in different types of olive groves. We also studied the time when *Prays oleae* activity peak occurs on several nights to compare with the bat species.

Our results suggest that the intensification of olive grove management practices does not equally compromise the biocontrol service in the different seasons. In summer, we found that only in olive groves with low structural complexity there is no overlap between the time when the two peaks of activity occur but during autumn, we found that there is always a phenological mismatch, regardless of management practices.

Keywords: Bats; *Pipistrellus Kuhlii*; Biocontrol Services; *Prays oleae*; Olive farming.

Phenological mismatches disrupt bat-mediated biocontrol services in olive groves

Resumo

Sabe-se que a intensificação agrícola compromete o serviço de biocontrole providenciado por morcegos em olivais devido à incompatibilidade espacial gerada entre estes e a praga. No entanto, não existem estudos sobre como a incompatibilidade temporal afeta este serviço de ecossistema.

Para preencher esta lacuna de conhecimento, analisámos a distribuição das passagens de *Pipistrellus kuhlii* ao longo da noite em três estações e em diferentes tipos de olival. Estudámos igualmente o pico de atividade de *Prays oleae* ao longo da noite para comparar com a espécie de morcego.

Os nossos resultados sugerem que a intensificação das práticas de gestão não compromete igualmente o serviço de biocontrole nas diferentes estações do ano. No verão e apenas nos olivais com baixa complexidade estrutural, constatamos que não há sobreposição entre o momento em que os dois picos de atividade ocorrem. Durante o outono, verificamos que há sempre incompatibilidade fenológica, independentemente das práticas de gestão.

Introduction

Land conversion for agricultural purposes and the intensification of farming practices is increasingly leading to the degradation and destruction of important habitats for wild species (Mickleburgh *et al*., 2002). In the 1960s, with publications such as Carson's Silent Spring (1962), public recognition of the implications of changes in agricultural management practices for wildlife emerges (Park, 2015). In the following decades, evidence of the catastrophic effects of this progressive intensification on biodiversity has accumulated. At global scale, agricultural intensification has been considered a major cause of biodiversity losses (Benton *et al*., 2002, 2003; Frey-Ehrenbold *et al*., 2013; Tilman *et al*., 2001; Tscharntke *et al*., 2007; Wickramasinghe *et al*., 2003). World population is expected to reach 9.7 billion in 2050 and could peak at nearly 11 billion around 2100 (United Nations, Department of Economic and Social Affairs & Population Division, 2015). In this way, agriculture tends to be progressively more intensive and mechanized with increased chemical inputs, such as non-selective synthetic pesticides and fertilizers (Firbank *et al*., 2008; Matson *et al*., 1997; Stoate *et al*., 2001). On the other hand, intensive agriculture requires simplification of farming landscapes associated to a significant increase in the size of parcels (Petit *et al*. 2003b). It's well known that extensive monocultures of high-yielding varieties coupled leads to the loss of landscape connectivity therefore negative environmental impacts on soil, air, water and biodiversity (Donald *et al*., 2001; Firbank *et al*., 2008; Herrera *et al*., 2018; Matson *et al*., 1997; Stoate *et al*., 2001, 2009; Tilman *et al*., 2001; Tscharntke *et al*., 2005).

In the Mediterranean region, one of the major drivers of landscape modification is olive (*Olea europaea*: L., 1753) farming. Traditionally, olive farming was achieved with relatively low impacts of management practices. The intensification of production was encouraged by the past Common Agricultural Policy (CAP) because subsidies were allocated based on the quantity of olive oil produced (de Graaff *et al*. 2010). Olive groves were categorized as intensive or traditional depending on their management (Beaufoy, 2001). Currently, a new category has been created, superintensive, where agricultural practices, such as mechanization and recurring pesticide application, has become even more intense. Euro-Mediterranean region contributes with three quarters of the annual production of olive oil in the world and the total waste generation is nearly 75% of the olive harvest (Azbar *et al*., 2004). The sustainability of this intensification is questionable. Therefore, olive-production regions currently face the great challenge of combining environmentally sustainability with economic profitability. The loss of structural complexity is expected to affect species diversity and how they use these extensive areas. Paradoxically, the decrease in landscape heterogeneity over time and the remaining consequences of this progressive intensification are threatening species that provide ecosystem services for these very same agricultural landscapes, including pest control (Paredes et al., 2013; Rusch *et al*., 2016).

Pest control is an important, valuable and currently recognized ecosystem service provided by biodiversity (Cleveland *et al*., 2006; Landis *et al*., 2000; Schlapfer, 1999; Tschumi *et al*., 2015). But several studies indicate that agricultural intensification and consequent simplification of spatial patterns cause a decrease in natural enemy diversity (Andersen & Eltun 2001; Brown & Schmitt 2001; Rusch *et al*., 2016). Consequently, the stability of pest suppression may be affected, directly and indirectly, by the landscape structure (Martin *et al*., 2013; Rusch *et al*., 2013, 2016). According to Sandhu *et al*. (2008), the value of ecosystem services in general, and biological control in particular, are significantly higher in organic fields than in conventional crops. Within agricultural areas, some natural enemy species are unable to sustain positive population growth, however, they may use prey resources present in these plots (Tscharntke *et al*., 2007). The importance of having a landscape perspective and combining studies of natural and managed systems to understand population dynamics and trophic interactions has been increasingly accepted (Bianchi *et al*., 2006; Landis *et al*., 2000; Tscharntke *et al*., 2007).

