

RESEARCH ARTICLE

Preserving wintering frugivorous birds in agro-ecosystems under land use change: Lessons from intensive and super-intensive olive orchards

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Abstract

1. Fleshy fruit production is becoming more intensive worldwide, but how this affects frugivorous birds is poorly known. In the Mediterranean region, intensive and super-intensive olive orchards are fast expanding, potentially affecting millions of wintering songbirds. Here, we test the idea that intensification may benefit frugivorous birds, at least locally, due to increased fruit availability, while negatively affecting the wider wintering bird community due to intensive management, structural simplification and landscape homogenisation.
2. We estimated olive abundance and surveyed birds in early, mid- and late winter, at traditional, intensive and super-intensive orchards in southern Portugal. We used Hierarchical Modelling of Species Communities to relate species richness, prevalence and abundance to management intensity, winter period, olive availability and landscape context, and evaluated the role of frugivory in modulating observed responses.
3. Olive availability was much higher throughout the winter in more intensive than in traditional orchards, both in trees and on the ground. Frugivorous bird abundance was higher in more intensive orchards, and the most abundant frugivorous species (blackcap, song thrush, robin) were positively affected by olive availability and/or increasing landscape cover by olive orchards, while intensification level had relatively minor effects after accounting for other variables. Non-frugivorous richness and abundance were higher in traditional orchards, and many non-frugivorous species had lower prevalence in more intensive orchards or were negatively affected by landscapes dominated by olive cultivation.
4. *Synthesis and applications.* While negatively affecting the wider bird community, our results suggest that olive farming intensification can contribute to sustaining large numbers of frugivorous birds in the Mediterranean region. As frugivorous birds are not seen as damaging by olive farmers, there is an opportunity to promote their conservation in intensive and super-intensive orchards, which requires

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management to increase habitat heterogeneity, and to reduce risks such as mortality associated with mechanical harvest and contamination with pesticide residues. Overall, we recommend that efforts to manage farmland biodiversity should consider the impacts and conservation opportunities of fruit crop intensification.

KEYWORDS

agricultural intensification, farmland birds, frugivory, fruit crops, Mediterranean, resource tracking, super-intensive olive orchards, wintering birds

1 | INTRODUCTION

Fleshy fruit crops (e.g. grapes, olives, berries) represent an abundant food source that can contribute to sustain frugivorous birds in agricultural landscapes (Rey, 2011), which can result in conflicts with farmers (Lindell, 2020). Olive orchards provide food to millions of frugivorous songbirds wintering in the Mediterranean region, potentially affecting their populations at the continental scale (Rey, 1993, 2011; Tellería et al., 2005), while bird economic damages seem to be negligible (but see Berraï et al., 2017). Like other fruit crops (Rime et al., 2020), olive cultivation has fast intensified during the past decades (Sánchez-Martínez & Paniza Cabrera, 2015; Tous et al., 2010), but little is known about how this affects wintering birds. Gaining such understanding is important to inform bird conservation and management in intensive fruit crops.

Traditional olive orchards have low densities of often old and large trees (ca. 100 tree/ha), low levels of mechanisation and chemical inputs and no irrigation (Infante-Amate et al., 2016). Progressively, this system has been replaced by more intensive orchards, with smaller and shorter lived tree varieties, planted at higher densities (c. 200–500 trees/ha) and increased irrigation, mechanisation and chemical inputs (Tous et al., 2010). Super-intensive orchards have expanded more recently, involving very high densities (1,000–2,500 trees/ha) of highly productive dwarf trees, planted in a hedgerow-like pattern, with drip irrigation, heavy mechanisation and major use of agrochemicals (Connor et al., 2014; Tous et al., 2010). Intensification has increased productivity from <2.5 tonnes/ha in traditional, through 3–10 tonnes/ha in intensive, to 8–11 tonnes/ha in super-intensive orchards (Connor et al., 2014; IOC, 2015; Silveira et al., 2018), but concerns have been raised on the ecological sustainability of these changes (Beaufof, 2001; Moreira et al., 2019), mainly due to strongly negative biodiversity impacts (Carpio et al., 2016; Herrera et al., 2015; Morgado et al., 2020; Solomou & Sfougaris, 2011, 2015).

