RESEARCH ARTICLE

Temporal mismatches in flight activity patterns between *Pipistrellus kuhlii* and *Prays oleae* in olive farms: Implications for biocontrol services potential

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Abstract

1. Biocontrol services are widely recognized to provide key incentives for bat conservation. However, we have virtually no information on whether and how disruptions in bat-mediated biocontrol services are driven by mismatches between the temporal activity patterns of insectivorous bats and insect pests.

2. We investigated the temporal relationship between the nightly activity patterns of the common pipistrelle bat (*Pipistrellus kuhlii*) and the olive fruit moth (*Prays oleae*). Temporal mismatches between species pairs were estimated as the time difference (expressed as a percentage of the night) at which *P. kuhlii* and *P. oleae* reached 50% of their abundance.

3. The study was carried out during spring, summer, and fall between 2017 and 2019 in 60 olive farms representing increasing levels of structural simplification (as a surrogate of agricultural intensification). Olive farms were classified as exhibiting high (i.e. HIGH olive farms; $n = 27$), intermediate (MID; $n = 18$), and low (LOW; $n = 15$) structural complexity.

4. Temporal mismatches between the activity levels of *P. kuhlii* and *P. oleae* varied between seasons and types of olive farms, being comparatively lower in summer than in spring and fall. Furthermore, summer was the only season in which temporal mismatches between species pairs differed between types of olive farms, with higher temporal mismatches found in LOW than in HIGH and MID olive farms.

5. Overall, our work demonstrates the existence of temporal mismatches between the nightly activity patterns of *P. kuhlii* and *P. oleae*. Furthermore, it demonstrates

that the structural simplification of olive farms increases temporal mismatches between species pairs, particularly in summer when bat-mediated biocontrol services are most needed.

6. *Synthesis and applications.* Future research should consider mismatches between the temporal activity patterns of insectivorous bats and insect pests. Otherwise, the actual impact of agricultural intensification on bat-mediated biocontrol services as well as the economic impact of their loss on the agriculture industry might be underestimated. To enhance biocontrol services, we propose increasing the availability of suitable roosting and foraging sites as well as conserving areas of remnant native woodland and scattered hollow-bearing trees.

1 | INTRODUCTION

Bats are widely recognized as effective agents for controlling insect pests in agroecosystems around the world. Bat-mediated biocontrol services (defined as the impact of bats on the population density of pests) have proven to affect both yield quantity and quality in crops as diverse and economically relevant as cotton (e.g. Boyles et al., 2011), rice (Puig-Montserrat et al., 2015), coffee (Classen et al., 2014), grapes (Charbonnier et al., 2021) and cacao (Maas et al., 2013). Paradoxically, bats are currently under unprecedented threat from agricultural intensification (Voigt & Kingston, 2016). In fact, widespread population declines of many bat species have been reported throughout the world, increasing awareness of concomitant adverse effects on biocontrol services (Williams-Guillén et al., 2016). Previous studies have considered bat population declines in response to agricultural intensification as the main cause of disruption of biocontrol services (e.g. Herrera et al., 2021; Puig-Montserrat et al., 2015; Williams-Guillén et al., 2016). However, despite while for biocontrol services to occur effectively both bats and pests must co-occur in space and time, whether and how the disruption of biocontrol services are driven by temporal mismatches between species pairs still remain understood.

Disruptions in biocontrol services driven by bat population declines in response to agricultural intensification have been reported in agroecosystems around the world. On the one hand, research consistently demonstrates that high-intensity farming systems, characterized by reduced structural complexity and limited key resources such as foraging and roosting sites, exhibit low overall bat activity levels (e.g. Cleary et al., 2016; Faria et al., 2006; Fill et al., 2022; Herrera et al., 2015; Wickramasinghe et al., 2003; Williams-Guillén & Perfecto, 2011). In contrast, low-intensity farming systems, which resemble structural complexity as well as natural and seminatural habitats to some extent, tend to exhibit higher overall bat activity levels and thus greater biocontrol potential (Costa et al., 2020; Maas et al., 2015). On the other hand, agricultural intensification has been reported to increase pest abundance (primarily due to larger farm sizes and higher cropping densities), thereby exacerbating the spatial mismatch between the abundance of bats and pests (Rosemheim et al., 2022).

Despite the importance of understanding the temporal activity patterns of insectivorous bats and insect pests, we have virtually no information on whether and how disruptions in biocontrol services are driven by temporal mismatches between species pairs (Heim et al., 2016). On the one hand, bats are expected to show shorter and later peaks of activity in high-intensity farming systems compared to those in low-intensity farming systems. This is mostly because intensification of management—by increasing farm size and decreasing the availability of suitable roosting sites—will unavoidably force bats to fly over longer distances to reach high-intensity farming systems than those required to reach low-intensity farming systems (Morgado et al., 2022). On the other hand, pest activity timing is expected to be independent of grove-level management intensification, this being exclusively expected to shift across seasons in response to changes in climatic conditions (Chaplin-Kramer et al., 2011). Moreover, seasonal variations in the timing of activity have been widely reported in bats, driven not only by changes in climatic conditions but also by variations in the foraging strategy they exhibit along their life cycles (Heim et al., 2016). As such, the probability of occurrence and severity of mismatches between the temporal activity patterns of bats and pests are expected to be season-dependent (Paquete et al., 2013).

Here, we focus on olive (*Olea europaea* subsp. *europaea*) as a study crop to investigate the impact of agricultural intensification on the timing of flight activity of a common bat species, the Kuhl pipistrelle *Pipistrellus kuhlii* (Vespertilionidae; Kuhl 1817). We investigated flight activity patterns of bats during spring, summer and fall, which correspond to distinct periods of the bat's life cycle; Dalhoumi et al., 2018) and the three main seasonal activity peaks of the olive fruit moth *Prays oleae* (Praydidae; Bernard 1788; González et al., 2015). Our main aim was to investigate potential mismatches

between the temporal activity patterns of *P. kuhlii* and *P. oleae* and their concomitant implications on biocontrol services along an agricultural intensification gradient across seasons. To achieve this, we compare the interspecies flight activity in olive farms representing an increasing gradient of structural simplification (as a surrogate for agricultural intensification; see Costa et al., 2020 for a similar approach), ranging from structurally complex olive farms (low-intensity farming systems) to structurally simplified olive farms (high-intensity farming systems).