The olive fruit moth, *Prays oleae* (Bernard, 1788) (Lepidoptera: *Praydidae*), is one of the pests that cause the greatest economic damage in olive groves worldwide. This monophagous species registers three peaks of activity annually, but only the larvae of the carpophagous generation cause economic loss to that year's harvest. (Lopes *et al*., 2008; Ramos *et al*., 1998). In autumn, the phyllophagous larvae hibernate during the winter and in the following spring, during the onset of flowering, adults of this generation appear. In this first annual peak of the pest the eggs are placed on the buds, allowing the larvae of the anthophagous generation to emerge and feed until they pupate between June and July. During the peak of spring, only the flowers fall. In summer, adults of the anthophagous generation lay their eggs on the undeveloped fruits, close to the stem. Part of the olive pulp is consumed by the larvae of the carpophagous generation, which subsequently leads to premature fruit fall. Between September and October, carpophagous larvae emerge from the fruit to pupate on branches, leading to another fruit drop. These adult females lay their eggs on the leaves and this posture is responsible for restarting the cycle. (Gonzalez *et al*., 2015). Therefore, the effectiveness of the biological control of this pest, performed by different groups of vertebrates and invertebrates, is economically extremely important (Bento *et al*., 2001a; Villa *et al*., 2016).

In this context, the potential of bats, as non-selective predators, to provide pest suppression services has been proven through recent technological advances and its economic value has been estimated (Boyles *et al*. 2011; Brown *et al*., 2015; Cleveland *et al*., 2006; López-Hoffman *et al*., 2014). Several studies demonstrated that some of the most destructive agricultural pests are often among prey for insectivorous bats (Brown *et al.*, 2015; Cleveland *et al*., 2006). In this way, bats can offer biocontrol services that ultimately culminates in substantially more productive crops, corroborating their functional importance (Maas *et al*. 2013). The loss or disruption of roosting and foraging sites or landscape elements identified as important for bats is mainly due to urbanization and agriculture intensification (Mickleburgh *et al*., 2002). Although some bat species may exhibit marked foraging flexibility to feed in man-made habitats or success in exploring urban roosting sites, the response to habitat changes is highly species-specific (Russo & Ancillotto, 2015). Nevertheless, Herrera *et al*. (2015) suggested that large and homogeneous olive monocultures may serve more as commuting areas than true foraging habitats for bats. Thus, the absence of these predators on olive groves could lead to a decreased probability of their interaction with olive pests and, in turn, biocontrol services.

Routine ecological disturbances in crop fields constitute a requirement for the long-term persistence of species. The dispersal and repopulation dynamics originated can interfere with biological phenomena dependents on synchrony between interacting elements (Welch *et al*. 2011; Welch & Hardwood, 2014). Despite the structural complexity and agricultural intensification, biological control is also dependent on the temporal coincidence between the activity of predators and pests. Therefore, the importance of this component has started to achieve some recognition. According to Collins *et al*. (2018), spatial heterogeneity may be a predictor of temporal heterogeneity in ecological communities. Authors such as Welch & Hardwood (2014) have warned about the importance of recognizing the crucial role of temporal dynamics in predator-prey interactions in agroecosystems. How biological control can be provided, according to Welch & Hardwood (2014), is determined by the degree of overlap between all ecological cycles and their relative timing. In order that ecosystem services can be provided, the importance of phenological cycles is undeniable because the nature and magnitude of the ecological interactions among organisms depends on them. In addition to this, Lundgren *et al.* (2009) considered diel activity rhythms a determining factor of predator-prey interaction.

According to Welch & Hardwood (2014), prey animals can escape completely from guilds of active-hunting predators by simply changing the timing of their activity patterns. Lundgren *et al*. (2006) found that beneficial ground-dwelling arthropods that reside in less intensified agroecosystems have a more consistent diel activity patterns, suggesting that natural enemy communities behaved differently according to the intensity of management. Wickramasinghe *et al*. (2003) did not found statistically significant differences on bat species richness between farm types, however, total bat activity was significantly higher on organic farms than on conventional farms. In addition to this threat, Stepanian & Wainwright (2018) describe gradual changes in migration and reproductive phenology among the 23 years studied. Although knowledge gaps still exist in nightly, seasonal, and interannual variability in colony size, the phenological changes demonstrated indicate probable and inevitable implications for pest management.