Olive orchards are important for frugivorous birds because they provide high abundance of particularly nutritious fruits, and they are widely available across Mediterranean rural landscapes (Rey, 2011). Moreover, variations in ripening phenology and harvest timing across cultivars and locations create a continuous supply of olives (Rey, 1995, 2011), which can be tracked in space and time by frugivorous birds (Tellería & Pérez-Tris, 2003; Tellería et al., 2005). Intensification may thus bring benefits through

increased olive availability in highly productive orchards (Muñoz-Cobo & Montesino, 2003; Rey et al., 1996), though consequences may also be negative, particularly for non-frugivorous species, due to structural orchard simplification (Costa et al., 2020; Morgado et al., 2020) and landscape homogenisation reducing the availability of alternative habitats (Santana et al., 2017). Moreover, intensification is associated with specialisation on a few cultivars (Tous et al., 2010), which together with landscape homogenisation through intensive olive farming may reduce temporal continuity in fruit availability (Rey, 2011). Finally, birds in intensively managed orchards are exposed to significant risks, including mortality associated with mechanical night harvesting (Silva & Mata, 2019), reduced availability of alternative plant (Bergmeier & Strid, 2014; Solomou & Sfougaris, 2011) and arthropod foods (Cárdenas et al., 2006; Ruano et al., 2004) and contamination with pesticide residues (Cabras et al., 1997). It is thus important to understand how wintering birds use intensive and super-intensive orchards during the harvest and post-harvest periods, and how this is affected by olive availability and landscape composition.

Here, we investigate bird use of traditional, intensive and super-intensive olive orchards in southern Portugal, where intensive olive farming is fast expanding (Rodríguez-Cohard et al., 2020; Silveira et al., 2018). Although focusing on frugivorous species, we also considered the entire bird community to compare responses to intensification across trophic groups. We tested the following hypothesis: (a) The availability of ripe olives is higher in more intensive olive orchards, though it may decline rapidly due to high harvest efficiency; (b) olive abundance and landscape coverage by olive orchards positively affect the richness and abundance of frugivorous species; and (c) structural simplification in more intensive orchards and landscape coverage by olive farming negatively affects overall species richness and abundances, particularly that of non-frugivorous species.

2 | MATERIALS AND METHODS

2.1 | Study area

The study was carried out in Alentejo (Southern Portugal), within about 15,000 km² (37°38'–39°01'N, 7°02'–8°16'W, Figure S1). The climate is Mediterranean, with hot dry summers, mild winters and

annual rainfall concentrated in October–March. The landscape is flat or gently undulating (100–450 m a.s.l.), and dominated by open agricultural land, oak woodlands, olive orchards and vineyards. Alentejo is one of the European regions with the steepest growth in intensive olive cultivation, and accounted in 2018 for 52.5% (184,936 ha) of olive area and 75% (81,965 t) of olive oil production in Portugal (Rodríguez-Cohard et al., 2020). More intensive olive cultivation is mainly replacing traditional orchards and annual crops (Ribeiro et al., 2014), and has been favoured by the expansion of irrigation infrastructures, agricultural policies and global market demand (Silveira et al., 2018). Olive harvest occurs from October to January, though about 90% of olives are harvested in November (~35%) and December (~53%; GPP, 2021). The yield in our area was comparatively low in the sampling winter, due to the alternate fruit-bearing phenomenon characteristic of olive trees, with no or only partial harvest in some traditional orchards, but probably much lower impacts in more intensive orchards (Lavee, 2007).

2.2 | Orchard selection

A total of 78 orchards were selected, following a stratified random procedure to obtain an equal number of traditional, intensive and super-intensive orchards (Morgado et al., 2020). This categorisation was based on structural orchard features, mainly tree density, because they are strongly related to intensification (e.g. Tous et al., 2010) and biodiversity levels (Costa et al., 2020; Morgado et al., 2020), and because direct information on management intensity (e.g. agrochemicals use, mechanisation) could not be obtained. Structural features allowed a preliminary selection of orchards based on remote imagery, which was validated in the field. We constrained orchards to be on different farms, thereby reducing eventual dependencies due to management similarities.