2 | MATERIALS AND METHODS

2.1 | Study site and system

This study was carried out between 2017 and 2019 in the Alentejo region of southern Portugal (Figure 1a). Alentejo is the most important olive growing region in Portugal and one of the most important in Europe (Eurostats, 2021). Over the last decade, olive farming in this region has experienced a fast and large-scale agricultural intensification process, with associated impacts on biodiversity and ecosystem services (Jiménez-Navarro et al., 2023; Morgado et al., 2022). This intensification process is characterized by strong changes in grove structure (e.g. increased tree density and reduced tree age) and associated management activities (irrigation, and increased mechanization and use of agrochemical inputs) as well as a strong simplification of olive growing landscapes through homogenization of land cover types (Morgado et al., 2022).

The regional climate is Mediterranean, characterized by mild and rainy winters, as well as warm and dry summers with temperatures commonly reaching up to 40°C. The topography is markedly flat, with altitudes ranging between 100 and 400m. Natural and semi-natural vegetation throughout the study region occurs mainly in the form of extensive savanna-like cork (*Quercus suber* L.) and holm oak (*Q. rotundifolia* L.) forests in varying densities, composing the characteristic Portuguese *montado*, which is classified as a High Nature Value Farming System by the European Environmental Agency (Pinto-Correia et al., 2011). In addition to olives, dominant crop types include almond orchards (*Prunus dulcis*), vineyards (*Vitis vinifera* subsp. *vinifera*), and open areas allocated to cattle grazing and cereal farming.

2.2 | Study system

Prays oleae is one of the main olive pests worldwide (Eurostats, 2019). It is a monophagous species (i.e. it feeds almost exclusively on *Olea*
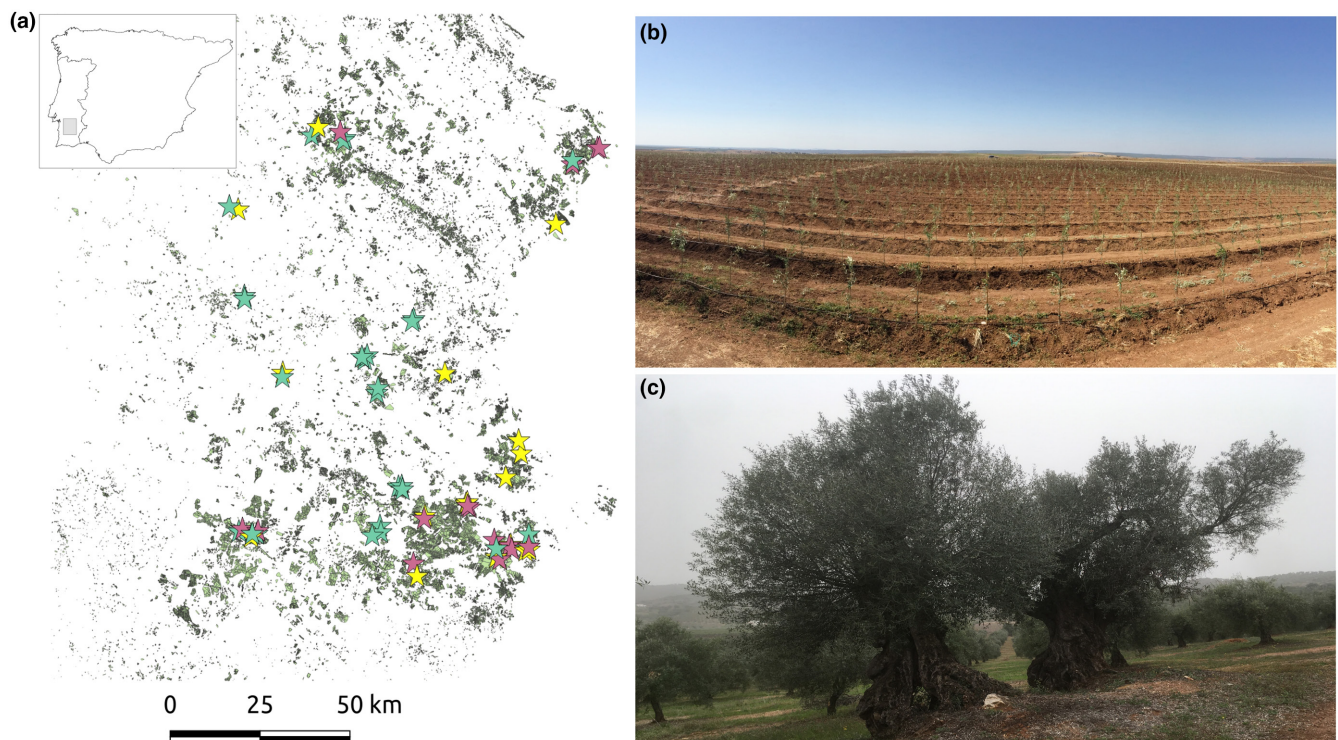
FIGURE 1 In (a) the spatial location of the study region (Alentejo, Portugal), framed into a grey square. In (b), the spatial distribution of the sampled olive farms throughout the study region. Red stars represent olive farms as LOW, while yellow and green stars represent olive farms classified as MID and HIGH olive farms, respectively (see the main text for details). In (c), a recently planted LOW olive farm is shown. It can be appreciated the large extent of the plantation as well as the high density planting system (above 1500 olive trees per hectare). Panel (c) shows a centenary olive tree, which are widely reported to provide suitable foraging and roosting sites for insectivorous bats. The occurrence of these trees typically decreases with increasing management intensification, contributing to the structural simplification of olive farms.

spp.), with three generations per year: phyllophagous, anthophagous, and carpophagous. The eggs of the phyllophagous generation hibernate during winter within the olive leaves. Then, eggs hatch in late winter, and phyllophagous larvae feed on olive leaves until adult emergence in early spring, just before flowering. Adults of this generation lay their eggs on flower buds and the resulting larvae feed on the recently emerged flowers until their pupation in late June. Farmers do not perceive this anthophagous generation as particularly harmful due to the large amount of inflorescences produced by olive trees. In early summer, the resulting adults from this anthophagous generation lay their eggs on still immature fruits, and later the emerged larvae penetrate the olive fruits, bore into the stone, and feed on the seeds. By emerging close to the fruit stems between late summer and early autumn (just before the harvest period in late autumn), they cause premature fruit fall. The carpophagous generation is therefore already considered by farmers as that of highest economic relevance, as they may drive significant yield losses (e.g. Ramos et al., 1998). Adults emerging from carpophagous larvae lay their eggs on olive leaves, closing the annual life cycle. The wingspan of adults of the three generations is between 11 and 15 mm and the body length between 6 and 7 mm. While the abundance patterns of *P. oleae* and their seasonal variations have been extensively investigated in olive farms (e.g. Costa et al., 2020; González et al., 2015; Kumral et al., 2005), there is no information available regarding the daily activity timing of this species.

