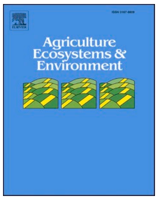
Agriculture, Ecosystems and Environment 343 (2023) 108280

Contents lists available at ScienceDirect

Agriculture, Ecosystems and Environment

journal homepage: www.elsevier.com/locate/agee



Disentangling the seasonal effects of agricultural intensification on birds and bats in Mediterranean olive groves

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ARTICLE INFO

Keywords:
Agricultural intensification
Olive groves
Birds and bats
Grove structural complexity
Biodiversity conservation in agroecosystems

ABSTRACT

Assessing the spatio-temporal impact of agricultural intensification on species and communities is key for biodiversity conservation. Here, we investigated the seasonal effects of olive grove intensification at both local (farming practices and grove structural complexity) and landscape scale (land-cover diversity) on birds and bats, at species and community-level. Both groups were surveyed during spring, summer, and autumn in 60 sites representing varying levels of olive grove intensification throughout the Alentejo region (southern Portugal). At the local scale, the number of chemical applications was used as a proxy for the intensification of farming practices and a Structural Index, which accounted for within-grove variability in tree density and features, was used as a measure of grove structural complexity. At landscape scale, we quantified the proportion of the major land-cover types potentially affecting birds and bats. We found that the abundance of ca. 77% of the species analyzed (ca. 84% and 55% of birds and bats respectively) was negatively related to olive grove intensification in at least one season. The Structural Index was the most influential factor at both species and community-levels, especially for birds, with a consistent and strong effect across seasons. Chemical applications had a stronger negative effect on birds, whereas the amount of olive grove cover had a stronger detrimental effect on bats. Birds and bats showed a variable response to predictor variables depending on the season, particularly for the bat community. Our study shows differences in bird and bat responses associated with the spatio-temporal variability of the agricultural intensification components. On the one hand, birds and bats showed a seasonal pattern of association with the different components of olive grove intensification, probably due to their ecological and biological requirements. On the other hand, the responses of both groups also appear to be scale-dependent: while birds seem to respond to in-farm or local intensification more strongly, bats seem to be more influenced by landscape-scale simplification. Overall, we highlight the importance of the structural complexity of olive groves for birds and bats, an aspect that should be considered in the design of agricultural policies aiming to promote biodiversity conservation.

1. Introduction

Agricultural intensification is widely recognized as a major driver of biodiversity loss worldwide (Foley et al., 2005; Chaudhary et al., 2016), with concomitant impacts on key ecosystem services in agroecosystems (Tscharntke et al., 2005). Despite current agricultural policies promoting biodiversity conservation, the agri-environmental measures implemented until now seem to be often inefficient (Kleijn et al., 2004;

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https://doi.org/10.1016/j.agee.2022.108280
Received 27 May 2022; Received in revised form 12 November 2022; Accepted 15 November 2022

Leventon et al., 2017). To a large extent, this has been attributed to the scarce inclusion of spatio-temporal factors when assessing species responses to agricultural intensification. (e.g., Benton et al., 2003). On the one hand, agricultural intensification takes place at different spatial scales, ranging from local (in-farm intensification as a consequence of management practices) to landscape level (i.e. landscape simplification resulting from reductions in land-cover heterogeneity); on the other hand, agricultural intensification presents a high temporal variability due to the seasonality of farming practices, with effects, in the case of tree-like crops, ranging from permanent (up to several years, such as grove structure) to temporary (few months, e.g., harvesting, tillage or agrochemical applications). This spatio-temporal variability may unevenly affect species responses (Tscharntke et al., 2005; Firbank et al., 2008), which depend on species-specific landscape perception due to their life history traits and mobility (e.g., Burel et al., 2004; Gonthier et al., 2014) as well as the time of year (Payne and Wilson, 1999). It is therefore crucial to include spatio-temporal variability in multi-faceted approaches to better understand the impact of agricultural intensification on biodiversity.

In the Euro-Mediterranean region, biodiversity conservation is particularly urgent in olive (*Olea europaea* L. 1753) production landscapes, because this crop represents a significant share of agricultural land area, estimated at ca. 4.6 million ha in Europe (Eurostat, 2019). Driven by both EU agricultural subsidies and by an ever-increasing global demand for olive oil, farming has shifted from small-scale extensively managed groves (which are of high conservation value, Loumou and Giourga, 2003) to large-scale intensive management (Neves and Pires, 2018), including major changes in agricultural practices such as greater chemical applications, irrigation and mechanization (Beaufoy, 2001). Likewise, olive grove intensification also leads to a strong structural simplification occurring at two spatial scales: (a) at local (in-fam) scale, where groves with old and heterogeneous olive trees planted at low densities (ca. 100 trees ha^{-1}) are replaced by shrub-like trees planted at very high densities (ca. 1500–2000 trees ha^{-1}; Beaufoy, 2001; Diez et al., 2016; Morgado et al., 2022); (b) at landscape scale, where olive grove expansion simplifies surrounding landscapes by reducing the area occupied by other agroecosystems and natural habitats (Stoate et al., 2009; Herrera et al., 2016). This simplification results in landscape homogenization, which acts as an important filter to biological diversity (e.g., Carpio et al., 2016; Gkisakis et al., 2016; Rey et al., 2019). Considering that Mediterranean countries are recognized as biodiversity hotspots (Myers et al., 2000; Cuttelod et al., 2009; Moran and Kanemoto, 2017), olive groves should be the focus of decision-making policies for promoting species conservation throughout the Mediterranean basin.

Birds and bats are the target of conservation measures since they include many threatened species, many of them declining because of agricultural intensification (e.g., IUCN, 2022). Additionally, they are suggested to provide biocontrol services in different crops worldwide (e.g., Maas et al., 2016; Boesing et al., 2017; Kemp et al., 2019), including olive groves (Rey et al., 2019; Costa et al., 2020). Although several works have shown an overall negative effect of olive grove intensification on birds (e.g., Castro-Caro et al., 2014; Morgado et al., 2020; but see Morgado et al., 2021) and bats (e.g., Davy et al., 2007; Herrera et al., 2015), there is a current lack of multi-faceted studies investigating how the different components of agricultural intensification, as well as their spatio-temporal variability, influence both groups simultaneously.