According to previous studies, bat activity levels are negatively affected by landscape homogenization and natural non-crop habitat fragmentation (Obrist *et al*. 2011; Wickramasinghe *et al*., 2003; Williams-Guillén & Perfecto, 2011). Although it is known that this intensification causes spatial mismatch, which consequently disturbs the biological pest control (Costa *et al*., 2020; Paredes *et al*., 2013), there is a lack of knowledge about the temporal synchrony of different species in the same place that also influences the effectiveness of the ecosystem service. In the present study, we investigated the impact that management intensification in Mediterranean olive farms have on the daily and seasonal phenology of a bat species occurrence and its potential impact on biological pest control provided against a major olive pest. Specifically, we compared *Pipistrellus kuhlii* (Kuhl, 1817) and *Prays oleae* (Bernard, 1788) diel activities in three types of olive groves. The categories of olive farms were defined based on their structural complexity. That is, olive groves with low intensive management, therefore with high structural complexity, are grouped in the same category and the remaining olive groves were divided into two more categories according to the same criteria. Then, to determine the potential biocontrol service, we compared the phenological match between the two species. In addition to being able to identify the difference in the time throughout the night when peak activity in different types of olive groves occurs, we have also been able to study the difference between seasons.

Material and Methods

Study area, sampling design and sampling sites characterization

The area under study comprised about 4,000 hectares, throughout Alentejo, southern Portugal (Fig. 1). The regional climate is Mediterranean, characterized by mild and rainy winters and by warm and dry summers (Miranda *et al*, 2002). The research area has a flat topography where the natural and semi-natural vegetation occurs at different densities in a large-scale mosaic of cork (*Quercus suber*) and holm oak (*Quercus ilex rotundifolia*) trees. In this complex agroforestry system, *montado*, the complementary of multiple productions grants the permanence of biodiversity and related ecosystem services (Costa *et al*, 2009; Pinto-Correia *et al*., 2011; Surová *et al*., 2011). Open areas for cattle grazing and cereal farming are also dominant landcover types in region. Currently, extensive areas allocated to olive groves (*Olea europaea L.*) is one increasingly type of landcover.