Pipistrellus kuhlii is one of the most common and abundant bat species in the Mediterranean zone of the Palaearctic region. It is widely considered a habitat generalist, capable of thrive in a wide variety of environments, including both natural and human-impacted landscapes (Amichai & Korine, 2021). Previous studies also suggest that *P. kuhlii* is the bat species most frequently recorded in Mediterranean agroecosystems including olive farms, regardless of their level of agricultural intensification (Herrera et al., 2015). *P. kuhlii* is also considered a trophic generalist, including in its diet a great variety of taxa. Due to its small size (with tail ranging between 30 and 40 mm and wingspan between 210 and 230 mm), most of its prey are small flying insects, including diptera and lepidoptera. *P. oleae* is indeed already known to be part of the diet of *P. kuhlii* (Mata et al., 2021), and recent studies demonstrate that predation rate significantly increases during peaks of insect abundance (author's unpublished data). There is no much published information explicitly focused on the movement ecology of *P. kuhlii*, and only some references about its seasonal activity patterns and habitat use are available (Amichai & Korine, 2021 and references therein). The activity levels of *P. kuhlii* have been reported to vary throughout the seasons according to its life cycle (Maxinová et al., 2016). For example, in spring, the activity levels exhibited by this species are typically low and mostly restricted to the vicinity of maternity sites or nursery colonies. Later, in summer, both activity levels and flight distances increase significantly mainly because juveniles have already gained independence and females can therefore leave the maternity roost to track insects and build up a store of body fat to survive the winter. Then, in fall, activity levels drop markedly and

movements are restricted to particularly suitable resource-rich land cover types such as natural and semi-natural habitats (Dalhoumi et al., 2018). The daily activity pattern of *P. kuhlii* is poorly known, though there is some evidence for an activity peak about 30 min after sunset, which rapidly decreases after 90 min, regardless of season (Dalhoumi et al., 2018).

2.3 | Sampling design

In 2017, following a stratified random design, a total number of 60 sampling points within 38 olive farms were selected across the study region aimed to represent the greatest possible range of structural complexity at grove-level. The maximum number of sampling points within a given olive farm was $n = 2$, always ensuring a distance of 500 in-between them. Each olive farm was characterized using a set of structural features describing both planting patterns and tree characteristics. 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 farm, we measured *tree_dist*, *row_dist*, *dbh*, *t_height*, and *canopy* from ten olive trees in order to obtain representative means and deviations (i.e. *dbh_SD*, *t_height_SD*, *canopy_SD*). In doing so, two olive trees (separated by a distance of 5 m each other) were selected at each sampling point. Additionally, four olive trees within a buffer of 10 m radius around each sampling point were selected following the four cardinal directions. To account for any potential spatial aggregation of tree features within farms, four olive trees using a 50 m buffer were additionally selected ($n = 10$).

For an easier interpretation of the results, we classified olive farms based on their structural attributes (see Costa et al., 2020 for a similar approach). To group olive farms as a function of their structural properties, we used a multivariate clustering method, the k-means clustering algorithm, using function kmeans (R-package "cluster") (Maechler et al., 2022). Therefore, farms within the same cluster are more similar to each other than to farms in another cluster (Celebi et al., 2013). The optimal number of clusters was obtained via the gap statistic (Tibshirani et al., 2001), using function clusGAP (R-package "cluster") (Maechler et al., 2022). This approach clearly identified three types of olive farms, corresponding to olive farms exhibiting high variability in both planting patterns and tree features (hereinafter referred as HIGH olive farms; $n = 27$), an intermediate structural complexity (MID olive farms; $n = 18$), and a significant low variability in both planting pattern and tree features (LOW olive farms; $n = 15$).

The mean pairwise distances between sampling points located within olive farms classified as HIGH, MID and LOW were 69.6 ± 2.6 km (range: 0.7–136.2), 49.2 ± 1.5 km (range: 0.8–117.2), and 46.6 ± 1.5 km (range: 0.5–126.5), respectively. The mean pairwise distances between the different types of olive farms were lower

between HIGH and MID olive farms, mainly because olive farms classified as HIGH were mostly concentrated in the southern region of Alentejo (Figure 1b).

We also accounted for landscape-level structural simplification, by accounting for the diversity of land cover types around each sampling point. Using a geographical information system (QGIS Development Team, 2016), the proportions of the two dominant types of land cover that occur throughout the study region (i.e. olive farms and holm-oak forests) were extracted within a 1000-m circular buffer around each sampling point. To this end, we used the CORINE Land Cover (CLC2018) database. The 1000-m radius was selected based on the foraging distances regularly covered by *P. kuhlii* (Davidson-Watts & Jones, 2006).

2.4 | Bat monitoring

In 2017, the temporal activity patterns of *P. kuhlii* were determined using ultrasound recording devices (Pettersson D500x; Pettersson Elektronik AB, Uppsala, Sweden) equipped with microphones with a sensitivity range of 10–190 kHz. Ultrasound samples were digitized at 300 kHz with a resolution of 16 bits. We consistently used the same auto-recording mode setting for 3 s without pre-trigger. The records were then used to identify species and determine species-specific activity patterns of *P. kuhlii*. Surveys were conducted in spring (mid-April), summer (mid-June), and fall (mid-September) in order to overlap the seasonal peaks of abundance exhibited by *P. oleae*. At each sampling point, a single bat detector was mounted on a tripod at a height of approximately 1.5–2.0 m from the ground, facing upward at 45° and oriented toward the space between rows of olive trees to maximize the number and quality of bat calls. We monitored bat activity during three consecutive nights at each sampling point per season, starting 30 min before sunset and ending 30 min after sunrise (Costa et al., 2020).