Here, we examined the impact of olive grove intensification on birds and bats, at both species and community levels, during three consecutive seasons. Specifically, we investigated how their occurrence and abundance patterns are affected by in-farm intensification (as resulting from increased agrochemicals use and reduced grove structural complexity) and landscape simplification (as resulting from reduced land-cover heterogeneity). We anticipated an overall negative response of bird and bat communities to both in-farm intensification and landscape simplification, although the strength of such responses is expected to be species-specific (e.g., Ducci et al., 2015; Doherty and Driscoll, 2018). We also predicted that these impacts will be season-dependent, mainly related to the seasonal variations in species composition of bird communities in Mediterranean ecosystems (e.g. Herrera, 1978; Farina, 1989), the adjustment of foraging and activity levels of bats according to their annual reproductive life cycle (Dietz et al., 2009; Heim et al., 2016) and the annual variability in the intensity of farming practices (such the number of chemical applications). Finally, as the responses of both groups to agricultural intensification may be spatial-dependent due to their relative differences in foraging ranges, we hypothesize stronger effects of in-farm intensification on birds and landscape simplification on bats.

2. Methods

2.1. *Study area*

The study was carried out in the Alentejo region, Southern Portugal – one of the main olive-producing regions in Europe (European Commission, 2012; Neves and Pires, 2013) –, in an area of ca. 400,000 ha (see Fig. S1a in Supporting Information). The topography is largely flat, with altitude ranging from 100 to 450 m a.s.l. The climate is typically Mediterranean, characterized by mild winters and a hot dry season from June to September. The landscape is dominated by large patches of olive groves, and, to a lesser extent, open areas allocated to cattle grazing and cereal farming. Natural and semi-natural areas are mostly composed of the characteristic Portuguese 'montado' – evergreen forests of cork (*Quercus suber*) and holm oaks (*Q. rotundifolia*) –, considered a High Nature Value Farming System (Pinto-Correia et al., 2011). Additional land cover types include vineyards (*Vitis* sp.), timber plantations (mainly of *Pinus pinaster* and *Eucalyptus* sp.), riparian vegetation and small urban areas.

The Alentejo region has experienced substantial land-cover changes in the last decades, associated with the intensification and expansion of olive farming (Morgado et al., 2022). In fact, the region currently accounts for ca. 75% of national olive oil production (Rodríguez-Cohard et al., 2020), owing to the plantation of more than 85,000 ha of new intensive and super-intensive groves since 1990, that now represent more than 40% of the region's total olive area (EDIA, 2022; RGA, 2021; Morgado et al., 2022). Despite the rapid process of intensification, olive farming based on traditional and extensive practices still coexists with more intensive modes of production in the region (Silveira et al., 2018), generating a wide intensification gradient. Alentejo is therefore a convenient region to study biodiversity responses to olive grove intensification.

2.2. *Sampling site characterization*

In 2017, a total of 60 sites were selected within 38 olive groves throughout our study region (see Fig. S1a in Supporting Information), representing a gradient of agricultural intensification (Fig. S1b). The maximum number of sites within groves was three, always ensuring a minimum distance of 500 m between them. In each site, olive grove intensification was estimated at two scales: i) in-farm intensification, accounting for potential variability of management at local scale, and ii) landscape simplification due to olive grove expansion at larger scales.

2.2.1. *Local scale: in-farm intensification*

For each site, we decomposed in-farm intensification according to i) farming practices and ii) grove structural complexity. We used the number of chemical applications (i.e., herbicides and pesticides), that varies among seasons (see Table S1a in Supporting Information) as a proxy for farming practices (e.g., Kleijn et al., 2009).

The structural complexity of olive groves was estimated in terms of variables describing both planting patterns and tree features. To do that, we randomly selected five olive trees (one coinciding with the center of the sampling site and four following the four cardinal directions) within a 10 m buffer and took measures related to tree features (i.e., trunk perimeter, trunk height, tree height, canopy area and canopy volume) and their spatial arrangement (i.e., 'area among trees', defined as distance among trees x distance among tree rows, used as a proxy for tree density). As a measure of tree variability, we calculated the mean and the standard deviation of the tree feature variables. We then checked for potential correlations among the 11 variables by computing Pearson's correlation for all possible pairs of independent variables. First, we discarded all pairs highly correlated ($r > 0.6$; Table S1b), and then, in a second round, those variables with lower number of high pairwise correlation among variables. We finally retained six structural variables not highly correlated among them: 'area among trees', mean tree height and standard deviation, mean trunk height and standard deviation and canopy area standard deviation (Table S1c). By normalizing the selected variables, we computed a Structural Index (SI), similarly to the intensity index calculated by Herzog et al. (2006):

$$SI_s = \frac{\sum_{i=1}^{n} (y_i - y_{\min}) \Big/ (y_{\max} - y_{\min})}{n}$$

where SI_s is the overall SI at each site s, y_i the observed value of each structural variable, y_{min} the minimum observed value, y_{max} the maximum observed value and n is the number of structural variables. Higher SI_s values indicate higher grove structural complexity in terms of more scattered, taller and heterogeneous trees, whereas lower SI_s values indicate more aggregated, smaller and homogeneous trees. We considered that the Structural Index can account for the structural complexity of olive groves while avoiding over-parametrized models in statistical analyses, which can lead to more complex interpretations, despite the loss of specific information about the specific structural components.

Since the seasonal number of chemical applications and the SI have $r < 0.6$ (Table S1d), and due to the variability found in both variables across sites (even within traditional EU categories of olive groves; Fig. S2), our approach of assessing the effects of in-farm intensification by separately testing the impact of the two components on birds and bats appears to be appropriate.

2.2.2. *Landscape scale: landscape simplification*

We estimated the amount of olive grove area surrounding sites as a measure of landscape simplification resulting from crop expansion. For each site, we generated a 1-km radius buffer, as this spatial scale is suitable for studying bird and bat responses to landscape heterogeneity (e.g., Sánchez-Oliver et al., 2014; Herrera et al., 2016; Kerbiriou et al., 2018). Land-cover data was obtained from the Land Use and Land Cover of Continental Portugal 'COS2015' (DGT, 2015). For each buffer, we extracted the amount of olive groves, which represent the greatest proportion of land-surface in the study area (54.10% ± 23.53). Likewise, we estimated cover by open areas (22.99% ± 17.85), including grasslands, pastures, cereal crops and other open areas with little or no vegetation, as well as cover by natural and semi-natural woodlands of *Quercus* spp (14.53% ± 17.13; hereafter 'agroforests'). Both were selected as they are frequently used by birds (e.g., Godinho and Rabaça, 2011) and bats (e.g., Fuentes-Montemayor et al., 2013) in Mediterranean ecosystems. Finally, we obtained cover by water bodies (rivers, dams) as an important resource for birds and bats. Data extraction was performed using Quantum GIS v. 3.0.3 (QGIS Development Team, 2016).