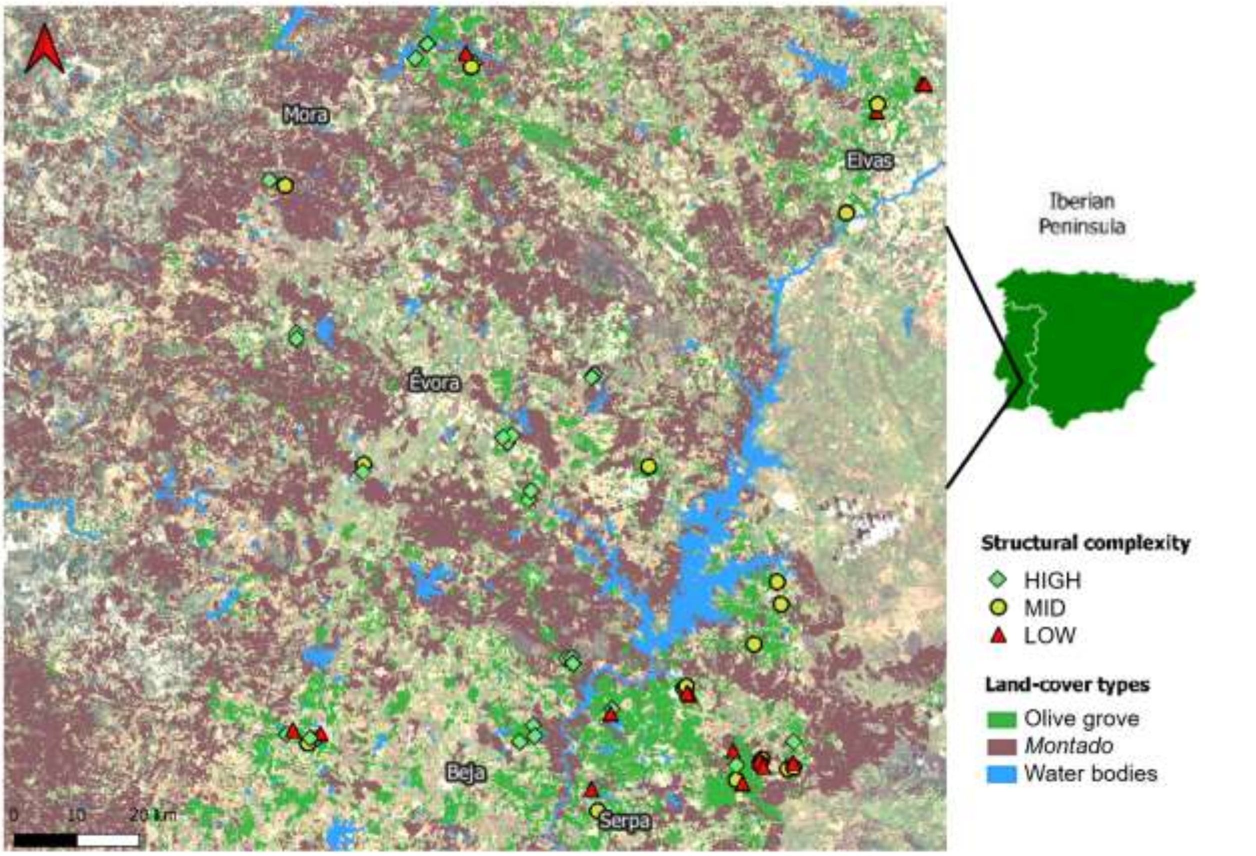

Figure 1. Map of Iberian Peninsula showing the location of the study area in Southern Portugal (right) and the location of the 60 sampling points within the study area (left).

Following a stratified random design, we selected 60 sampling points within 38 olive groves across the study region aimed to represent the greatest possible range of structural complexity (Fig. 1). Each olive grove was characterized using a set of structural characteristics describing both planting patterns and tree features. We used the distance between olive trees along rows (tree_dist), the distance between tree rows (row_dist), the diameter at breast height of olive trees (dbh), the standard deviation of the diameter of the tree trunks (dbh_SD), height of the trunks (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). Within each olive grove, we measured 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). In doing so, two olive trees were randomly selected within 10 m buffers around each sampling point as well as around points 50 m further away following the four cardinal directions.

Olive groves were then assigned to single categories based on their structural features using a multivariate clustering method, the k-means clustering algorithm. The optimal number of clusters was obtained via the gap statistic. This approach clearly identified three types of olive groves, corresponding to olive groves showing a (1) high structural complexity (henceforth referred to as HIGH; i.e., olive groves exhibiting the highest variability in both planting patterns and tree features), (2) intermediate structural complexity (MID; olive groves with intermediate variability) and (3) low structural complexity (LOW; exhibiting the lowest variability). For further detail please refer to Costa *et al*. (2020).

Bat monitoring

Bat activity sampling was performed in three different seasons (mid-April, mid-June, mid-September) during the year of 2017. Recordings were made during three consecutive nights at each location per season. Bat detectors were programmed to start recording 30 minutes before sunset and finish 30 minutes after sunrise. Auto-recording mode was configured for 2 seconds without pre-trigger. Surveys were always conducted when temperature was above 15°C and wind speed below 3.5 m s^{-1}.

We used acoustic recording devices (Peterson D500x; Pettersson Elektronik AB, Uppsala, Sweden) equipped with microphones with a sensitivity range of 10 to 190 kHz. All ultrasound samples were digitized at 300 kHz with a resolution of 16 bits. In order to maximize the number and recording quality of bat passes, detectors were always deployed at about 1.5 - 2.0 meters above the ground, mounted on a tripod, facing upwards at 45° and orientated towards the space between rows of olive trees.

Through a custom-built R script, nineteen spectral and temporal parameters of bat echolocation calls were measured. A semi-automatic classification system (Silva *et al*., 2013, 2014) classified recordings to species level or assigned them to genus complexes, followed by user validation using published data on bat calls (Rainho *et al*., 2011), as recommended by Russo & Voigt (2016). After determining species-specific activity levels, using the number of passes, we selected data only for *P. kuhlii*, the most abundant species in olive production systems in our study region (Herrera *et al*., 2015).

Pest monitoring

To determine the daily patterns of activity of *P. oleae* during each season, we placed modified Delta Traps (ECONEX; model TA118; 20 × 28 × 11,5 cm), equipped with a HD infrared camera (PiNoir, 1, CSI-2). Traps were placed in three previously selected sampling sites, each one corresponding to a type of olive grove structural complexity (i.e., HIGH, MID and LOW). All three traps were photographed hourly for several nights and for each generation we selected data for seven consecutive nights during peak moth activity. Every glued specimen was counted in each photograph. At each location, data from the seven nights was pooled together and the number of glued specimens per hour was obtained. All the traps were baited with synthetic sex pheromone [(Z)-7-14: Ald] contained in a polyethylene capsule (Mazomenos *et al*., 1999) to maximize captures. Additionally, alongside each bat recorder, a non-modified Delta trap baited with synthetic sex pheromone was also deployed to obtain the abundance levels of *P. oleae* regarding each bat sampling.

Data analyses

Along the year, night length varied from 8h to 12h (10.4h +- 1.0h). To account for these differences, time in hours was standardized as percentage of the night, with 0% corresponding to sunset and 100% to sunrise. Considering mean night length, it is possible to infer that 10% of night time corresponds approximately to 1 hour across all seasons.

In our study we considered two dependent variables. One to describe *P. kuhlii* phenology (accum50) and another to describe the phenological mismatch between *P. kuhlii* and *P. oleae* (dif_accum50). We considered peak activity time, for both *P. kuhlii* and

P. oleae, as the time of night (expressed as percentage of the night) where half the passes (*P. kuhlii*) or captures (*P. oleae*) in a particular night occurred. Accum50 was then defined as peak activity time of *P. kuhlii* and dif_accum50 as the difference between peak activity time of *P. kuhlii* and *P. oleae*.