To avoid sampling biases, we simultaneously monitored three sampling points belonging to each types of olive farms ($n = 9$) during three consecutive nights per season. Bat passes were defined as a search-phase echolocation sequence of at least three consecutive echolocation calls belonging to *P. kuhlii*. The reason why we focused on search-phase calls instead on feeding buzzes was twofold. First, the number of search-phase calls was much higher ($n = 2039$; see Section 3) than that of feeding buzzes ($n = 148$). Second, we found a strong correlation between the number of search-phase calls and feeding buzzes (linear relationship; $r = 0.76$, p-value < 0.01). For the identification of bat species in the recordings, a convolutional neural network (CNN) was trained using a reference database of European bat echolocation calls. The database consists of 16,000 individual calls from more than 1600 bats (totalling 26 species) recorded in multiple locations in Portugal and Spain. The trained network was obtained using soundClass (Silva et al., 2022), a package R specifically designed to train CNNs from reference databases to automate sound classification and species identification. All predictions of the trained

CNN were manually revised to minimize identification errors. Only bat passes unequivocally identified as belonging to *P. kuhlii* were considered. Bat activity at each sampling point and season was estimated hourly by pooling the number of passes from the three sampling nights.

2.5 | Pest monitoring

In 2017, the abundance of *P. oleae* at each sampling point and season was estimated using Delta traps (ECONEX; model TA118; $20 \times 28 \times 11.5$ cm) baited with species-specific synthetic sex pheromone [(Z)-7–14: Ald]. Pest monitoring was performed in spring (mid-April), summer (mid-June), and fall (mid-September), thereby overlapping the period of bat monitoring (see above). Traps were placed in the field during 15 days per season, and hung about 1.5 m above-ground on the Southwest facing side of the tree canopy. At the end of the 15 days, the number of *P. oleae* individuals captured (glued) in each trap was counted and used to determine the abundance of the pest population at each sampling point and season.

To determine the nightly timing of activity of *P. oleae* we used modified Delta traps incorporating a HD infrared camera (PiNoir, 1, CSI-2), which took pictures of the insect collection platform placed at the bottom of the trap (unpublished data of the authors). Cameras were programmed to take pictures hourly, starting 30 min before sunset and ending 30 min after sunrise. The modified Delta traps were placed in the field for 30 days in spring (mid-April), summer (mid-June) and fall (mid-September), in 2017, 2019 and 2021. In each study year, two modified Delta traps were placed in two olive farms belonging to distinct production systems. The nightly activity patterns of *P. oleae* were determined twice in each farm category ($n = 6$), alternating the type of olive farm across all three study years. The timing of nightly activity of *P. oleae* was estimated hourly by pooling all glued specimens counted per type of olive farm, year, and season.

2.6 | Data analysis

We followed two main steps to determine the species-specific nightly activity timing for *P. kuhlii* and *P. oleae* and, ultimately, the extent of temporal mismatches between their activity patterns (Figure 2). First, the number of bat passes and glued insect specimens were pooled hourly to determine the nightly activity timing of each species per type of olive farm (i.e. HIGH, MID and LOW) and season (spring, summer and fall). Because night-time length in our study region significantly varied across seasons (ranging from 9 to 12 h), the temporal activity patterns for both species were calculated along the percentage of night time with 100% corresponding to the entire period between sunset and sunrise (Buxton et al., 2016). Second, we estimated the percentage of the night at which *P. kuhlii* and *P. oleae* reached 50% of their abundance (i.e. median), using this estimate as the period of at which both species exhibit their highest abundance along the night. This estimate is henceforth referred to as *accum50*
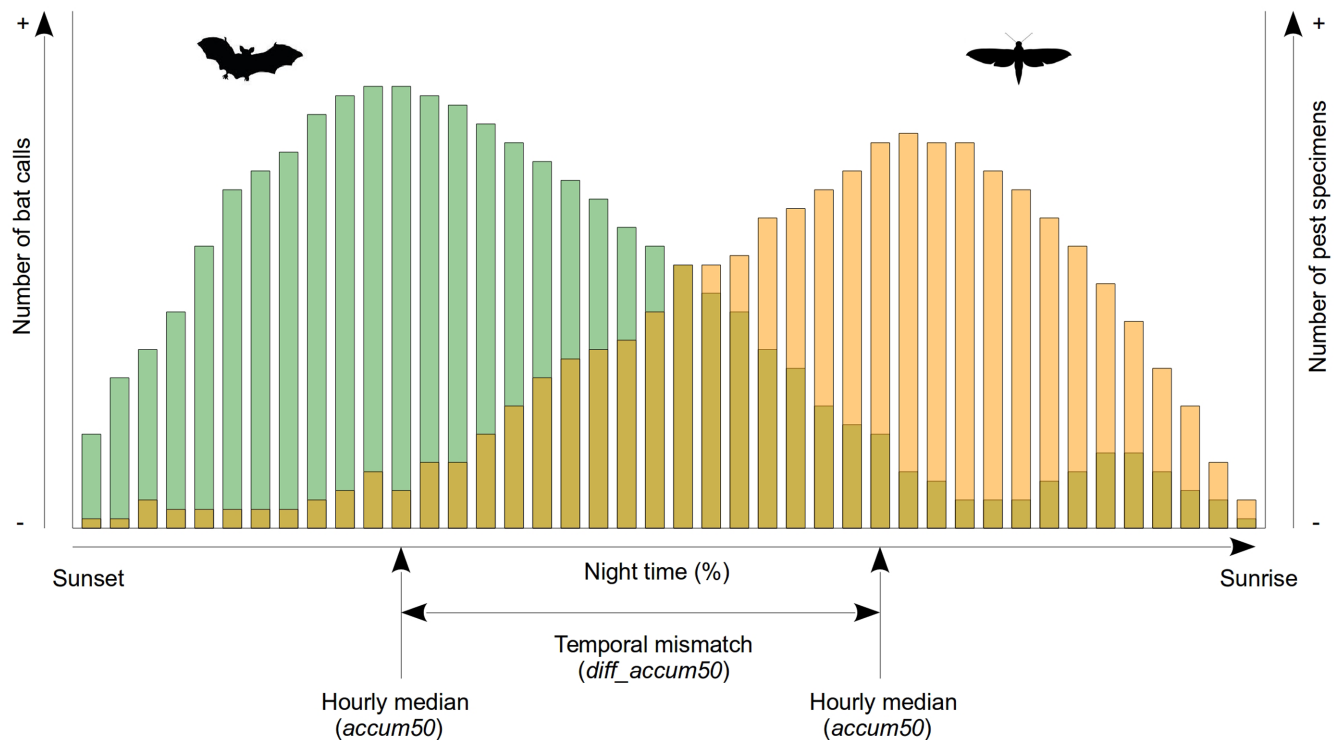
FIGURE 2 Conceptual diagram illustrating our approach to determine mismatches between the flight activity patterns of *Pipistrellus kuhlii* and *Prays oleae*. Vertical (*y*) axes represent the temporal activity patterns of *P. kuhlii* (as estimated by the number of bat calls; green bars; left axis) and *P. oleae* (number of specimens; orange bars; right axis), while the horizontal (*x*) axis represents the night time (as estimated by the percentage of night from sunset). Temporal mismatches in flight activity patterns between *P. kuhlii* and *P. oleae* were estimated as the difference in the nigh time at which each species reached their median abundance.