2.3. *Bird and bat surveys*

In each site, we surveyed birds and bats during spring (April - May), summer (June - July) and early-autumn (September – October) of 2017. Bird surveys were performed twice (two rounds) for each season and site. Each survey consisted of 10-minute point counts, where the presence of every individual or flock visually or acoustically detected within a radius of 50 m was recorded. For avoiding double counting, we used five distance bands (0 –5 m, 5 – 10 m, 10 – 25 m, 25 – 50 m, > 50 m) to better track bird presence and movements. Additionally, a distance of at least 500 m between sampling sites also avoided double counting across sites. Surveys were carried out in early morning (from one hour after sunrise until midday), avoiding hot weather, rain or strong wind conditions, and always by the same observer (GJ-N). We discarded aquatic species and birds of prey as they were poorly sampled, except for the little owl (*Athene noctua*), due to its strong preference for olive groves and other Mediterranean agroecosystems (Martínez and Zuberogoitia, 2004). Owing to the difficulty in reliably distinguishing *Galerida cristata* from *G. theklae*, both species were pooled into '*Galerida* sp'. For each season and site, we computed species-specific abundance, total abundance, and species richness.

Bat surveys were performed during three consecutive nights for each season and site. Each survey was performed with ultrasound recording devices (Pettersson D500x; Pettersson Elektronik AB, Uppsala, Sweden), equipped with microphones with a sensitivity range of 10–190 kHz following procedures detailed in Costa et al. (2020). Bats were monitored from 30 min before sunset until 30 min after sunrise. Recordings were then used for bat group identifications – i.e., bat species, genera, or phonic groups– using reference collections of calls (Lisón, 2011; Rainho et al., 2013), and to determine species-specific activity levels. For each season and site, we calculated bat richness (estimated by the minimum number of identifiable species recorded) and total activity (as a surrogate of total abundance), by pooling data from the three surveyed nights. While the species belonging to the genus *Rhinolophus* were considered individually when calculating bat richness and total activity, for species-specific analyses these species were pooled into '*Rhinolophus* sp' due to their low detectability in sampling sites and their similarity in ecological requirements (Dietz et al., 2009). For species-specific analyses, we discarded phonic groups including different genera (e.g., *Nyctalus leisleri / Eptesicus* sp.).

2.4. *Statistical analyses*

We performed analyses at species-level, aimed at detecting species-specific responses to olive grove intensification, and at community-level, aimed at detecting general properties related to community assembly. Species-level analyses were performed separately for each species, considering either bird abundances or bat activity (bats) as response variables. Analyses at community-level considered either total abundances or species richness for each taxonomic group. In the case of bats, we measured "total activity", but we will use, hereafter, 'total abundance' for a similar terminology used for birds. Analyses were independently computed for spring, summer, and autumn, aimed at testing potential differences in the effects of olive grove intensification across seasons. Before analyses, we checked for possible outliers, homogeneity of variance and collinearity among the explanatory variables (Zuur et al., 2010), with a maximum value of $r < 0.6$. Statistical analyses were performed in R 3.5.2 (R Core Team, 2019).

2.4.1. *Species-level*

In each season, we analyzed the abundance and activity of bird and bat species occurring in at least 10% of sites ($n = 6$). As recommended by Zuur et al. (2009) and O'hara and Kotze (2010), we did not transform count data because conclusions could differ when analyzing transformed and untransformed data. We therefore fitted raw abundances to Generalized Linear Mixed Models (GLMM) using the 'glmmTMB' package (Brooks et al., 2017), which allows to fit mixed models and specifying the most adequate family distributions used for count data and zero-inflation (Zuur et al., 2009; Coly et al., 2016). In all models, we included 'Chemical applications', 'Structural Index', 'Olive grove cover', 'Agroforest cover', 'Open areas' and 'Water bodies' as predictor variables (all previously scaled). We additionally included 'farm' and 'site' as random factors, to account for similarities between sites belonging to the same olive grove (farm), and to control for repeated visits or nights in the same site.

For each species and season, we performed preliminary analyses aimed at retaining the most appropriate family distribution fitting count data (i.e., Poisson or Negative Binomial). To accomplish this, we compared the most parsimonious model with Poisson or Negative Binomial distributions based on Akaike Information Criterion corrected for small sample sizes (AICc) value (Burnham et al., 2011). Model selection was computed using *dredge* function in the 'MuMIn' package (Barton, 2018). When models with Poisson distributions were overdispersed, we used the Negative Binomial distribution. If overdispersion persisted, models were discarded. Models additionally included the zero-inflation parameter when needed.

Once the family distribution was selected, for each species and season we computed a set of candidate models with all possible combinations of predictor variables. We subsequently retained models with ΔAICc < 2, which are considered equally supported or not differentiable from the top ranked model (Burnham and Anderson, 2002). To avoid models with 'uninformative parameters' (*sensu* Arnold, 2010), we only retained those with informative parameters (i.e., with 95% confidence intervals not overlapping zero). For species models not fulfilling this criterion, we selected the null model when included in the top rank (ΔAICc value was < 2), or the best model (lowest ΔAICc value) when the null model was excluded. In any case, we fully report all models with ΔAICc values < 2, including the null model.

The most parsimonious models were subsequently evaluated and validated by diagnostic tools in the 'DHARMa' package (Hartig, 2019), testing for uniformity, dispersion, outliers and zero inflation by means of residual simulations ($n = 1000$). We also tested for multicollinearity among predictor variables by using the 'performance' package (Lüdecke et al., 2021). Additionally, spatial correlation tests were performed (DHARMa Moran's I test). Models were discarded in case of violation of any assumption.

2.4.2. Community-level

Species richness and total abundance of birds and bats were used to analyze the potential effects of in-farm intensification and landscape simplification at community-level. These measures included all species registered in our sampling sites. To control for the proportionally high effect of the most abundant species within the community, we computed the 'standardized relative abundance' for each species using the *decostand* function in the 'vegan' package (Oksanen et al., 2018). We use the Hellinger transformation, which applied the squared root to the proportional abundance values of each species, giving less weight to abundant species (Legendre and Gallagher, 2001). For each season and site, we then calculated the 'total abundance' as the summed 'standardized relative abundance' of all the species.

To test for potential seasonal differences at community level, we first performed post-hoc comparisons of species richness and total abundances among seasons using Tukey contrasts with the *glht* function in the 'multcomp' package (Hothorn et al., 2018). We subsequently analyzed species richness and total abundance following the procedure described for species (see above). For birds and bats, we checked for the family distribution best fitting total abundance (i.e., Gaussian and gamma distributions) and species richness (Poisson distribution in every case). In addition, we estimated the seasonal importance of each predictor variable, by calculating the relative importance of the variables included in the selected species-specific abundance models. For species with only one competing model, a relative importance value of '1' was assigned to the variables present in those models. If there was more than one competing model, we computed model-averaging (*model.avg* function in the 'MuMIn' package), estimating the relative importance of each predictor variable by summing the Akaike weights over all models in which the variable was present. For each season, we then computed the mean importance values of the variables analyzed for birds and bats as a measure of the importance of in-farm intensification and landscape composition at community level, as well as its potential seasonal variability.