We used generalized linear mixed models (GLMMs) with Gaussian distribution (function lmer; R-package "lmerTest"; Kuznetsova *et al*., 2017) in order to investigate the effect of season, olive groves structural complexity, prey abundance, landscape context (distance to water, forest and olive grove cover- obtained from COS2018) and potential interactions between season and olive groves structural complexity on the phenology of *P. kuhlii* and on the phenological mismatch between *P. kuhlii* and *P. oleae*. The structural complexity of olive groves (HIGH, MID, LOW), the amount of *P. oleae* adults caught at each sampling point (prey abundance) as well as the minimum distance to water and amount of forest cover and olive grove cover were included as fixed effects. To account for any potential constraints related to their spatial distribution, we included the identity of each olive farm as random effect. The best model was obtained using a backward stepwise model selection. Post-hoc pairwise comparisons based on Tukey's tests were applied to test comparisons not evaluated in the main model (function glht; R-package "multcomp"; Horthorn *et al*., 2008). The fit of the GLMM was evaluated by calculating conditional (regarding fixed effects plus random effects) and marginal (regarding only fixed effects) Pseudo R^2 values (function r.squaredGLMM; R package "MuMIn"; Barton, 2019). 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. The analysis were conducted within "R" software environment, version 3.5.3 (http://www.r-project.org).

Results

We recorded a total of 2049 bat passes belonging to *P. kuhlii'*s in the 60 locations that were sampled evenly distributed across seasons: spring (N = 750; 36.9%), summer (N = 753; 37.0%) and autumn (N = 528; 25.9%). In spring, 41 locations, in summer 37 locations and in autumn 47 locations presented at least three *P. kuhlii* passes and were considered for the analysis.

In autumn, *P. kuhlii* activity tends to happen earlier than in the remaining seasons, regardless of the structural complexity of the olive groves. In summer and autumn, the activity of these bats occurs earlier in olive groves classified as LOW, followed by MID and

HIGH, respectively. During spring, we did not identify the same relationship between the variables since the activity occurs later in the MID olive groves (Table 1).

Table 1. Mean (%) ± SE (%) of *Pipistrellus kuhlii* phenology (accum50) and Mean (%) ± SE (%) of phenology mismatch between *Pipistrellus kuhlii* and *Prays oleae* (dif_accum50), per season and structural complexity. HIGH, MID and LOW correspond to olive groves showing a high, intermediate and low structural complexity, respectively.

	Season								
	Spring			Summer			Autumn		
	Structural complexity								
	HIGH	MID	LOW	HIGH	MID	LOW	HIGH	MID	LOW
accum50	53.34 ± 4.76	38.87 ± 3.63	55.27 ± 5.76	59.59 ± 4.42	49.98 ± 5.78	33.72 ± 8.40	36.12 ± 3.57	32.42 ± 3.99	28.89 ± 5.55
dif_accum50	29.58 ± 3.39	39.32 ± 3.63	23.23 ± 5.55	22.83 ± 3.55	28.81 ± 5.78	45.07 ± 8.40	35.55 ± 3.16	38.27 ± 3.99	41.80 ± 5.55

The phenological mismatch between *P. kuhlii* and *P. olea*e (dif_accum50) is the consequence of the alteration of the activity pattern of bats (accum50) according to the season and type of olive grove. The time at which the peak activity of the pest is recorded is 78.2% in the spring, 78.8% in the summer and 70, 7% in the autumn. Thus, the later the activity of *P. kuhlii* occurs, the less is the phenological mismatch between the two species (Table 1). The activity of these bats exhibits an overall trend to occurs earlier with the simplification of the structural characteristics of olive groves and, consequently, the phenological mismatch between the bats and the pest increases (Fig. 2). Considering only the activity and the season, the activity tends to occur later in the summer, followed by spring and finally by autumn. Consequently, the phenological mismatch between the two species is greater in the autumn and lesser in the summer season (Fig. 3).