(Figure 2). The median was used mainly because this parameter is widely recognized to better represent the central tendency of the data than do other parameters (e.g. mean). This is particularly true when the frequency distribution of the data is not symmetrical such is the case of the temporal activity patterns exhibited by both *P. kuhlii* and *P. oleae* in this study (see Section 3). We found no differences between the temporal activity patterns of *P. oleae* across types of olive farms (see Section 3). Thus, a single estimate of *accum50* for *P. oleae* was estimated for each season regardless of the type of olive farm. The difference between *accum50* estimated for *P. kuhlii* and *P. oleae* was used to determine the temporal deviations between their timing of flight activity and, ultimately, the extent of temporal mismatches between species pairs across types of olive farms and seasons. This metric is henceforth referred to as *diff_accum50* (Figure 2).

Generalized linear mixed models (GLMMs) with Gaussian distribution (function lmer; R-package "lmerTest"; Kuznetsova et al., 2017) were used to investigate the effects of the structural complexity of olive farms, season, and their interaction on *accum50* and *diff_accum50*. The sampling site was included as a random effect in these models. Variables on the landscape scale (i.e. the proportion of natural forests and olive farms on the 1000 m scale from sampling sites) and the abundance of *P. oleae* (as a surrogate of prey availability for *P. kuhlii*) were included as covariates. Post hoc pairwise comparisons across types of olive farms and seasons were applied

using Tukey's tests (function glht; R-package "multcomp"; Hothorn et al., 2008). The performance of GLMM models was evaluated by calculating pseudo-r2 values for conditional (fixed effects plus random effects) and marginal (only fixed effects) (function r.squared; R package "MuMIn"; Barton, 2009). Spatial independence between localities in model residuals was assessed applying a Mantel's test for spatial autocorrelation (function mantel.rtest; R package "ade4"; Dray & Dufour, 2007). Ethical approval to conduct this study was not required. Field work within all olive farms was carried out with the landowners' permission.

3 | RESULTS

We recorded a total of 2039 bat passes and 905 insect-glued specimens, all of which were used to determine the temporal activity patterns of *P. kuhlii* and *P. oleae*, respectively (Table 1). Neither the amount of oak forest cover and the olive cover surrounding the sampling sites nor the abundance of *P. oleae* were found to influence the temporal activity patterns of *P. kuhlii* and were therefore excluded from subsequent analysis. Analysis of spatial autocorrelation using Mantel's test yield no spatial signal in model residuals, thereby suggesting the spatial independence of our response variables regardless of study season (*p*-value > 0.05 in all three seasons).

TABLE 1 Parameter estimates (mean±SE) of the night time at which *Pipistrellus kuhlii* and *Prays oleae* reached their median abundances (*accum50*) and the difference between species-specific estimates (*diff_accum50*) across types of olive farms and seasons. Night time was estimated as the percentage of the night from sunset. Between parentheses are reported the number of bat passes belonging to *P. kuhlii* and the number of specimens belonging to *P. oleae* used for parameter estimations.

	Season								
	Spring			**Summer**			**Autumn**		
	Structural complexity			Structural complexity			Structural complexity		
	LOW	MID	HIGH	LOW	MID	HIGH	LOW	MID	HIGH
accum50									
P. oleae	83.83±2.57 (88)			71.07±0.79 (488)			69.42±1.22 (329)		
P. kuhlii	55.27±5.76 (44)	38.87±3.63 (41)	53.34±4.76 (665)	33.72±8.40 (18)	49.98±5.78 (90)	59.59±4.42 (649)	28.89±5.55 (37)	32.42±3.99 (66)	36.12±3.57 (429)
diff_accum50	28.54±5.77	44.95±3.63	33.34±3.84	37.35±8.41	22.22±5.33	18.75±3.09	40.52±5.55	36.99±3.99	34.47±3.09

Overall, we did not find significant differences in the percentage of the night at which *P. kuhlii* reached its median abundance (i.e. *accum50*) between the types of olive farms, ranging between 28.89±5.55 in LOW olive farms in fall and 59.59±4.42 in HIGH olive farms in summer (Table 2; Figure 3). Significant differences in *accum50* were found between seasons, with *P. kuhlii* reaching hourly median abundances earlier in fall (69.42±1.22) than in summer (71.07±0.79) and spring (83.83±2.57) (Table 2; Figure 3). The interaction term between type of olive farm and season was also statistically significant (Table 2). To a large extent, this was related to the earlier activity period exhibited by *P. kuhlii* in LOW olive farms (33.72±8.40) compared to MID (49.98±5.78) and HIGH (59.59±4.42) olive farms in summer (Table 2; Figure 3). *accum50* for *P. oleae* decreased slightly over seasons, ranging from 83.83±2.57 in spring to 69.42±1.22 in fall (Table 2; Figure 3).