3. Results

3.1. General results

Overall, 14,609 birds belonging to 61 species were counted (Table S2a), of which 37 were registered in $n \geq 6$ sites in at least one season and round. Bird species richness was higher in summer (pairwise summer-spring z-value $= 5.597$, $p < 0.001$) and autumn (pairwise autumn-spring: z-value $= 3.576$, p=0.00102) than in spring (Fig. 1a). Bird total abundance was higher in summer than in spring (pairwise summer-spring: z-value $= 6.290$, $p < 0.001$) or autumn (pairwise autumn-summer: z-value $= -5.040$, p=0.009; Fig. 1b).

Overall, 5329 bat passes belonging to 27 groups were recorded (Table S2b). A total of 11 identifiable groups were registered –all single species along with groups including species belonging to the same genera: eight single species, two genera (*Eptesicus* sp. and *Rhinolophus* sp.) and one phonic group (*M. myotis / M. blythii*). We did not find seasonal differences in bat richness ($p \geq 0.19$; Fig. 1c), while total activity was higher in spring (pairwise autumn-spring: z-value $= -4.174$, $p < 0.001$) and summer (pairwise autumn-summer: z-value $= -4.141$, $p < 0.001$) than in autumn (Fig. 1d).

3.2. Influence of olive grove intensification on bird and bat communities

Overall, olive grove intensification, mediated by in-farm intensification (i.e., number of chemical applications and Structural Index) and/or landscape simplification (i.e. amount of olive grove cover), was negatively related to 37 of the 48 analyzed bird and bat species (ca. 77%; Table 1 and S3; abundance models of bird and bat species are detailed in Tables S4 and S5 respectively).

3.2.1. Responses to in-farm intensification

In-farm intensification was negatively related to the abundance of 28 bird and bat species in at least one season (ca. 58% of total species; Table S3), with 18 bird species and three bat species positively responding to the Structural Index, and 13 bird species and one bat species negatively responding to the number of chemical applications (Fig. 2; Table 1 and S3). The Structural Index was consistently and positively related to the abundance of five bird species across seasons (i.e., short-toed treecreeper *Certhia brachydactyla*, blue tit *Cyanistes caeruleus*, great tit *Parus major*, Eurasian collared dove *Streptopelia decaocto* and blackbird *Turdus merula*), while only the short-toed treecreeper was negatively related to chemical applications in all seasons (Table S3). Conversely, the Structural Index was negatively related to the abundance of five species (i.e., greenfinch *Chloris chloris*, linnet *Linaria cannabina,* goldfinch *Carduelis carduelis*, the crested/Thekla larks *Galerida* sp., and lesser noctule *Nyctalus leisleri*) in at least one season, while chemical applications were positively related to two bird species (i.e., the linnet and the goldfinch) and three bat species/groups (i.e., *Myotis daubentonii*, *M. escalerai* and *Nyctalus leisleri;* Table S3). At community level, the Structural Index was positively related to bird richness and abundance in all seasons and to bat activity in spring and summer (Tables S3a). Chemical applications were negatively related to bird abundance in spring and summer (Table S3b), while no effects were found for the bat communities.

3.2.2. Responses to landscape composition

Landscape-scale variables were related to the abundance of 35 bird and bat species in at least one season (ca. 73% of total species; Table S3). Greater cover by olive groves was negatively related to the abundance of eight bird species and three bat species (Fig. 2; Table 1 and S3). Conversely, the abundance of six bird species increased with cover by

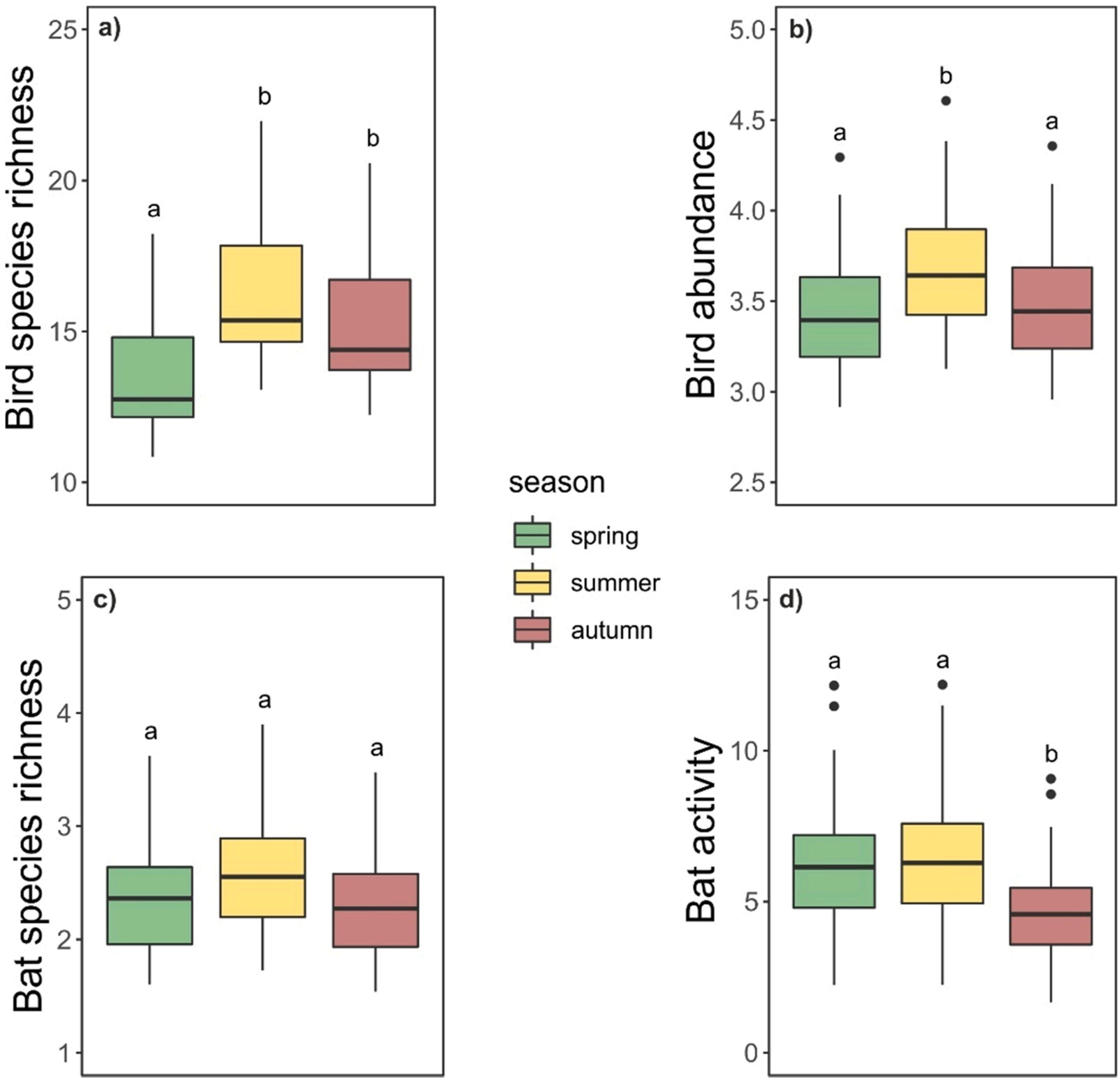

Fig. 1. Effects of season on bird (a-b) and bat (c-d) species richness and total abundance. Different letters denote significant differences between seasons ($p < 0.05$). Values of variables in y-axis are the model predicted values.

