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RESEARCH PAPER

Olive grove intensification negatively affects wintering bird communities in central Spain

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Abstract

Agricultural intensification is a persistent and growing threat to biodiversity worldwide. Olive groves cover extensive areas in the Mediterranean basin and play a fundamental role as refuge and wintering quarters for many bird species, but the effects of their current intensification on bird communities remain unclear. This study aims to evaluate the response of wintering birds to the management of olive groves with different degrees of intensification (traditional, intensive and super-intensive management) in central Spain. Based on two bird censuses conducted in 25 groves in early and late winter, we examined the influence of habitat structure and composition at different spatial scales on species richness and abundance of the entire farmland bird community, and of the diet-based functional groups. Total species richness tended to decrease with intensive olive grove management, probably due to reduced habitat heterogeneity, whereas total abundance did not, indicating the capacity of intensive and super-intensive olive groves to sustain large numbers of wintering birds. The negative effect of intensification was particularly evident in frugivore species richness, while frugivore abundance was positively (but marginally) associated with olive fruit availability. Granivorous species were positively associated with lower vegetation cover, but insectivorous species did not respond to intensification gradients. Species richness and abundance (total and by diet-based functional groups) also decreased from early to late winter, which may be due to the effect of olive harvest, but also to an extreme cold event. Overall, our findings show how olive grove intensification and the associated management practices result in significant changes in habitat structure and composition at different spatial scales, thus affecting wintering bird communities.

Keywords: Agricultural intensification; Bird diet-based functional groups; Landscape context; Mediterranean agroecosystems; Microhabitat; extreme cold event

Introduction

Olive groves are one of the main agricultural systems in the Mediterranean basin, a region considered a biodiversity

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hotspot (Myers et al., 2000; Rey, 2011). Covering over 4.6 million hectares, olive groves are the most widespread woody crop in Europe, with great environmental, socioeconomic and cultural importance (Loumou & Giourga, 2003; Rey et al., 2019). Spain produces 60% of the olive oil in the European Union (EU) and 45% worldwide (MAGRAMA, 2015). The EU production is growing due to economic incentives of the Common Agricultural Policy (CAP) and the increasing global demand for olive oil (Morgado et al., 2022), which leads to the expansion of irrigated olive groves, the overuse of fertilizers and pesticides (Guerrero-Casado et al., 2021), and the homogenization and simplification of these landscapes (Castro-Caro et al., 2015). In contrast, low intensity, rainfed olive groves under traditional management constitute key biodiversity refuges (Bouam et al., 2017). These olive crops are characterized by larger old trees (easily over 100 years) holding a more complex morphology (two or three trunks with many hollows and cavities) that act as refuge and high-quality habitats for arthropods (de Paz et al., 2022), reptiles (Carpio et al., 2017; Kazes et al., 2020), small mammals (Barão et al., 2022) and birds (Morgado et al., 2020). Yet these traditional olive groves are currently threatened by their conversion into irrigated, more densely planted and intensively managed olive groves (ESYRCE, 2020; Guerrero-Casado et al., 2021; Morgado et al., 2022), compromising their essential ecosystem services.

Birds are widely considered indicators of ecosystem health due to their trophic breadth, as well as their physiological and behavioral responses to changes in the environment (Bouam et al., 2017; Rey et al., 2019). Agroecosystems harbor a significant portion of European bird species (Emmerson et al., 2016), but agricultural intensification severely impacts farmland birds, whose populations are declining throughout Europe (PECBMS, 2021; Traba & Morales, 2019). Olive groves are a key breeding and wintering habitat for birds, providing refuge and food for sensitive species (Muñoz-Cobo Rosales et al., 2001; Assandri et al., 2017). For example, olive groves harbor important wintering populations of frugivorous species due to the highly nutritious and energetic olive content (Rey, 2011; Morgado et al., 2021). Furthermore, the presence of insects in olive groves also attracts many insectivorous bird species (Poirazidis et al., 2011), which can contribute to the control and regulation of agricultural pests (Rey-Benayas et al., 2017; Herrera et al., 2021; but see Martínez-Núñez et al., 2021). In winter, many bird species alternate their diet or adopt mixed diets, thus directly benefiting from the availability of fruits in olive groves (Senar & Borras, 2004; Rey, 2011).

Intensively and super-intensively managed olive groves are characterized by increased mechanization, irrigation and agrochemical inputs (Castro-Caro et al., 2014a; Guerrero-Casado et al., 2021). This management is generally associated with landscape simplification and the cultivation of smaller and more simple trees, related to both the canopy and the trunk (Guerrero-Casado et al., 2021), thus contributing to the decrease of trophic and spatial resources required by birds (Castro-Caro et al., 2015). Therefore, intensive or super-intensive olive groves can become less suitable habitats for bird species or even ecological traps (Castro-Caro et al., 2014b). As a result, bird communities in olive groves can be dominated by common granivorous generalist species to the detriment of the rarest species of greater conservation interest, while functional diversity is reduced (Morgado et al., 2020).