The differences in *accum50* estimates between *P. kuhlii* and *P. oleae* (that is, *diff_accum50*) varied significantly between types of olive farms and seasons (Table 2; Figure 4, right panel). Thus, the temporal mismatches between *P. kuhlii* and *P. oleae* were, on average, lower in summer than in spring and fall (Figure 4, right panel). Moreover, the interaction term between type of olive farm and season was found to be statistically significant, mainly related to the higher estimates of *diff_accum50* across types of olive farms that were found in summer than in spring and fall (Figure 4, right panel).

4 | DISCUSSION

We investigated the nightly activity patterns of the common insectivorous bat *Pipistrellus kuhlii* in olive farms representing decreasing grove-levels of structural complexity (HIGH, MID and LOW) during three sampling seasons (spring, summer, and fall). By simultaneously investigating the nightly activity patterns of the olive fruit moth, *Prays oleae*, we also explored concomitant impacts on potential biocontrol services resulting from temporal mismatches between species pairs. We found that temporal mismatches between the activity levels of *P. kuhlii* and *P. oleae* varied between seasons and types of

TABLE 2 Results of the generalized linear mixed models (GLMMs) testing for the effect of type of olive farm, season and its interaction on the night time at which *Pipistrellus kuhlii* and *Prays oleae* reached their median abundances (*accum50*) and the difference between species-specific estimates (*diff_accum50*). Significant effects ($p < 0.05$) are showed in bold.

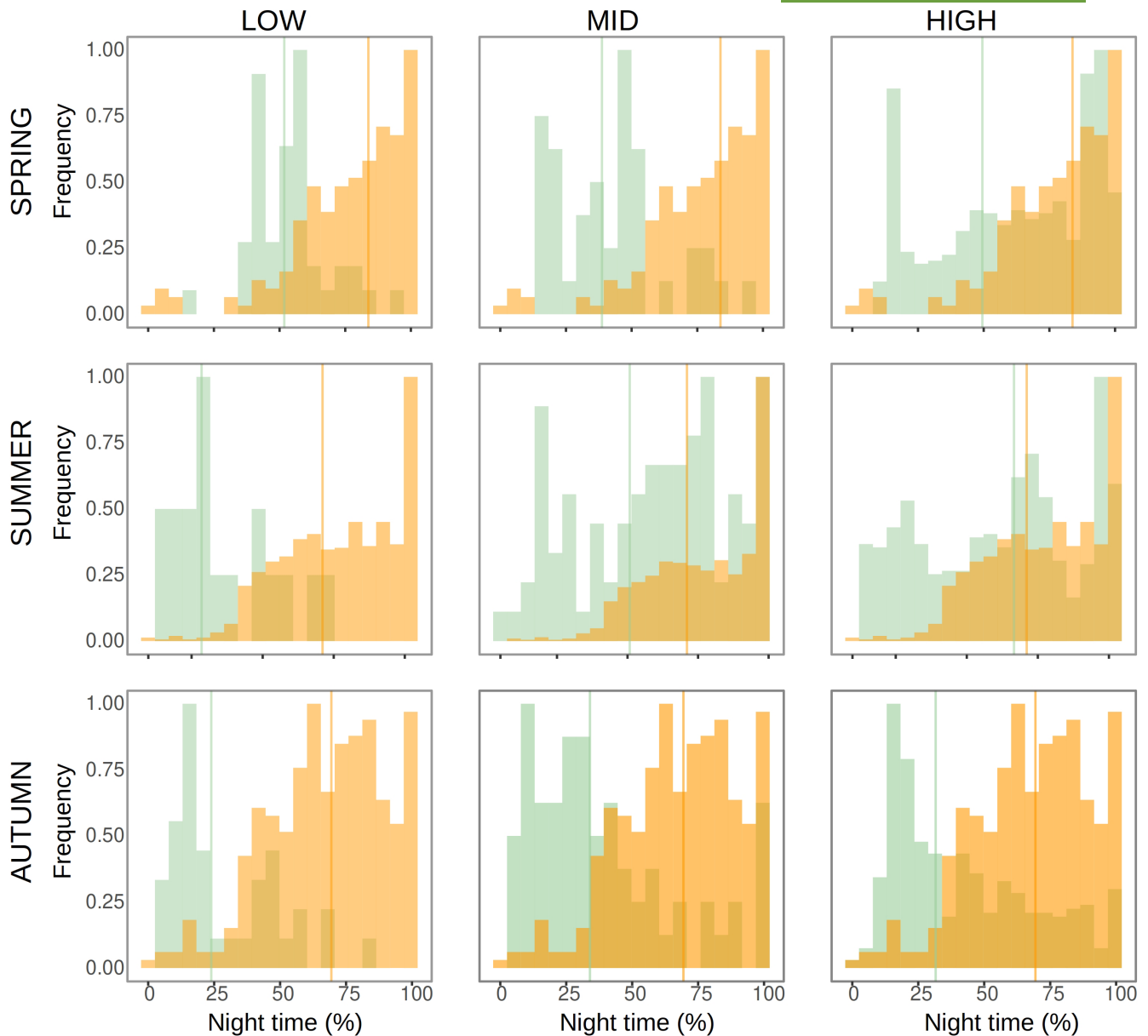|	*accum50*			*diff_accum50*		
	χ^2	df	*p*-value	χ^2	df	*p*-value
Structural complexity	4.536	2	0.104	7.046	2	**0.030**
Season	12.535	2	**0.002**	4.749	2	0.093
Structural complexity × season	10.223	4	**0.037**	12.355	4	**0.015**

FIGURE 3 Temporal patterns displayed by *Pipistrellus kuhlii* (green bars) and *Prays oleae* (orange bars) across types of olive farms (columns) and seasons (rows). Vertical bars represent the frequency of bat calls belonging to *P. kuhlii* (green bars) and the frequency of specimens belonging to *P. oleae* (orange bars), along the night time as estimated by the percentage of night from sunset. Vertical continuous lines depict the night time at which each species reached the hourly median abundance (*accum50*).

olive farms, being comparatively lower in summer than in spring and fall. Furthermore, summer was the only season in which temporal mismatches between species pairs differed between types of olive farms, with higher temporal mismatches found in LOW than in HIGH and MID olive farms.