olive groves, whereas no positive response was found for bats. Bird and bat richness were lower in sites surrounded by larger amounts of olive groves in summer and autumn (Table S3). The total abundance of both groups was lower in such sites, although only in summer (Table S3).

Regarding the remaining land-cover types, cover by open area and agroforests was related to the abundance of 20 (ca. 42% of total species) and 18 (ca. 38%) species, respectively. Birds were most related to agroforests (i.e., 16 species, 11 of which were positively related; Fig. 2a), whereas bats were most related to open areas (five species, two positively and three negatively related; Fig. 2b; Table S3). Bird species richness and total abundance were higher in sites surrounded by more agroforests, but only in spring, while bat species richness and total abundance were unrelated to agroforests and open areas (Table S3).

A total of nine bird and one bat species had higher abundances in sites with larger amounts of water bodies in at least one season (Fig. 2; Table S3). Eight bird species were negatively related to water bodies, and no response was found for bat species. Species richness and total abundance were never related to the amount of water bodies (Table S3).

3.3. Seasonal effects of olive grove intensification on bird and bat communities

The influence of in-farm intensification and landscape composition on birds and bats was variable depending on the season at both species (Fig. S3; Table S3) and community-levels (Fig. 3). For birds, the Structural Index was the most important factor in each season, particularly in summer. Chemical applications and the amount of olive groves were most important in autumn and spring, respectively. The importance of open areas and agroforests on bird communities was higher in spring, and the amount of water bodies had consistent importance, although slightly higher in spring.

Chemical applications were the most important factor affecting bat communities, although only in summer. The importance of the Structural Index was relatively high across seasons, with a peak in spring, while the importance of landscape cover by olive groves peaked in autumn. The highest importance of the open areas was in spring, whereas the amount of water bodies had minimal importance for bats (and only in autumn).

Table 1
Bird and bat species affected by at least one component of olive grove intensification ('OG intensification component') in at least one season: olive grove expansion ('grove expansion'), number of chemical applications ('chemicals') or the structural complexity of the grove ('structure'). Values of 'Agricultural impact score' were obtained from IUCN (2022) and vary between 0 (no impact) to 8 (high impact). 'Threat category' and population trend ('Pop trend') of the species were also obtained from IUCN. We only presented those species detected in n ≥ 6 sites in at least one season. We used information of IUCN about *Galerida cristata* and *Galerida theklae* for '*Galerida* sp', *Saxicola torquatus* for *Saxicola rubicola* (previously lumped together) and *Rhinolophus ferrumiquenum*, *R. hipposideros*, *R. mehelyi* and *R. euryale* for *Rhinolophus* sp.

	Group	Threat category	Pop trend	Agricultural impact score	OG intensification component
Alecoris rufa	bird	Near Threatened	decreasing	6	structure
Apus apus	bird	Near Threatened	decreasing	0	chemicals
Carduelis carduelis	bird	Least Concern	increasing	0	grove expansion
Cecropis daurica	bird	Least Concern	increasing	0	structure
Certhia brachidactyla	bird	Least Concern	increasing	5	structure / chemicals
Cisticola juncidis	bird	Least Concern	stable	4	structure / chemicals
Columba livia domestica	bird	Unknown	unknown	0	chemicals
Columba palumbus	bird	Least Concern	increasing	0	structure / chemicals
Cyanistes caeruleus	bird	Least Concern	increasing	0	structure
Cyanopica cooki	bird	Least Concern	increasing	5	structure / chemicals
Delichon urbicum	bird	Least Concern	stable	0	grove expansion
Emberiza calandra	bird	Least Concern	decreasing	6	grove expansion / chemicals
Erithacus rubecula	bird	Least Concern	stable	0	chemicals
Ficedula hypoleuca	bird	Least Concern	decreasing	0	structure
Galerida sp	bird	Least Concern	–	6	chemicals
Hirundo rustica	bird	Least Concern	decreasing	6	grove expansion
Lanius senator	bird	Near Threatened	decreasing	6	structure
Linaria cannabina	bird	Least Concern	increasing	6	grove expansion
Lullula arborea	bird	Least Concern	decreasing	6	structure
Luscinia megarhynchos	bird	Least Concern	stable	5	structure
Merops apiaster	bird	Least Concern	stable	5	structure
Parus major	bird	Least Concern	stable	0	structure
Phylloscopus trochilus	bird	Least Concern	decreasing	5	chemicals
Pica pica	bird	Least Concern	stable	0	grove expansion
Saxicola rubicola	bird	Least Concern	decreasing	6	grove expansion / chemicals
Serinus serinus	bird	Least Concern	decreasing	0	grove expansion
Streptopelia decaocto	bird	Least Concern	stable	0	structure / chemicals
Sturnus unicolor	bird	Least Concern	stable	0	structure
Sylvia melanocephala	bird	Least Concern	stable	0	structure / chemicals
Turdus merula	bird	Least Concern	increasing	4	structure
Upupa epops	bird	Least Concern	stable	6	structure
Myotis daubentonii	bat	Least Concern	stable	0	grove expansion
Nyctalus leisleri	bat	Least Concern	unknown	0	grove expansion
Pipistrellus kuhlii	bat	Least Concern	increasing	0	structure / chemicals
Pipistrellus pipistrellus	bat	Least Concern	stable	4	structure
Pipistrellus pygmaeus	bat	Least Concern	unknown	0	structure
Rhinolophus sp	bat	Near Threatened / Vulnerable	decreasing	–	grove expansion

4. Discussion

Overall, our findings are in line with previous studies evidencing a strong negative impact of olive grove intensification on birds and bats (e.g., Muñoz-Cobo et al., 2001; Davy et al., 2007; Herrera et al., 2015; Solomou and Sfougaris, 2015; Morgado et al., 2020, but see Morgado et al., 2021). However, to our knowledge, this is the first work in such agroecosystems demonstrating season-dependent effects of in-farm intensification and landscape simplification on these two taxonomic groups, simultaneously. Further, our study gets to distinguish the effects caused by agrochemical applications from those derived from grove structural complexity. Examining the impact of specific components of agricultural intensification is of great relevance in management decisions aimed at promoting animal conservation in agroecosystems.