Thus, determining how species richness and abundance of farmland birds in olive groves are affected by agricultural intensification is key for designing efficient conservation plans. Indeed, the number of studies on the effect of intensification on birds in olive groves has rapidly grown in recent years (see e.g., Rey et al., 2019; Martínez-Núñez et al., 2020, 2021; Morgado et al., 2021). Despite the relevance of winter for bird survival (Morales et al., 2015), studies of winter bird communities in olive groves are still scarce. Morgado et al. (2021) found that olive grove intensification favored frugivorous birds through increased olive availability, whereas structural grove features played a secondary role, and reported a negative effect of intensification on non-frugivorous bird species. Birds might respond to changes in crop management, such as grass cover and herbicide use (Muñoz-Cobo & Montesino, 2003; Castro-Caro et al., 2014b), as well as in landscape heterogeneity (Rey et al., 2019). To counteract the effects of intensification and enhance biodiversity in agricultural systems, agri-environment and climate change-mitigation CAP measures currently include the maintenance of grass cover (Castro-Caro et al., 2015; Rey et al., 2019). Studying their effects on bird communities is therefore crucial to orient these measures in the future CAP 2023−2027, so that olive farming can be environmentally, socially and economically sustainable.

Here, we evaluate the response of farmland bird communities and of diet-based functional groups to intensification in olive grove management and to habitat features at microhabitat, field and landscape scales. We expect a decrease in bird species richness and abundance with increased intensification as well as changes in species richness and abundance associated with vegetation structure and composition at local and landscape scales. We also expect frugivorous species to be more strongly affected by olive grove management than other diet-based functional groups.

Materials and methods

Study areas

The study was carried out in 25 olive groves (10 traditional, 7 intensive and 8 super-intensive) located in central Spain Fig. 1. The climate is dry continental Mediterranean, characterized by cold winters and hot, dry summers, with an average annual temperature of 15 °C and annual precipitation ranging 350−600 mm (Rojo & Pérez-Badia, 2014). The landscape is dominated by arable and woody crops,

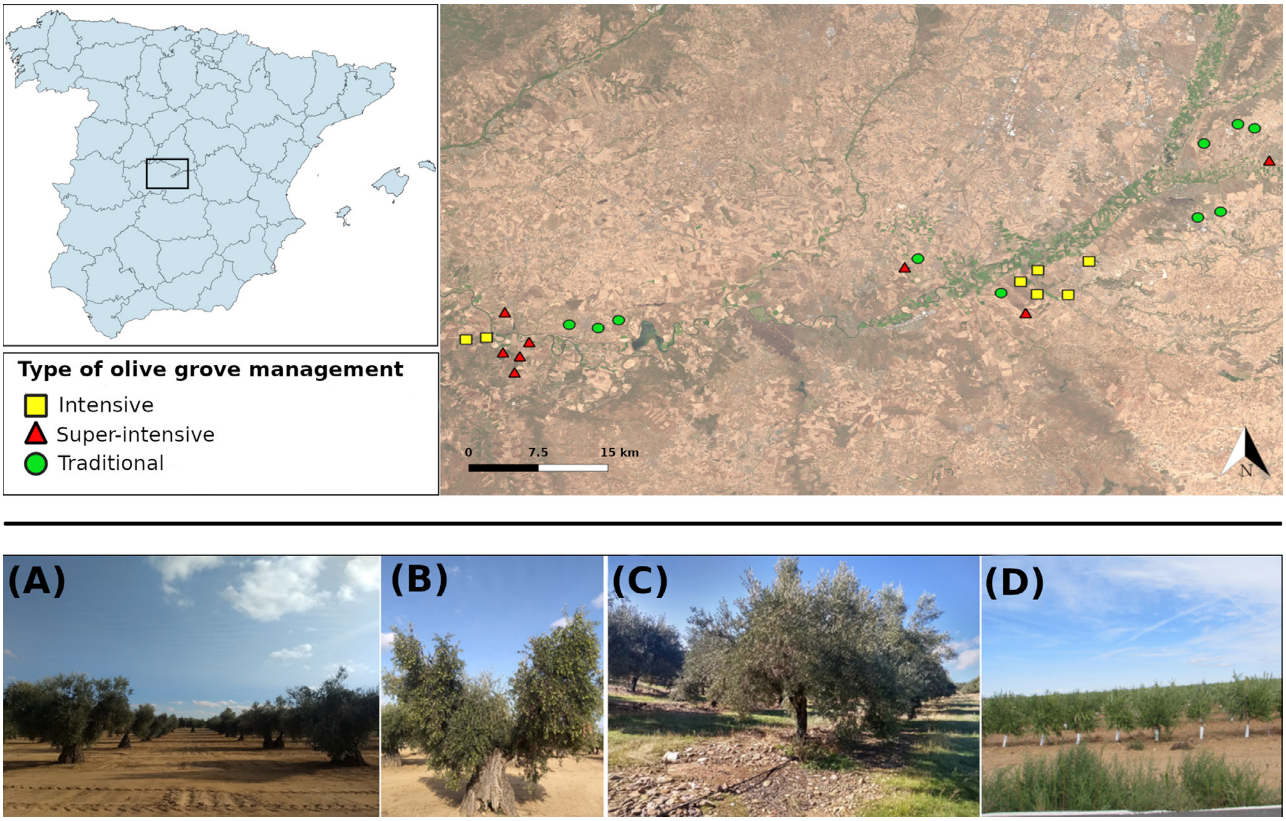

Fig. 1. Location of study areas in the middle part of Tagus Basin (provinces of Madrid and Toledo, central Spain), where sampled groves are plotted according to the type of olive grove (upper panels). *Traditional* (A, B), *intensive* (C) and *super-intensive olive groves* (D; bottom panels).

with scattered urban areas and small patches of natural vegetation, such as forests, scrubs and grasslands, forming a mosaic of land uses. Olive grove is the dominant woody crop, with harvesting occurring between October and January.