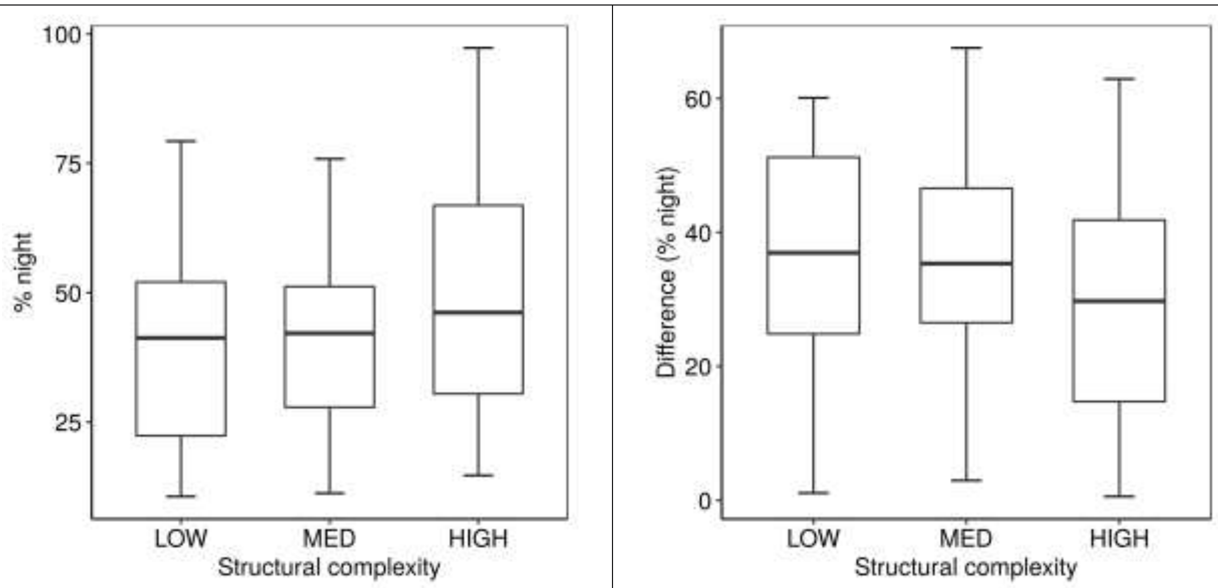

Figure 2. Graphical representation of the effect of the olive groves structural complexity on *Pipistrellus kuhlii* phenology (left) and phenology mismatch between *Pipistrellus kuhlii* and *Prays oleae* (right). A value of 10% corresponds approximately to 1 hour.

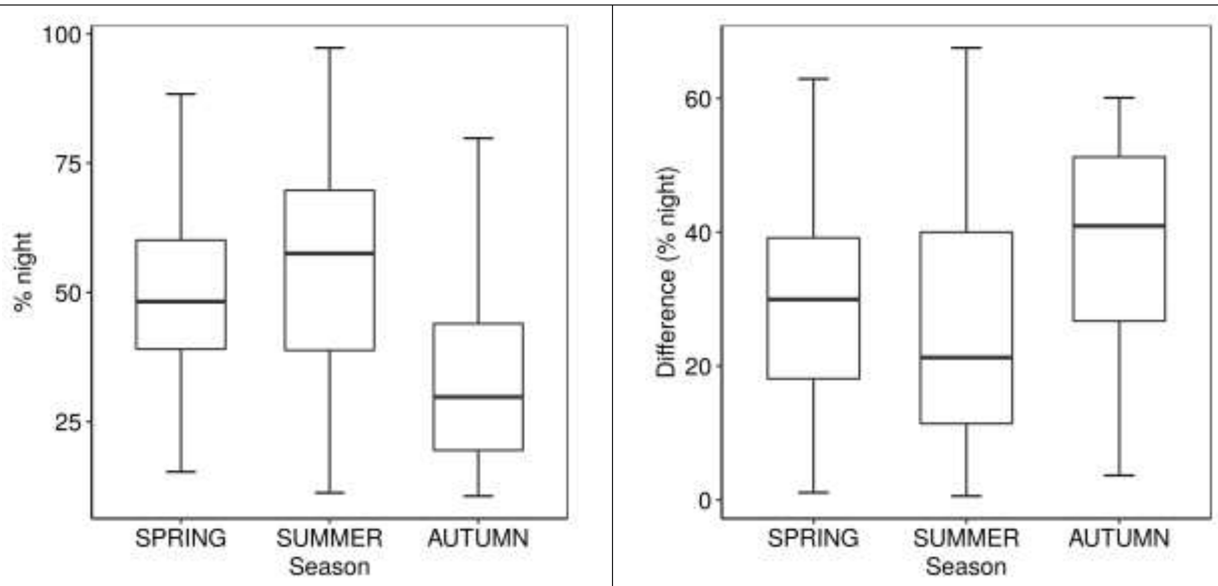

Figure 3. Graphical representation of the effect of season on *Pipistrellus kuhlii* phenology (left) and phenology mismatch between *Pipistrellus kuhlii* and *Prays oleae* (right). A value of 10% corresponds approximately to 1 hour.

The interaction between structural complexity and season is significative both for the phenology of *P. kuhlii* (accum50) and for the mismatch between *P. kuhlii* and *P. oleae* (dif_accum50) (Table 2).

Regarding the biological phenomenon (accum50), during the summer we found significant differences between the structural complexities HIGH and LOW (*p-value*= 0.0186). Considering the phenological mismatch between the two species (dif_accum50) we found significant differences during the summer between the structural complexities MID and LOW (*p-value*= 0.0474) and between the categories HIGH and LOW (*p-value*= 0.0296) (Fig. 4).