4.1. In-farm intensification

Our findings highlight the importance of the structural complexity of olive groves in explaining species composition and abundance of birds and bats at both species and community-level, affecting the abundances of ca. 44% of the species analyzed in at least one season. Although other studies also found positive effects of structural features of olive groves on birds (e.g., Morgado et al., 2020, 2021) and bats (e.g., Costa et al., 2020), our results further stress their role on both groups ahead of other components of agricultural intensification such as farming practices or landscape simplification. Structurally complex olive groves could play a similar role to natural or semi-natural ecosystems in the Mediterranean region, as reported by Solomou & Sfougaris in Central Greece (2015), likely providing a broad span of biological resources for insectivorous species, such as birds and bats (e.g., Zahn et al., 2009).

Regarding farming practices, our results show negative effects of chemical applications on birds and bats, consistent with previous studies (e.g., O'Shea and Johnston, 2009; Geiger et al., 2010; Jeliazkov et al., 2016; Barré et al., 2018). However, the number of chemical applications had a lower influence than the Structural Index, both at species- (ca. 39% vs 54% of the species analyzed respectively) and community-levels (Table 1 and S3, Fig. 3). In our case, whilst the lack of detailed information about the quantity, timing or type of agrochemicals used could have compromised the ability to detect their influence on birds and bats, these groups seem to be more influenced by the permanent impact of grove structure, rather than by occasional disturbances during the year caused by farming practices. Contrary to what we expected, there were positive effects of chemical applications on two bird (namely, the linnet and the goldfinch) and three bat species (*Myotis daubentonii*, *M. escalerai* and *Nyctalus leisleri*). These finches and the two *Myotis* species seem to be flexible in terms of adaptation to agricultural disturbances, as they commonly forage in conventional and intensified fruit orchards, including olive groves (e.g., Muñoz-Cobo et al., 2001; Davy et al., 2007; Morgado et al., 2020, 2021). Plausible explanations could include indirect correlations (not tested in this study) between chemical inputs

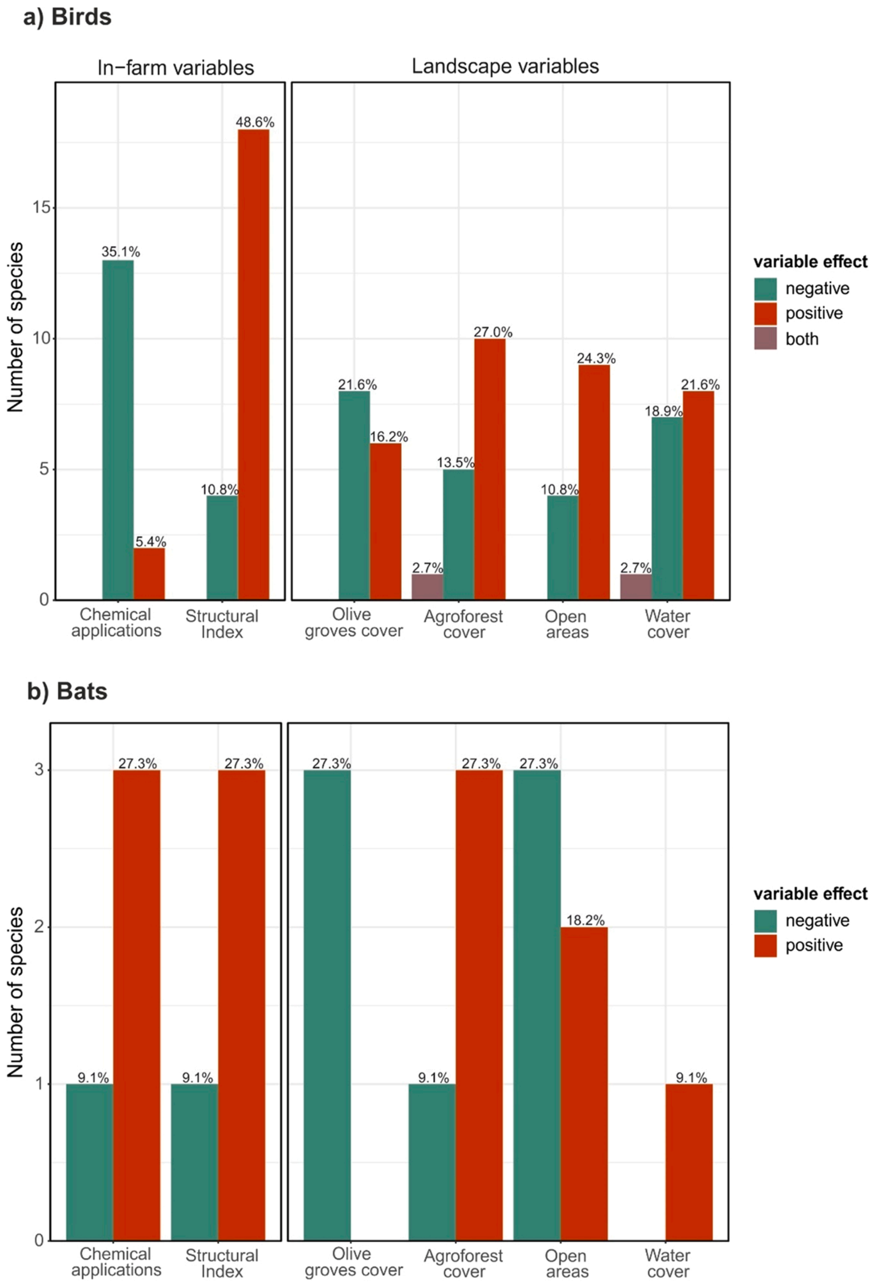

Fig. 2. Number and percentage of species of a) birds and b) bats influenced by predictor variables in at least one season, distinguishing between in-farm and landscape variables. Each variable was additionally split into two according to the sign of their effect (either positive, negative or both) on species abundance models.

and other farming practices that could benefit these species. Note that species such as the linnet appears to be affected by agricultural practices (IUCN, 2022), and therefore identifying which components of in-farm intensification threaten such farmland species may be an urgent task.