4.1 | Season-dependent effects of structural simplification on potential biocontrol services

We hypothesized that *P. kuhlii* would exhibit longer periods of activity in structurally complex (i.e. HIGH) olive farms, leading to lower

temporal mismatches with *P. oleae* consistently across seasons. However, our results report a very different response pattern, with significant season-dependent variations in the strength of these mismatches across types of olive farms.

In spring, the temporal activity patterns displayed by *P. kuhlii* did not differ between the types of olive farms. We suggest that this response pattern could be related to the shortage of suitable roosts for bats within olive farms such as ancient large-canopied olive trees and native hollow-bearing trees (Figure 1), something that is true even within low-intensity farming systems (i.e. HIGH olive farms). In fact, the availability of suitable roosts is expected to be particularly relevant for activity timing in spring, mainly
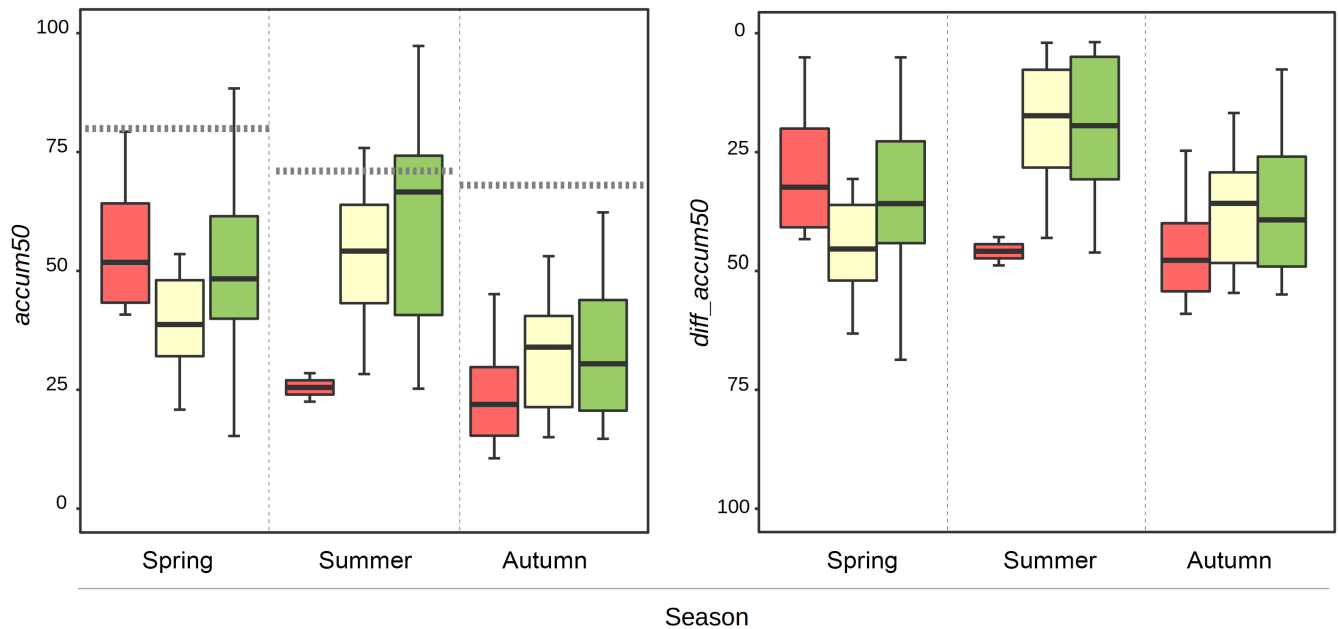
FIGURE 4 Left panel include box plots illustrating the night time at which *Pipistrellus kuhlii* reached the hourly median abundance (*accum50*) across types of olive farms (LOW, red; MID, light yellow; HIGH, green) and seasons. The dashed horizontal lines indicate the night time at which *Prays oleae* reached the hourly median abundance (*accum50*) at each season. Right panel include box plots illustrating the differences in the night time at which *P. kuhlii* and *P. oleae* reached the hourly median abundance across types of olive farms (*diff_accum50*). See the main the main text for details.

because during this season bats tend to restrict their movements to areas close to maternity sites or nursery colonies (Schloesing et al., 2020). In close agreement with this hypothesis, previous studies in the same study region suggest that olive farms support low levels of bat activity (including *P. kuhlii*), regardless of their structural complexity (Herrera et al., 2015). Therefore, our study suggests that the structural simplification of olive farms not only drives spatial mismatches, but also temporal mismatches between the flight activity patterns of *P. kuhlii* and *P. oleae*, ultimately strengthening the loss of biocontrol services potential during a particularly intake-demanding season.

In summer, the temporal activity patterns of *P. kuhlii* and *P. oleae* and, consequently, the strength of the temporal mismatches between species pairs changed markedly. On the one hand, the temporal mismatch between the activity patterns of *P. kuhlii* and *P. oleae* markedly decreased, particularly in HIGH and MID olive farms. To a large extent, this was because the activity levels displayed by *P. oleae* advanced considerably compared to those displayed in spring, while the opposite was true for *P. kuhlii*. At least for *P. kuhlii*, this temporal shift in can be well explained by its higher movement opportunities in this particular season, as bat juveniles have already left the maternity sites. This ultimately allows bats (both juveniles and adults) to forage at greater distances from roosting sites and for longer time periods and, in turn, increases the likelihood of matching the temporal activity patterns displayed by *P. oleae*. On the other hand, the activity patterns displayed by *P. kuhlii* differed markedly between the types of olive farms. Thus, bat activity levels in LOW olive farms concentrated earlier in the night, leading to higher temporal

mismatches compared with HIGH and MID olive farms. We do not have a robust explanation for this response pattern. We suggest that bats, even showing higher movement opportunities in summer (see above), would concentrate their foraging time on comparatively more suitable land cover types such as MID and HIGH olive farms, using LOW olive farms exclusively as commuting areas rather than true foraging habitats (Herrera et al., 2015).