Three levels of olive grove intensification were determined based on tree structural features (IOC 2019; Tous et al., 2010; Fig. 1): (i) traditional olive groves are characterized by low tree density (50−100 trees per ha), generally large trees and low level of mechanization and inputs; (ii) intensive olive groves have an intermediate density (200−600 trees per ha), smaller tree size, are generally irrigated and require higher input use; and (iii) super-intensive hedge-like olive groves are always irrigated, present a very high density of trees (>1000 trees per ha), an extreme degree of mechanization and high use of chemicals. Small trees in super-intensive olive groves are usually replaced after 15 years.

Additionally, we selected groves according to the following criteria: (a) groves surrounded only by olive crops of similar management within a buffer of at least 150 m; and (b) groves separated by at least 1 km from each other to minimize the effect of spatial autocorrelation. Due to access constraints, sampling was not totally balanced across types of olive groves.

Bird surveys

Two bird censuses per grove were conducted during winter 2020−2021: early winter (November-December 2020) and late winter (February 2021). We used fixed-width transects (Bibby et al., 1992) of 100 m length and 30 m width, set at 50 m away from any grove edge. This band width was chosen because the proximity of olive rows to transect lines impeded full detection of birds beyond 15 m, particularly in intensive and super-intensive groves. Therefore, this width allowed detection of all individuals within the band without biasing counts. These data were used for statistical analyses. Birds spotted out of band were also recorded and used for descriptive results. Individuals in flight were not recorded. Each transect was surveyed by experienced observers walking at approximately constant speed in dry, windless weather, between 9:00 and 18:00 h, excluding central hours of the day. All individuals detected (seen or heard) were identified and georeferenced. The Crested Lark *Galerida cristata* and Thekla Lark *Galerida theklae*, both resident in the study area (Martí & Del Moral, 2003), were classified at genus level to avoid species misidentification. In addition, we classified all bird species into four diet-based functional groups: frugivores, granivores, insectivores and omnivores (see Appendix A: Table 1), according to their winter diet

Table 1. Summary of descriptive statistics of variables measured at microhabitat, grove and landscape level according to olive grove type. Different letters (superscripts) indicate significant differences ($p<0.05$) between olive grove types (HSD Tukey). SD: Standard deviation. E: early winter; L: late winter.

Variables	Traditional (n = 10) Mean ± SD	Intensive (n = 7) Mean ± SD	Super-intensive (n = 8) Mean ± SD	Season
Grove (field)				
Field size (ha)	9.73 ± 6.33^{a}	23.87 ± 20.19^{a}	27.23 ± 17.80^{a}	E
Tree density (Trees/ha)	69.02 ± 13.57^{a}	291.86± 42.53^{b}	1164.63 ± 309.59^{c}	E
Tree height (m)	3.91 ± 0.31^{a}	3.59 ± 0.37^{a}	2.68 ± 0.42^{b}	E
Distance between tree rows (m)	12.66 ± 1.64^{a}	4.84 ± 1.39^{b}	1.96 ± 0.51^{c}	E
Distance within tree rows (m)	11.76 ± 1.88^{a}	7.13 ± 0.61^{b}	4.09 ± 0.52^{c}	E
Diameter breast high	145.2 ± 43.85^{a}	58.29 ± 13.44^{b}	26.69 ± 12.56^{c}	E
Microhabitat				
Bare ground (%)	63.60 ± 22.48^{a}	30.71 ± 33.96^{b}	41.63 ± 34.69 ^{a,b}	E
	50.90 ± 22.51^{a}	15.66 ± 31.36^{b}	20.50 ± 29.54^{a,b}	L
Litter (%)	11.80 ± 13.04^{a}	25.00± 23.55^{a}	33.10 ± 29.04^{a}	E
	13.56 ± 11.12^{a}	27.57 ± 19.87^{a}	33.13 ± 25.44^{a}	L
Grassy vegetation (%)	23.00 ± 21.57^{a}	36.29 ± 31.07^{a}	24.75 ± 20.44^{a}	E
	32.84 ± 21.13^{a}	56.77 ± 27.72^{a}	46.25 ± 26.48^{a}	L
Dry vegetation cover (%)	1.00 ± 3.03^{a}	3.14 ± 7.96^{a}	0 ± 0^{a}	E
	2.00 ± 6.93^{a}	0 ± 0^{a}	0 ± 0^{a}	L
Moss cover (%)	0.60 ± 3.14^{a}	2.86 ± 7.10^{a}	0.50 ± 3.16^{a}	E
	0.30 ± 1.57^{a}	0 ± 0^{a}	0.13 ± 0.79^{a}	L
Total vegetation cover (%)	24.60 ± 22.40^{a}	44.29 ± 37.12^{a}	25.25 ± 21.30^{a}	E
	35.14 ± 23.53^{a}	56.77 ± 27.72^{a}	46.38 ± 26.38^{a}	L
Vegetation contacts <5 cm	3.14 ± 3.82^{a}	0.69 ± 1.89^{a}	0.58 ± 0.84^{a}	E
	7.14 ± 4.28^{a}	12.34 ± 5.61^{a}	9.48 ± 6.10^{a}	L
Vegetation contacts 5−10 cm	1.28 ± 3.42^{a}	0.23 ± 0.55^{a}	0.55 ± 0.99^{a}	E
	1.24 ± 2.53^{a}	1.66 ± 2.83^{a}	2.25 ± 3.95^{a}	L
Vegetation contacts 11−30 cm	0.44 ± 1.21^{a}	1.14 ± 1.78^{a}	0.10 ± 0.38^{a}	E
	2.10 ± 3.95^{a}	1.20 ± 2.75^{a}	1.43 ± 3.63^{a}	L
Vegetation contacts >30 cm	0.02 ± 0.14^{a}	0.11 ± 0.47^{a}	0 ± 0^{a}	E
	0.80 ± 2.20^{a}	0.03 ± 0.17^{a}	0.03 ± 0.16^{a}	L
Total Vegetation contacts	4.88 ± 6.22^{a}	2.17 ± 2.35^{a}	1.23 ± 1.27^{a}	E
	11.28 ± 8.22^{a}	15.23 ± 6.48^{a}	13.18 ± 8.93^{a}	L
Maximum vegetation height (cm)	6.90 ± 10.19^{a}	9.49 ± 11.80^{a}	4.50 ± 5.45^{a}	E
	14.12 ± 15.44^{a}	11.51 ± 10.87^{a}	10.65 ± 9.06^{a}	L
Olives in tree canopy	57.64 ± 11.74^{a}	46.49 ± 28.13^{a,b}	24.90 ± 15.87^{b}	E
Olives on the ground	9.26 ± 16.91^{a}	14.60 ± 12.42^{a}	16.78 ± 19.11^{a}	E
Landscape				
Arable crops (ha)	18.63 ± 18.64^{a}	17.50 ± 9.78^{a}	24.33 ± 14.32^{a}	
Woody crops (ha)	48.60 ± 22.95^{a}	42.50 ± 11.46^{a}	37.71 ± 14.90^{a}	
Natural forest (ha)	0.23 ± 0.57^{a}	3.46 ± 4.68^{a,b}	5.91 ± 7.27^{b}	
Shrublands (ha)	7.16 ± 10.87^{a}	8.35 ± 6.86^{a}	4.94 ± 6.62^{a}	
Grasslands (ha)	1.48 ± 4.06^{a}	5.43 ± 9.43^{a}	1.46 ± 2.85^{a}	
Artificial (ha)	2.40 ± 3.89^{a}	1.25 ± 1.25^{a}	4.15 ± 8.02^{a}	