2.3 | Bird data

Birds were counted along two or three 100-m transects per orchard (mean: 2.9 ± 0.4 SD, $n = 223$), depending on orchard size. Transects were located consecutively along the longest axis crossing each orchard, at least 100 m away from its border to reduce edge effects. We used multiple transects to account for variability within orchards, and they were placed consecutively to allow the survey of multiple transects even in small orchards. Counts were made in early (15–30 November), mid- (1–15 January) and late (15–28 February) winter of 2016–2017, covering the harvest and post-harvest periods (GPP, 2021) and thus temporal changes in olive availability. Counts were made throughout the day, except between c. 12.00 and 14.00 hr when bird activity declined, by two experienced ornithologists (RM, RP), avoiding heavy or persistent rain and strong wind. Birds were identified and counted within a small band (30 m) to each side of transects (Bibby et al., 1992), to minimise variations in bird detection across habitat types and sampling occasions (e.g. weather,

time of day, observer; Shave et al., 2018; Westgate et al., 2021). This detection distance was set considering other bird studies in olive (Rey, 1995) and other fruit orchards (Shave et al., 2018), and following a preliminary study consistently showing high bird detectability within this band width. Care was taken to avoid double counting birds moving between nearby transects. We discarded birds flying over but not landing, and birds poorly sampled such as raptors, nocturnal birds, aquatic birds and aerial feeders (swallows). Crested and Thekla larks *Galerida cristata* and *G. theklae* were categorised to genus to avoid misidentification problems. Bird species feeding primarily on fruits during winter were categorised as frugivorous and non-frugivorous otherwise (Table S1).

2.4 | Environmental data

Orchards were characterised considering olive tree density, height and diameter at breast height, orchard age and the presence of drip irrigation, estimated from remote imagery (Google Earth, version 7.1.2.2041), field measurements and enquiries to landowners (details in Table S2). These variables were used to assign orchards to intensification categories based on hierarchical clustering on principal components (Lê et al., 2008), following Morgado et al. (2020). We retrieved three well-defined clusters matching the initial assignment (Table S3; Figures S2 and S3), each with 26 orchards. These categories were used to describe structural changes along the intensification gradient, due to high multicollinearity among the original variables.

In each sampling period, we estimated olive availability on trees and on the ground separately, because they may be used differently according to species foraging preferences. We only considered ripe olives, discarding unripe (rigid and not black coloured) or damaged (dry, infested by insects or partly eaten) ones. Olive availability was estimated on each tree closest to each of five points located at 10, 30, 50, 70 and 90 m from the start of each bird sampling transect. The proportion of each tree crown with ripe olives was visually estimated to the nearest 5%, using a fully loaded crown as the 100% reference. We then estimated the total availability of olives on trees in tonnes per hectare (t/ha) for each transect, by averaging the crown proportions with ripe olives and then multiplying by the mean annual olive yield in Portugal (2009–2010 to 2011–2012), for traditional (1.5 t/ha), intensive (8 t/ha) or super-intensive (10 t/ha) orchards (IOC, 2015). We converted to t/ha instead of using the proportion of the crown, because the total amount of olives per tree and tree densities vary widely across intensification levels. This approximation enhanced comparability of fruit availability estimates across production systems over the winter, though it does not provide absolute estimate for any given year, due for instance to alternate bearing cycle of olive trees (Lavee, 2007).

On the same five trees, we counted all ripe olives on the ground inside 0.3×0.3 -m quadrats placed under each tree crown in each of the four cardinal directions (N, E, S, and W). The mean number of ripe olives per quadrat (4 quadrats \times 5 trees) was converted into

number per hectare, and multiplied by the proportion of orchard area under tree crown projections estimated using Google Earth imagery. The latter was needed because there were virtually no olives on the ground outside crown projections. Finally, we transformed the number of olives per hectare into t/ha, using the weight of olives from the predominant cultivars in each intensification level (Leitão et al., 1986; Tous et al., 1999).

Landscape context was described from the proportional cover of the main land uses within 1-km radius buffers around the centre of each orchard sampling area. Data were extracted in a Geographic Information System (GIS) from land cover maps for 2015 (DGT, Direcção Geral do Território, 2018), and updated where necessary from field surveys. Land uses were classified in three dominant categories that affect farmland birds in the region (Morgado et al., 2020; Santana et al., 2017): olive orchards, open agricultural land and natural and semi-natural vegetation (Table S2).