Regarding the biological phenomenon (accum50), but this time considering the structural complexity individually, we found significant differences between autumn and spring (*p-value*= 0.0065) in the LOW structural complexity, for the MID structural complexity between autumn and summer (*p-value*= 0.0145) and for the HIGH structural complexity between autumn and spring (*p-value*= 0.0104) and also between autumn and summer (*p-value*= 0.00001). In view of the phenological mismatch between the two species (dif_accum50), when the structural complexity is LOW, there are significant differences between summer and spring (*p-value*= 0.0371) and between autumn and spring (*p-value*= 0.0296). When the complexity is HIGH, we found it between autumn and summer (*p-value*= 0.0158) (Fig. 4).

Table 2. Results of the generalized linear mixed models investigating the effect of season, olive groves structural complexity and potential interactions between season and olive groves structural complexity on *Pipistrellus kuhlii* phenology (accum50) and phen ology mismatch between *Pipistrellus kuhlii* and *Prays oleae* (dif_accum50). Significant effects (P < 0.05) are showed in bold.

	accum50			dif_accum50		
	χ^2	d.f	*p-value*	χ^2	d.f	*p-value*
Structural complexity	4.536	2	0.104	6.032	2	**0.049**
Season	12.535	2	**0.002**	11.147	2	**0.004**
Structural complexity * Season	10.223	4	**0.037**	12.675	4	**0.013**

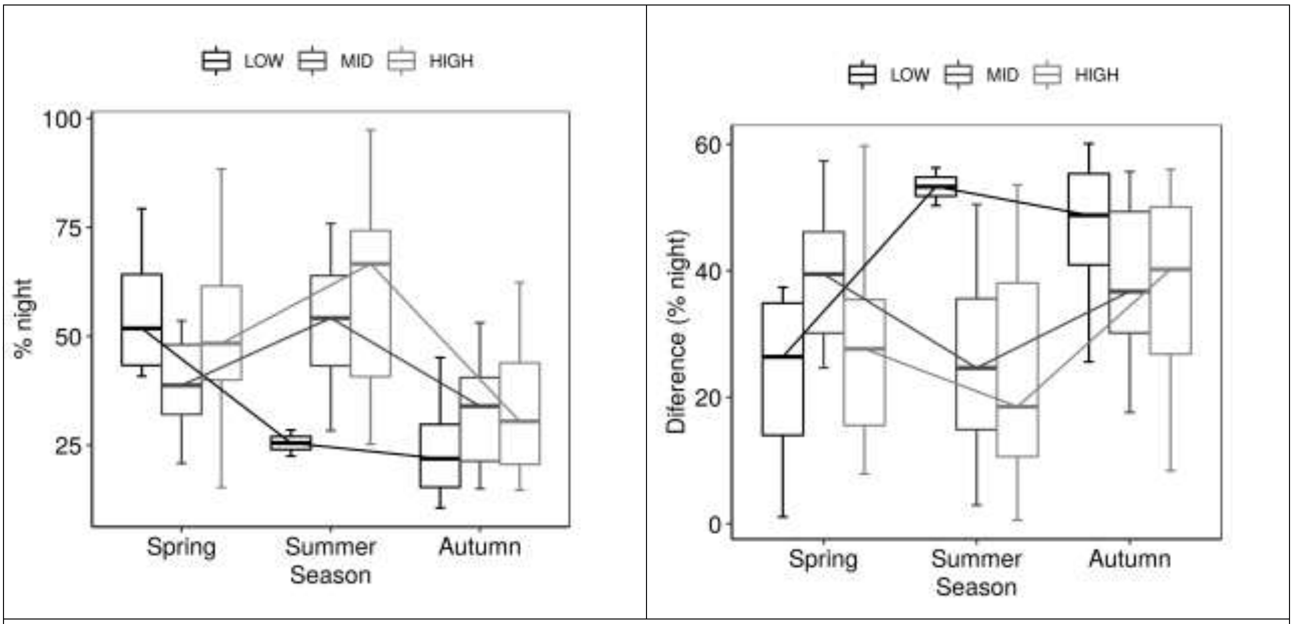

Figure 4. Graphical representation of the interaction between season and olive groves structural complexity on *Pipistrellus kuhlii* phenology (left) and phenology mismatch between *Pipistrellus kuhlii* and *Prays oleae* (right). A value of 10% corresponds approximately to 1 hour.

Discussion

In this study, we investigated the impact that intensification practices have on daily and seasonal phenology of *P. kuhlii* occurrence and its potential impact on biological pest control against the major olive pest *P. oleae*. During three consecutive seasons (spring, summer and autumn), we have sampled *P. kuhlii* and an olive pest, the olive moth *P. oleae*, in olive groves with different structural complexities. Olive production systems were classified based on their structural characteristics: high, mid and low structural complexity. The peak activity of the pest was detected (regardless of the season and the type of olive grove) between seven and nine hours after sunset, which corresponds to approximately between three am and five am.