(Snow & Perrins, 1998). The second census was conducted after the "Filomena" snowstorm (Smart, 2021), which was particularly intense in central Spain.

Olive grove characterization

Habitat structure and composition were characterized at three spatial scales: microhabitat, grove (field) and landscape level. At microhabitat scale, we estimated the percentage of grassy and dry vegetation, moss, litter, bare ground and total vegetation cover. These variables were measured in both censuses using five 1 × 1 m squares located within transects and separated 16 m from each other (see Appendix A: Fig. 1). We also estimated the maximum and mean vegetation height from the number of vegetation contacts at different heights (<5 cm; 5−10 cm; 11−30 cm; >30 cm). At grove level, we recorded field size (ha) and five metrics related to olive grove structure (Table 1): tree density (TD: number of trees/area), diameter at breast height (DBH, cm), tree height (TH, cm), distance between tree rows (DBR, m) and distance within tree rows (DWR, m). These variables were measured *in situ* based on five trees, except for tree density, which was estimated from satellite images (Google Earth Pro, version 7.3.3.). Landscape level characterization was carried out by measuring six land cover variables in 500 m radius buffers centered around each grove: arable and woody crops, natural forest, shrublands, pastures and artificial areas. Land covers were obtained from SIOSE cartography 2014 (http://www.siose.es; 1:25,000) and checked with the most recent aerial image (PNOA, 2020) and the Spanish version of the European Land Parcels Information System (SIGPAC). Landscape analyses were conducted with QGIS v3.12.3 (QGIS Development Team, 2020).

We further estimated the relative abundance of olive fruits per grove as a proxy of fruit availability for frugivorous birds, both in the canopy and on the ground. We counted the number of fruits observed in the canopy within 1 min (30 s for each half of the tree crown) in five trees separated approximately 16 m along each transect. We counted olives on the ground under the tree canopy in five squares of 50×50 cm (see Appendix A: Fig. 1). We conducted this sampling only in the first census, as most of the groves were already harvested in late winter. We also recorded whether the olive grove was irrigated or rain-fed and whether it was harvested at the time of the census.

Data analysis

We first conducted a Principal Component Analysis (PCA) using the R function “prcomp” to obtain interpretable ecological gradients from microhabitat (n = 11), grove (n = 6) and landscape features (n = 6). PCA enables us to identify key features that explain variability in habitat structure among the olive groves. Moreover, it synthesizes information and reduces the number of original predictors (n = 23), thus minimizing collinearity and saturation of the subsequent models. At microhabitat scale, we averaged data of vegetation and ground variables from early and late winter censuses. Previous to the PCA, original variables were scaled to have unit variance. We also conducted ANOVAS and Tukey’s HSD to test for differences in environmental variables between intensification levels.