4.2. *Landscape composition*

Our work also reflects the impact of landscape simplification on birds and bats, in line with other studies (e.g., Rey et al., 2019; Costa et al., 2020; Morgado et al., 2020, 2021). Specifically, we found that larger amounts of olive groves were negatively related to birds and bats at species (ca. 23% of species analyzed) and community-level (species richness and total abundance in summer and autumn). However, the strong influence of olive grove structure evidenced a potential shortcoming in our study at landscape-level: the difficulty to estimate the degree of grove structural complexity by using land-cover maps. Future works should aim at finding potential valid proxies or metrics of grove structure in remote sensing measures (i.e., photogrammetry, LiDAR) in conjunction with in-field measures to distinguish among groves with different structural complexity. In our study site, larger areas of olive groves usually match with intensive orchards with lower structural complexity (Rallo et al., 2013; Neves and Pires, 2018), suggesting that this limitation did not affect our key results in any significant way.

Regarding other dominant land-cover types, both birds and bats were positively influenced by open areas and agroforests, as suggested for other Mediterranean ecosystems (e.g., Godinho and Rabaça, 2011; Costa et al., 2020; Morgado et al., 2020). These results thus suggest that olive grove-dominated landscapes may affect birds and bats due to the loss of preferential habitats, especially for those species requiring additional resources provided in adjacent areas. Far from being trivial, olive grove expansion through the simplification of agricultural landscapes may be an important driver of biodiversity decline, occurring at

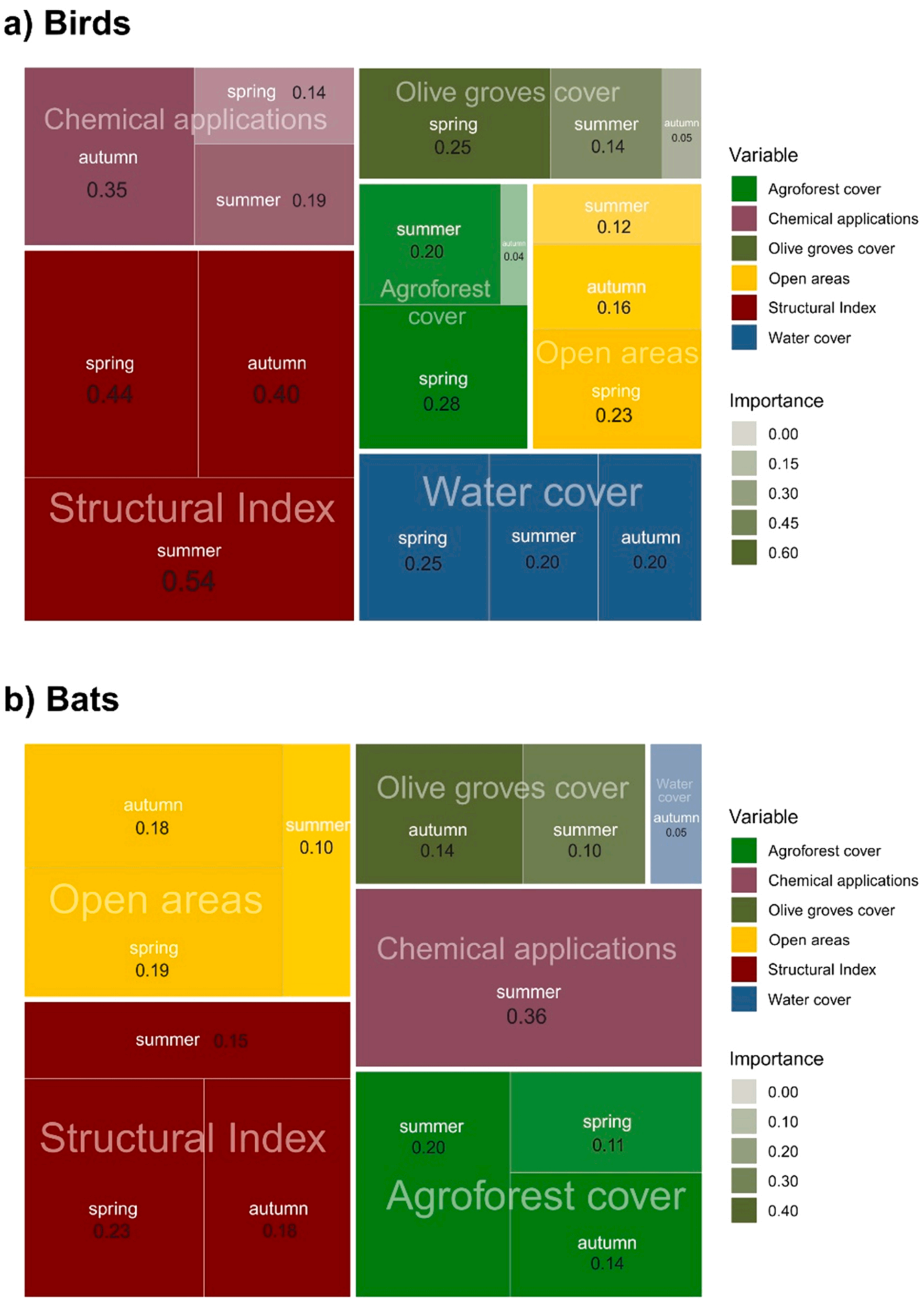

Fig. 3. Treemaps showing the seasonal importance of in-farm intensification of olive groves and landscape composition on a) bird and b) bat communities. For each season, the value in each box reflects the average of the relative importance of each explanatory variable on bird and bat species (see text for a detailed explanation).

regional (e.g., Herrera et al., 2016; Morgado et al., 2022) and global scales (Sirami et al., 2019). Additionally, crop heterogeneity has been linked to increased biodiversity in agricultural landscapes, even buffering the effects of in-farm intensification (Gámez-Virués et al., 2015). Thus, upholding heterogeneous mosaics in agricultural landscapes seems to be crucial for maintaining species-rich communities in Mediterranean ecosystems.

Our study also evidences the importance of water bodies for birds, with surprisingly minimal effects on bats, despite their strong dependence on aquatic habitats (Salvarina, 2016; Amorim et al., 2018). Due to a large proportion of small ponds and troughs throughout the region, water was probably not a limiting factor for flying vertebrates in the study area. While there is water provisioning for birds and bats, larger amounts of water bodies could have no (or even negative) influence on the studied species.

4.3. *Differences between bird and bat responses*

Despite the commonalities in bird and bat responses to the components of olive grove intensification, we also found relevant differences between them as expected. Firstly, although both groups were strongly influenced by grove structural complexity, birds responded more strongly than bats. The bird community positively and consistently responded to structurally complex olive groves regardless of the differences in species composition across seasons, suggesting a permanent effect of grove structure on the whole community.