In fall, mismatches between the temporal activity patterns of *P. kuhlii* and *P. oleae* did not differ between the types of olive farms. Moreover, temporal mismatches between species pairs increased markedly in this season, being significantly higher than in spring and summer. To a significant extent, this mostly occurred because the temporal activity patterns of *P. oleae* showed minimal changes, whereas those of *P. kuhlii* exhibited a notable shift toward earlier night-time concentration in all three types of olive farms. This consistent response pattern shown by *P. kuhlii* suggests that environmental constraints other than the structural properties of olive farms are behind the changes in its temporal activity patterns. Thus, for example, in fall temperatures drop much more rapidly than in spring and summer, ultimately leading foraging bats to restrict their activity to the early night, when the temperature is closer to optimal (Gorman et al., 2021). Another potential (and complementary) explanation is that in fall *P. kuhlii* could be tracking other locally abundant olive pests, including the olive fruit fly *Bactrocera oleae*, which has already been reported to be preyed by this bat species (Mata et al., 2021). Unfortunately, we do not have data to test this hypothesis, and further research on this topic is therefore necessary.

4.2 | Landscape-scale effects on potential bat-mediated biocontrol services

We found no effects of the surrounding landscape (that is, the proportion of oak forest cover and olive cover) on the temporal activity patterns of *P. kuhlii* and, in turn, on their potential biocontrol services against *P. oleae*. This suggests that the temporal activity patterns of *P. kuhlii* are mostly determined by the structural complexity of olive farms and, particularly, by the availability of suitable roosting and foraging sites (Davy et al., 2007; Froidevaux et al., 2021; Russo & Jones, 2003). The significance of the surrounding landscape on the potential for bats to provide biocontrol services in olive farms has, in any case, already been demonstrated (Herrera et al., 2021). Previous studies in our study region demonstrate, for example, that the amount of forest cover in the surrounding landscape has a significant positive influence on the activity levels of *P. kuhlii* and a significant negative influence on the abundance of *P. oleae* (Costa et al., 2020). Thus, by promoting high levels of activity of *P. kuhlii*, the amount of woodland cover would increase the potential for biocontrol services, particularly in olive farms in which the temporal activity patterns of *P. kuhlii* match those of *P. oleae*.

4.3 | Integrated pest management of Mediterranean olive farms using biocontrol services as incentives for bat conservation

The spatial match between the activity levels of insectivorous bats and insect pests has been widely used as a surrogate for effective biocontrol services provisioning in agroecosystems worldwide. However, our results conclude that estimations of biocontrol services potential based exclusively on the spatial match between bats and pests may well overestimate service delivery and, consequently, the economic value of bats for the agriculture industry (Boyles et al., 2011). This is because, on the basis of our results, the spatial match between bat and pest occurrence patterns does not guarantee biocontrol services due to temporal mismatches between species pairs. Therefore, future research should consider both spatial and temporal mismatches between the activity patterns of insectivorous bats and crop insect pests, especially if aimed at determining biocontrol services and providing robust estimations of their economic importance in agriculture.

Previous studies in our study region, for example, have reported that the activity levels of *P. kuhlii* consistently decrease with structural simplification of olive farms, while the abundance of *P. oleae* increases at intermediate levels of structural simplification (Costa et al., 2020). Therefore, bat-mediated biocontrol services in olive farms were proposed to be higher in structurally complex olive farms compared to those showing intermediate and low levels of structural complexity, regardless of the season. We now know that this conclusion was somehow overstated. Indeed,

this study suggests that potential biocontrol services by *P. kuhlii* against *P. oleae* can be compromised even in structurally complex olive farms due to mismatches between the temporal activity patterns of both species.

Currently, olive farming covers about 5.0 million acres in Europe alone. If the area devoted to olive production and the intensification of farming practices continues to expand to meet the growing global demand for olive oil, pervasive impacts could arise on bats and the potential biocontrol services they provide. However, our results suggest that biocontrol services provide clear incentives for bat conservation in olive farms by providing biocontrol services in summer when farmers need them most. These incentives, far from being exclusively economic, are also societal, as biodiversity-friendly management practices are rapidly infiltrating the olive industry in response to their increasing demand by olive oil consumers. This is particularly true in our study region, Alentejo, Portugal, where there is increasing social awareness around the cultural, environmental, and economic impact of intensive olive monocultures. At this point, we recognize that the way forward should focus on quantifying the economic impact of bats on the olive industry, as well as obtaining rigorous evidence to motivate olive farmers to integrate bats into daily farm management.

The economic impact of bats on the olive industry in our study region is currently being studied and we hope to have robust conclusions soon. Regarding how farmers can decrease temporal (and spatial) mismatches between bat activity patterns and pests and, in turn, increase biocontrol services potential, we are certain that both the availability of suitable roosting sites and the structural complexity of olive farms are pivotal. The availability of roosting sites can be increased both naturally (by conserving native hollow-bearing trees) or artificially (by placing man-made bat refuges; Mering & Chambers, 2014). To increase the structural complexity of olive farms, we propose to maintain (and even increase) the presence of highly suitable bat foraging sites such as those provided by native scattered trees, which are typically removed or ignored until they eventually die (author's personal observations). In our study region, these scattered trees mainly belong to *Quercus suber* and *Q. rotundifolia*, which are biological legacies retained from preexisting montado-dominated landscapes. Scattered trees will not only facilitate the movement of bats throughout the landscape but will also increase the number of natural refuges for native prey insects, thereby increasing the likelihood of bats entering olive farms and the time spent for foraging purposes.

AUTHOR CONTRIBUTIONS

José M. Herrera, Bruno Silva, Ana Carvalho, Sílvia Barreiro, Gerardo Jiménez-Navarro, Nereida Melguizo-Ruiz, Pedro Beja, Francisco Moreira, Sasha Vasconcelos and Rui Morgado conceptualized the study. Bruno Silva, José M. Herrera and Ana Carvalho collected and analysed the data; José M. Herrera led the writing of the manuscript. All authors critically contributed to the drafts and gave their final approval for publication.

CONFLICT OF INTEREST STATEMENT

The authors declare no conflict of interest.

DATA AVAILABILITY STATEMENT

All baseline data are publicly available via Dryad https://doi.org/10.5061/dryad.0rxwdbs6z (Herrera et al., 2023).

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