To test the effect of habitat structure of the olive groves on the whole bird communities, we fitted two linear mixed effects models (LMM) with Gaussian error structure, including total species richness or total abundance per transect as response variables. Model inference was established by full-null model comparisons using the R function “anova”, and predictor p-values with the function “lmerTest” from lmerTest package. We used the R function “model performance” to obtain the marginal R^2 from LMMs. All statistical analyses were performed with R version 3.6.3 (R Core Team, 2020). As the two response variables were count variables, and hence we log-transformed them to fit model assumptions. The first two PC axes and the census period (early vs. late winter) were added as predictors, and grove as a random factor to account for non-independent observations (two censuses per grove). Instead of using the IOC intensification categories, we included the PC axes since they provide information on specific environmental factors influencing bird communities. We also opted for the inclusion of census period, rather than harvest (harvested vs. not harvested), as the latter factor was relevant only for a part of the bird community (i.e., frugivorous birds). We further tested the effect of olive groves intensification on the diet-based functional groups through four additional LMMs, using the same set of predictors and total species richness and total abundance of granivorous and insectivorous birds as response variables. For frugivorous species, we replaced census period by olive fruit availability (canopy and ground) as predictor and fitted two linear models (LM) using only data from the first census (early winter), as fruit availability was only measured in that period. We discarded the omnivore group due to the low number of species (<15%). Normal distribution of model residuals and homocedasticity were visually assessed using diagnostic plots and no evident deviations from these assumptions were observed. We did not include interaction terms nor random slopes to reduce models’ complexity.

Results

General bird occurrence patterns

We recorded a total of 648 birds from 30 species, of which 359 birds from 20 species (67%) were detected within the transect band (see Appendix A: Table 1). The highest abundance was found in early winter (66.3% of the individuals recorded within the band). Thirty percent

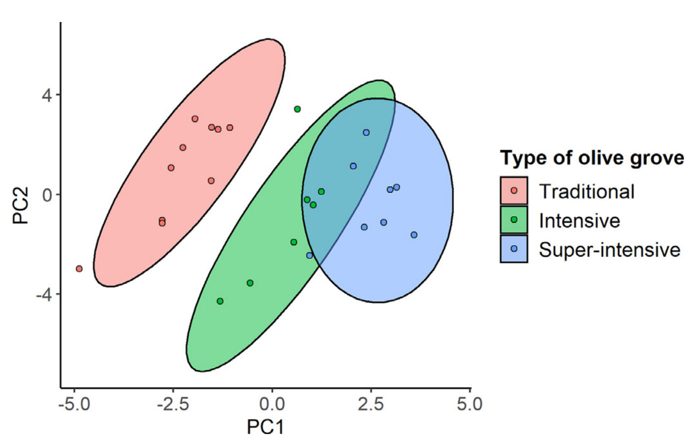

Fig. 2. Scatter plot showing the first two PCs calculated from 23 original environmental variables. Colored ellipses indicate grouping of olive groves according to the intensification category. See Table 2 for PCs interpretation.

of the total species recorded were frugivorous, 33% granivorous, 23% insectivorous and 10% omnivorous. Frugivorous species represented 43.5% of total birds detected and 56% of the birds detected within the band. We did not record any species exclusive to a single type of olive grove, but eight species (26.7% of total species) were not observed in super-intensive olive groves in at least one of the two winter periods: *Columba livia, Cyanistes caeruleus* and *Turdus merula* (both periods); *Serinus serinus, Fringilla coelebs, Chloris chloris, Parus major* (late winter); and *Turdus philomelos* (early winter). The most abundant species within the band were Eurasian Blackcap *Sylvia atricapilla*, Sardinian Warbler *Curruca melanocephala* and Chaffinch *F. coelebs*, all detected in the three types of olive groves, with Chaffinch being more abundant in super-intensive olive groves in early winter (see Appendix A: Table 1 and Fig. 2).

Olive grove characterization: ecological gradients

The PCA on the 23 variables yielded two axes that explained 46.9% of total variance (Table 2). These two axes are easily interpretable in terms of ecological gradients observed in the field, while the remaining PCs do not have a straightforward interpretation. PC-1 showed a clear gradient from groves characterized by high tree density and forest cover within the landscape buffer (positive values),

Table 2. Spearman correlation coefficients between the 23 original environmental variables and the PC axes. Correlation coefficients > 0.5 are highlighted in bold.

Spatial scale	Original variable	PC-1	PC-2
Grove (field)	Tree density	**0.933**	−0.167
	Field size	**0.529**	0.265
	Tree high	**−0.795**	0.200
	Distance between tree rows	**−0.890**	0.172
	Distance within tree rows	**−0.929**	0.169
	Diameter Breast High	**−0.836**	0.140
Microhabitat	Bare ground cover	**−0.572**	**−0.561**
	Litter cover	**0.539**	0.090
	Grassy vegetation cover	0.309	**0.874**
	Moss cover	−0.097	0.327
	Dry vegetation cover	−0.250	0.363
	Total vegetation cover	0.257	**0.897**
	Contacts at <5 cm height	0.145	**0.574**
	Contacts at 5−10 cm height	0.329	**0.601**
	Contacts at 11−30 cm height	−0.022	**0.692**
	Contacts at >30 cm height	−0.436	**0.562**
	Maximum vegetation height	−0.094	**0.773**
Landscape	Arable crop cover	0.294	−0.087
	Woody crop cover	−0.235	0.210
	Natural forest cover	**0.501**	0.173
	Shrubland cover	0.037	−0.194
	Pasture cover	−0.027	−0.184
	Artificial cover	−0.132	−0.402
	Explained variance (%)	24.7	22.2

Table 3. Estimates and SE (standard error) from linear mixed models testing for differences in bird richness and abundance of the entire bird community and of the four bird diet-based functional groups (response variables) between olive groves with increasing levels of intensification (represented by PC axes) and census periods (predictor variables).