In respect to structural complexity, during spring and autumn, our data reveals that the structural complexity of olive groves does not influence the time when *P. kuhlii*'s peak activity occurs. However, during summer, in the most intensive olive groves, the peak of activity occurs earlier, approximately three hours after sunset, which corresponds to midnight. Previous studies correlated the marked decrease in bat activity levels with the increasing landscape simplification (Costa *et al*., 2020; Herrera *et al*., 2015; Wickramasinghe *et al*., 2003; Williams-Guillén & Perfecto, 2011), subsequently, olive groves that already have little attractiveness to bats, become increasingly distinct from their natural or semi-natural habitats as management practices intensify. It is known that in addition to bats, there are other species of vertebrates and invertebrates that contribute to the suppression of *P. oleae* (Bento *et al*., 2001a; Villa *et al*., 2016). The effectiveness that each species has in fulfilling this role has consequences for the annual olive harvest. We have no data on the contribution that other species have to the suppression of this moth, but they maybe complement each other to perform this ecosystem service. However, in the most intensive and homogeneous olive monocultures during the summer, in which bats appear considerably earlier than the pest, it is possible that the biocontrol service may be disrupted. Probably with other species, the pattern is similar, since it is known that spatial simplification is correlated with the loss of biodiversity. (Donald *et al*., 2001; Firbank *et al*., 2008; Matson *et al*., 1997; Stoate *et al*., 2001, 2009; Tilman *et al*., 2001; Tscharntke *et al*., 2005). This indicates that the structural complexity should not be reduced too much so that the animals that provide biological pest control have sufficient conditions to inhabit these fields or, at least, to use them as hunting areas.

We also found that the season has a strong influence on the peak activity of these bats. Our results showed that in autumn, the *P. kuhlii*'s activity is always concentrated closer to the beginning of the night. Insectivorous bats emerge from the roosting sites around sunset and, shortly after, happens a first peak of activity. Later, there is a pause period used to digest the food already consumed. Closer to sunrise, a new and smaller peak of activity occurs before returning to the roosting sites. (Knight & Jones, 2009; O'Donnell, 2000). In the autumn, a bimodal pattern of activity was not observed. The second peak of activity was not recorded in any type of olive grove hence, the values are all closer to sunset than in the other two seasons. In relation to spring and summer, temperatures in this third season were lower, specially before sunrise, this being the most likely cause to the observed pattern. Previous studies have shown that temperature is a conditioning factor for the activity of different bat species (Bender & Hartman, 2015; O'Donnell 2000). Another possible factor that may be influencing these results is the annual cycle of the species. Mating takes place between September and October and this is also the period immediately before hibernation (Yom-Tov, 1991). We have no data to explain how these behaviors may cause this unexpected change in peak activity throughout the night, however, it is a hypothesis to consider. On the other hand, in relation to spring and summer, in the autumn the number of this moths is much lower. As generalist predators, the role of bats in controlling prey populations depends on the predator's ability to track and exploit available prey (McCracken *et al*., 2012). If *P. kuhlii* can track spatiotemporal fluctuations in insect abundance within olive groves, it is possible to hypothesize that in the autumn these bats prefer to explore more abundant food resources. Studies on the abundance of other insect species would be needed to prove that this may be a probable cause for the pattern found during autumn.

With these results we conclude that the pest control services may be compromised, due to the phenological mismatch found, in the summer in olive groves with low structural complexity and during autumn in any olive grove regardless of the olive grove's structural complexity. Despite these results, the larvae that exist in the autumn depend on the number of moths that laid eggs in the summer and these depend on the adults that existed in the previous spring. Therefore, this species of bats, by providing biocontrol service in the spring, may be indirectly decreasing the number of moths that exist in the following seasons where the greatest economic damage occurs (Gonzalez *et al*., 2015; Lopes *et al*., 2008; Ramos *et al*., 1998).

Conclusions

It is known that in the case of Mediterranean olive groves, bats can be very helpful for landowners by controlling pest populations that cause economic damage. Previous studies have shown that the intensification of management techniques have a negative impact on the biodiversity of these agricultural fields at a qualitative but also quantitative level. For several reasons already described, *P. kuhlii* is one of the species negatively influenced by the decrease in structural complexity. With this study we realized that the loss of structural complexity also has consequences on daily and seasonal phenology of *P. kuhlii*. As in the conclusion of previous studies, the maintenance of characteristics suitable to the presence of different pest control species is once again essential for this ecosystem service to continue to be performed in these areas.

On the other hand, we also conclude that the peak activity throughout the night of this bat species is strongly influenced by the season. Thus, it is essential to fill the knowledge gap regarding the presence of other species capable of exercising biological pest control throughout the night and throughout the year, in olive groves with different types of management. In this way, it will be possible to assess the complementarity between species throughout the year and ascertaining variables that influence the presence of each one of them in olive groves, to take more correct conservation actions to maintain the ecosystem service.

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