At landscape-level, bird and bat abundances seem to be similarly influenced by landscape composition, but they differed regarding the influence of olive groves. Proportionally, more bat species were negatively affected than birds (ca. 27% vs ca. 22% of species, respectively), suggesting a stronger response of bats to landscape simplification. Bats have higher mobility and wider home ranges than birds, which could reflect a stronger influence of landscape context when foraging, as evidenced in Mediterranean agroecosystems (Froidevaux et al., 2017; Costa et al., 2020). Our results are consistent with other studies revealing that, regardless of the impact arising from landscape context (e.g., Jeliazkov et al., 2016), bird communities seem to be more influenced by other components of in-farm intensification such as farming practices or olive grove structure (e.g., Castro-Caro et al., 2014; Rey et al., 2019; Morgado et al., 2020, 2021). Likewise, agroforests seem to positively affect both groups similarly (ca. 27% of species of both groups), whilst open areas seem to have a stronger influence on birds. In particular, we found that species usually associated to forests such as tits (*Paridae*) or the nightingale *Luscinia megarhynchos* were positively affected by agroforests as well as by the Structural Index (Table S3), highlighting the potential similarity between agroforests and structurally complex olive groves for birds. Greater structural differences between olive groves and open areas may promote higher richness and abundance of birds owing to increased habitat heterogeneity (Santana et al., 2017).

4.4. Seasonal differences in bird and bat responses

Our findings also revealed a seasonal pattern in bird and bat responses to in-farm intensification and landscape composition, which probably reflected changes in the ecological requirements of individual species across seasons. This seasonal response was also observed at the community level, especially for bats, which were strongly influenced by grove structure in spring, chemical applications in summer, and the amount of olive groves in autumn (Fig. 3b). This seasonal variability is probably due to the adjustment of bat activity according to their annual reproductive cycle (Dietz et al., 2009; Heim et al., 2016). Although to a lesser extent, bird communities also showed seasonal variation in responses to olive grove intensification. Olive groves had the strongest importance in spring, grove structure in summer, and chemical applications in autumn. These results are in line with other studies reporting seasonal variability in agricultural effects on avian diversity (e.g., Laiolo, 2005). A possible limitation of this study was the lack of sampling during winter, despite the importance of olive groves for wintering birds (e.g., Rey, 2011; Morgado et al., 2021) and the potentially high activity of bats during this period in Mediterranean ecosystems (e.g., Mas et al., 2022). However, we think our option was justified, because we were interested on the effects of chemical applications, which are very low (pesticides were not even applicated) during winter in our study area. In any case, although our results highlight the importance of considering seasonality when assessing the impact of agricultural intensification on species and communities, future studies may include annual population monitoring for a better understanding of the seasonal effects of agricultural intensification on biodiversity.

4.5. Further research and implications for biodiversity conservation

This study reveals the importance of identifying the different components of agricultural intensification affecting biodiversity, as well as the spatial and temporal variability of these effects. Our findings suggest that, among the different components of olive grove intensification, grove structure appears to be the most influential factor affecting birds and bats. Further studies should aim to investigate the influence of specific elements of crop spatial structure such as tree features and planting patterns on species distribution and community responses, by differentiating it from other components of agricultural intensification (e.g., Bailey et al., 2010). In addition, new analyses testing both additive and multiplicative effects of grove structure with other farming practices and landscape context should be performed for a better understanding of the impact of agricultural intensification on biodiversity.

Furthermore, our results also revealed species-specific responses to different intensification components, which is crucial to better implement targeted measures for their conservation. Bird species such as the Red-legged Partridge *Alectoris rufa* or the Woodchat Shrike *Lanius senator*, assessed as ’Near threatened’ in Europe and with agricultural intensification as a main threat (IUCN, 2022), seem to be influenced by grove structural complexity (Table 1); *Rhinolophus* sp, with European species categorized as ‘Near threatened’ or even ‘Vulnerable’, seem to be negatively affected by the expansion of olive groves; or species not analyzed due to their low presence such as the European Turtle-dove *Streptopelia turtur*, species ‘Vulnerable’ with high impact of agricultural intensification (IUCN, 2022), which was only present in olive groves with high values of Structural Index (17A, 18A, 19A, 23A, 24A, 26A, 37A and 38A; Fig. S2). Additionally, we evidenced the need for including or modifying the threat level of agricultural intensification for several species, at least in Mediterranean ecosystems: we found 37 species (31 birds and 6 bats) negatively affected by agricultural intensification, whilst only 17 include this factor at least as a minor threat according to the IUCN (Table 1). Hence, agricultural intensification should be included as a threat for species such as the short-toed treecreeper or tits among birds, or pipistrelles among bats.

Promoting more sustainable farming practices to enhance biodiversity conservation in agricultural landscapes is among the priorities of the European Common Agricultural Policy (CAP). However, some measures implemented by the CAP seem to be ineffective (Pe’er et al., 2014; Leventon et al., 2017). Multi-faceted studies assessing the spatio-temporal impact of specific intensification components on biodiversity constitute an important tool to generate valuable ecological information that can be used to create or fine-tune agricultural policy mechanisms focusing on reconciling agricultural production with biodiversity conservation (e.g., agri-environmental schemes). As this study suggests, the structural complexity of permanent crops appears to play a key role in enhancing biodiversity in agroecosystems and, consequently, in promoting ecosystem service provision. The maintenance of certain levels of structural complexity within olive grove-dominated landscapes should therefore be a priority for agricultural policies targeting biodiversity conservation and food security objectives in these Mediterranean ecosystems.

CRediT authorship contribution statement

GJ-N, JMH and JR-P conceived and designed the study; GJ-N collected bird data; BS and SB collected bat data; GJ-N, NM-R, SV, BS, SB and JMH collected the environmental variables; GJ-N performed analyses; GJ-N wrote the manuscript with substantial contributions from JMH, JR-P and NM-R. All the authors contributed to the final version of the manuscript.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data Availability

Data will be made available on request.

Acknowledgements

This research was funded by the Portuguese Foundation for Science and Technology (FCT) under PTDC/AAG-REC/6480/2014 project and by the regional European Program Alentejo 2020 through the ALT20-03-0145-FEDER-343 000008 project. The study has also received funding from the project SHOWCASE within the European Union's Horizon 2020 Research and Innovation Programme under grant agreement No. 862480. Authors were supported by the FCT through fellowships and contracts SFRH/BD/133017/2017 (GJ-N), SFRH/BD/137803/2018 (BS), SFRH/BD/121388/2016 (SV), SFRH/BD/99746/2014 (RM), IF/00001/2015 (JMH) and IF/01053/2015 (FM). JRP was funded from "la Caixa" and "Caja Navarra" Foundation, LCF/PR/PR13/51080004. We also thank the property owners and managers for granting us access to the surveyed olive groves.

Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.agee.2022.108280.

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