Variables	Estimate (SE)	*t*	*P*	Estimate (SE)	*t*	*p*
	Total bird species richness			**Total bird abundance**		
Intercept	4.720 (0.275)	17.052	<0.001	2.285 (0.128)	17.765	<0.001
PC-1	−0.194 (0.086)	−2.028	0.054	−0.037 (0.043)	−0.854	0.402
PC-2	−0.002 (0.090)	−0.015	0.988	0.013 (0.045)	0.287	0.777
Census (late winter)	−2.640 (0.390)	−7.634	**<0.001**	−0.791 (0.165)	−4.790	**<0.001**
	Frugivore species richness			**Frugivore abundance**		
Intercept	0.751 (0.184)	4.075	<0.001	0.714 (0.352)	2.025	0.056
PC-1	−0.115 (0.036)	−3.143	**0.005**	−0.107 (0.070)	−1.521	0.144
PC-2	0.043 (0.031)	1.385	0.181	0.042 (0.060)	0.701	0.491
Olive tree	0.001 (0.003)	0.496	0.625	0.013 (0.006)	1.933	0.068
Olive ground	0.012 (0.006)	1.888	0.073	0.025 (0.013)	1.937	0.067
	Granivore species richness			**Granivore abundance**		
Intercept	0.900 (0.094)	9.994	<0.001	1.171 (0.132)	8.832	<0.001
PC-1	0.013 (0.028)	0.480	0.633	0.046 (0.041)	1.118	0.269
PC-2	−0.061(0.029)	−2.082	**0.042**	−0.072 (0.043)	−1.665	0.103
Census (late winter)	−0.403 (0.127)	−3.169	**0.002**	−0.438 (0.187)	−2.335	**0.024**
	Insectivore species richness			**Insectivore abundance**		
Intercept	0.432 (0.061)	7.081	<0.001	0.485 (0.075)	6.463	<0.001
PC-1	−0.029 (0.021)	−1.394	0.177	−0.025 (0.028)	−0.864	0.397
PC-2	−0.017 (0.021)	−0.793	0.436	−0.037 (0.030)	−1.224	0.234
Census (late winter)	−0.348 (0.075	−4.603	**<0.001**	−0.386 (0.073)	−5.279	**<0.001**

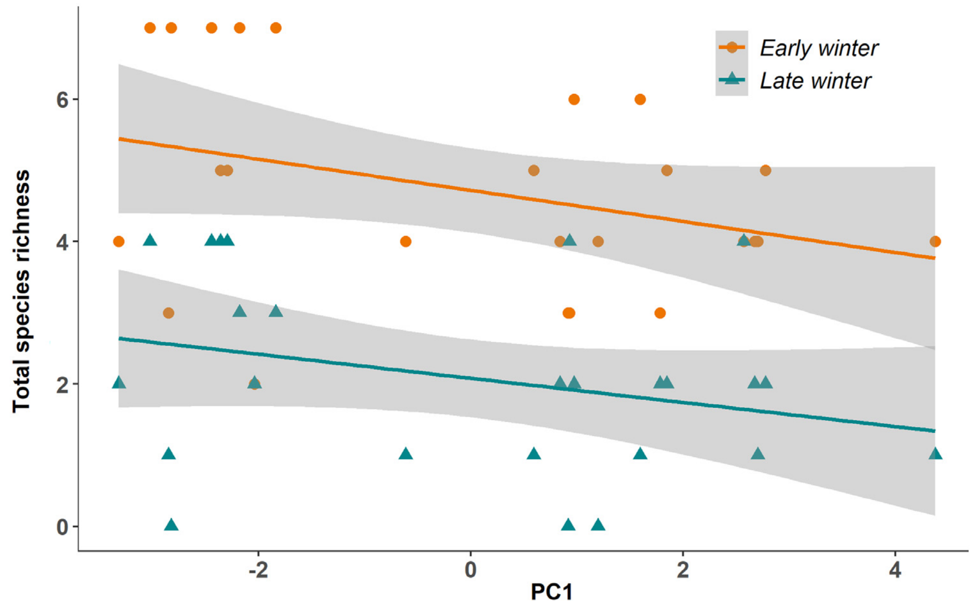

Fig. 3. Effect of PC-1 on bird species richness during early and late winter. The shaded area indicates the 95% confidence interval. PC-1 is correlated with high tree density and natural forest cover (positive values), and higher and more distanced trees (negative values).

corresponding to super-intensive olive groves, to groves of higher and more distant trees (negative values), corresponding to traditional olive groves (Table 2). PC-2 represented a gradient from groves with more total vegetation cover, including grassy vegetation and contacts at different heights (positive values), to fields with more bare ground cover (negative values), which indicates the intensity of field-level management. While the types of olive groves were clearly clustered along the PC-1, they mostly overlapped along the PC-2, as all types showed variation in vegetation and bare ground covers (Fig. 2). No clear patterns of land cover variation were associated with grove type, except for super-intensive ones, which were associated with higher forest cover (Table 1; PC-1, Table 2).

Environmental determinants of wintering bird communities

Total bird species richness decreased with the level of intensification (PC-1), from traditional to intensive and super-intensive olive groves (Table 3, Fig. 3), although this effect was marginally significant. Moreover, bird species richness clearly decreased over the winter period (R^2-marginal=51%; Table 3). We found no relationship between intensification and bird abundance, whereas the number of birds significantly decreased between winter periods (R^2-marginal=29%; Table 3).

Frugivores were the group most affected by the level of intensification, with a significant decrease in species richness related to PC-1 (Table 3). No significant effects on frugivore species richness were found regarding the availability of olive fruits in the canopy and on the ground. In contrast, for frugivore abundance only fruit availability had marginally significant positive effects (R^2-adj=30%; Fig. 4). Granivore species richness decreased with vegetation cover (microhabitat, PC-2) and in the late winter census (R^2-marginal=23%; Table 3). Both insectivore richness and abundance were affected by the census period, showing a decreasing trend from early to late winter (R^2-marginal (richness)=29%; R^2-marginal (abundance)=25%).

Discussion

Correspondence between olive grove type and environmental variables

The categorization of olive groves as traditional, intensive and super-intensive is based mainly on tree density and size. The environmental gradients identified in our PCA reasonably segregate olive groves according to intensification category (Fig. 2). Specifically, PC-1 adequately captures variation in the grove structural variables, so that olive groves previously classified in official categories tend to separate along the gradient. Therefore, this axis can be considered an adequate quantitative proxy of olive grove management intensification.

However, the level of intensification goes beyond physiognomy of olive groves. At microhabitat level, the differences in ground cover observed (e.g. grassy vegetation, bare ground, litter) are related to management practices that

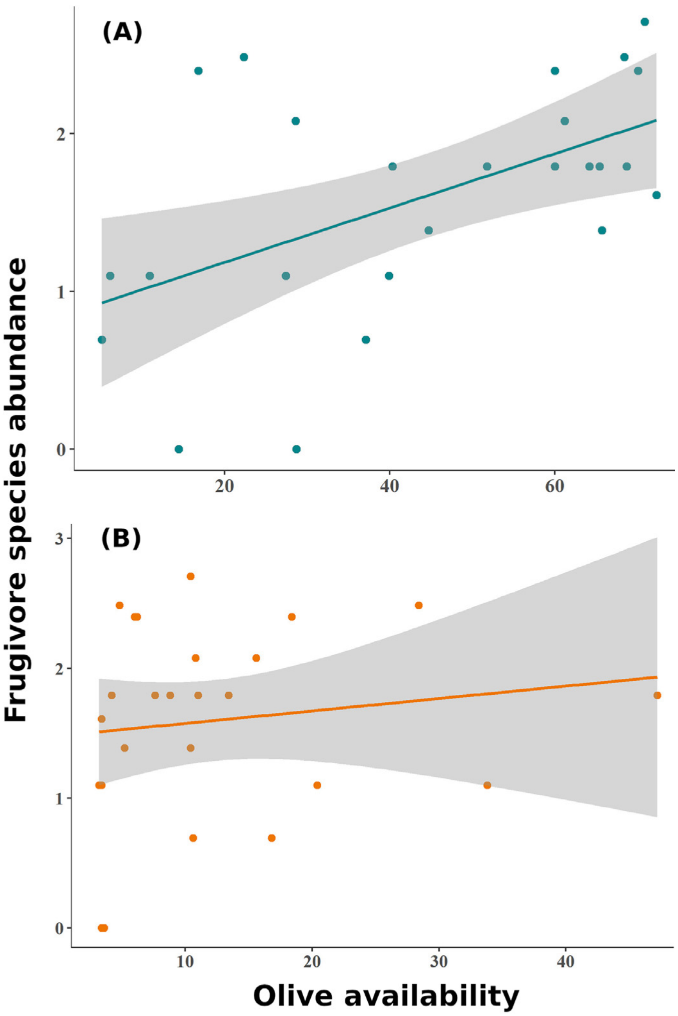

Fig. 4. Effect of olive availability in the tree canopy (A) and on the ground (B) on frugivore species abundance. The shaded area indicates the 95% confidence interval.

influence the structural complexity of olive groves and thus may buffer or increase the negative impact of intensification on biodiversity (Rey et al., 2019). For example, in super-intensive olive groves, the higher percentage of litter from shredded pruning debris (which correlated with PC-1) can contribute to improve soil structure and infiltration capacity by providing organic matter, although it can hinder the development of vegetation cover (Saavedra et al., 2015). This brings environmental and agronomic benefits by increasing soil fertility and reducing erosion (Moreno et al., 2009; Castro-Caro et al., 2014b).

On the other hand, traditional and intensive olive groves displayed a wider range of variation along PC-2, which indicates that the official categories do not fully capture intensification differences between groves at microhabitat scale, and thus they should be used cautiously in the context of grove management. Finally, it is interesting to note that, in our study area, super-intensive and intensive groves tend to be surrounded by a larger proportion of forest cover (Table 1). This may be explained by the more recent cultivation of these groves that are sparsely distributed in new areas, as opposed to traditional groves, which covered large areas for a long time, and therefore became the dominant land cover. The higher proportion of forests in landscapes surrounding intensive and super-intensive groves might have buffered the negative effects of grove intensification. This may also explain why only marginally significant effects of intensification on bird species richness were found.

Relationship between olive grove intensification and wintering bird communities

Our study partially supports the hypothesis that winter bird species richness tends to decrease with intensification of olive grove management (Fig. 3). This result is consistent with previous studies (Bouam et al., 2017; Morgado et al., 2021), reinforcing the known detrimental effect of intensive agricultural management on bird communities (Emmerson et al., 2016). Basically, species richness decreased as olive grove and canopy structure became denser and more hedgerow-like (i.e. super-intensive groves). This variation was captured by PC-1, indicating that the more complex grove structure favored by traditional management (two or three trunks with many hollows and cavities) offers greater number of conditions and resources to be exploited by a higher number of species (Rois-Díaz et al., 2006).

As found in other studies, diet-based functional groups seemed to respond differently to olive grove intensification (Morgado et al., 2021; García-Navas et al., 2022). Species richness of frugivorous birds was negatively related to olive management intensification. This reinforces the observed pattern of total species richness and thus is probably due to the dominance of frugivorous species such as Blackcaps and Sardinian Warblers (but also others like Thrushes and Robins) in the studied bird communities. However, olive fruit availability apparently did not influence richness, probably because the latter is governed by larger-scale environmental heterogeneity (as found by Morales et al., 2015 in cereal systems) rather than by food resources. Olive groves can harbor high densities of frugivorous birds in winter, functioning as habitats alternative to natural ones (Castro-Caro et al., 2014a), and offering an abundant key food resource in the form of ripe olives (Rey, 2011). Species such as Blackcap, Sardinian warbler or European Robin, are consumers of fat-rich fruits (Herrera, 1988), acting as seed dispersal agents (Assandri et al., 2017). This is supported by our results, which show that olive availability (both in the canopy and on the ground) tends to favor the abundance of wintering frugivorous birds. However, frugivorous bird abundance was not significantly associated with the degree of intensification represented by PC-1, suggesting that intensification does not necessarily reduce the suitability of intensive or super-intensive groves as winter habitat for this diet-based group. In fact, previous studies like Morgado et al. (2021) even found greater abundances of frugivorous birds in the more intensive groves that were associated with higher olive production. Nevertheless, a more detailed study of grove structure, olive availability and olive size (associated with variety, see also Rey et al., 1997) in different areas may be required to fully clarify this relationship. In addition, unlike intensive and super-intensive olive groves, traditional groves have a biennial bearing in olive production, and hence surveys covering more than one winter season would be desirable to confirm the patterns detected. In the same vein, larger sample sizes and larger number of groves of each type are recommended to detect more robust patterns.

Granivore species richness showed a significant negative relationship with PC-2. Variables measuring grass cover and vegetation complexity are correlated with high positive values of this component, and therefore species richness of granivorous birds would be higher in groves more intensively managed at microhabitat scale. Previous work has shown the importance of grass and plant litter cover for these birds, where they can find seeds for feeding (Senar & Borras, 2004). Again, a wide range of variation along this axis is found within intensification categories and thus the response of this functional group to small scale intensification should be further examined. For example, some studies have found that ploughing (i.e. grass removal) might benefit granivore birds by improving access to newly unearthed seeds and this way increase on-ground seed availability (Suárez et al., 2004).

Regarding insectivorous birds, none of the intensification gradients used in our study was correlated with either richness or abundance. Insectivore bird abundance in winter is limited by the lower activity rates of invertebrates (Senar & Borras, 2004) and this result is likely explained by a similarly low activity in all olive groves of the study area, regardless of invertebrate abundance and its potential relationship with intensification. Therefore, it may be inferred that olive groves are probably not a critical habitat for this functional group during the winter.

Differences between early and late winter censuses

Our results consistently show higher bird richness and abundance in early than in late winter. This difference may be explained by changes in olive availability that would benefit frugivorous species (Rey, 2011). In early winter, 44% of all olive groves were harvested, mainly in super-intensive (72.7%) and intensive groves (27.3%). At the time of late winter census, 84% had already been harvested. However, the effect of the "Filomena" heavy snowstorm, which occurred three weeks before the second sampling, and the extremely cold period that followed cannot be ruled out as an alternative or complementary explanation (Cano-Barbacil & Cano, 2017; Smart, 2021).

Conclusions

Olive grove intensification results in significant changes in habitat structure for wintering birds. Such changes can be summarized in quantitative ecological gradients that are useful proxies of intensification. Olive grove intensification has an important impact on the winter bird community, whose response may depend on the species' food requirements, and ecological gradients of grove and vegetation structure. Total winter bird richness tended to decrease with intensive olive grove management, probably linked to reduced habitat heterogeneity. However, total abundance remained unchanged among grove types, which indicates the capacity of intensive olive groves to sustain large numbers of birds. The effect of intensification was particularly strong in frugivorous species, whose abundance depends on olive fruit availability. Granivorous and insectivorous species did not seem to respond to intensification gradients, although richness of granivorous birds was associated with low grass cover and vegetation complexity. These latter results call for a more detailed examination of key food resources (invertebrates, seeds) within groves and their interaction with grove and landscape structure. Finally, our findings also show strong decreases of bird species richness and abundance after a snowstorm, highlighting the potential importance of extreme weather events in bird communities, which are forecasted to increase with climate change (Stott, 2016).

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.

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Supplementary materials

Supplementary material associated with this article can be found, in the online version, at doi:10.1016/j.baae.2023.04.005.

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