2.5 | Data analysis

Olive availability on trees and on the ground were modelled separately in relation to intensification level and sampling period, using generalised linear mixed models (GLMM) with Gaussian errors and identity link, with orchard and transect as random factors. The interaction between intensification and period was specified to account for differences in temporal patterns across intensification levels.

Bird data were modelled using the hierarchical modelling of species communities (HMSC) framework, whereby species occurrences or abundances can be related to environmental covariates, species traits and phylogenetic relationships, while accounting for study design and spatial dependencies (Ovaskainen & Abrego, 2020). Response variables were the species occurrences (0/1) or number of individuals in 669 transects (223 transects \times 3 periods). As covariates, we used intensification level (traditional as reference level), sampling period (early winter as reference level), their interaction, olive availability and landscape context. To reduce skewness and thus the potential influence of a few large values, we log- and arcsine-transformed olive availability and land cover data respectively (Legendre & Legendre, 1998). Multicollinearity was investigated with adjusted generalised variance inflation factors (GVIF), using function 'vif' of package *CAR* (Fox & Weisberg, 2019). Two land cover variables with $AGVIF > 2$ indicated multicollinearity problems, but all $AGVIF$ became < 2 when excluding open farmland and natural areas (Table S4). We retained cover by olive orchards, which was correlated with open farmland ($r = -0.79, p < 0.01$) and natural vegetation ($r = -0.40, p < 0.05$), because we were particularly interested on the effects of their expansion at the landscape scale. The species-trait matrix included a dummy variable coding frugivorous versus non-frugivorous species. The species-species phylogenetic matrix was created from a phylogenetic tree (Figure S4) based on Kumar et al. (2017), and it was used to assess the phylogenetic signal of residual variation in species environmental responses, potentially reflecting responses mediated by unmeasured species traits. To

control for dependency structures associated with study design, we specified three community-level random effects using a latent factor approach, which can be viewed as a model-based ordination that accounts for missing predictors influencing covariation across species at different design levels (Ovaskainen & Abrego, 2020; Warton et al., 2015). Two random effects corresponded to transects nested into orchards, thereby accounting for the hierarchical study design, with repeated measures in each transect during the winter and multiple transects sampled in each orchard. A third random effect was used to account for spatial autocorrelation resulting from orchard geographical location.

A probit model for occurrence data and a log-normal Poisson model for count data were fitted with the *Hmsc R*-package (Ovaskainen & Abrego, 2020), assuming the default distribution of priors. We sampled the posterior distribution with seven MCMC chains, using 300,000 iterations and a burn-in of 200,000 for the probit model, and 600,000 iterations and a burn-in of 500,000 for the abundance model. Each chain was then thinned by a factor of 100 to produce 1,000 posterior samples. After visually inspecting trace plots, we discarded due to convergence problems all species occurring in $< 5\%$ of transects (Table S1), and the blackbird *Turdus merula* from the abundance analysis.

The models' fit was evaluated using Tjur R^2 (Tjur, 2009) and AUC for occurrence models, and R^2 for abundance models (Ovaskainen & Abrego, 2020). Statistical support for the effects of environmental covariates was evaluated by verifying whether the 95% credible intervals of model's β coefficients crossed zero. HMSC models were used to estimate the posterior distributions of species prevalence or abundances in relation to environmental covariates, as well as their median and credible intervals. We then stacked individual species prevalence and abundance predictions to compute the posterior estimates of species richness and total abundance respectively (Ovaskainen & Abrego, 2020). Differences between intensification levels and periods in species richness, prevalence and abundances were assessed after setting the values of the remaining variables to the mean within each intensification-period combination, and their statistical support was estimated from the overlap between 84% credible intervals, as comparisons using 95% intervals are overly conservative (MacGregor-Fors & Payton, 2013). Effects of phylogeny were assessed with the phylogenetic signal parameter ρ .

3 | RESULTS

3.1 | Olive availability

Olive availability on trees was highest in early winter, when it was much higher in more intensive than in traditional orchards (Figure 1a; Table S5). From early to midwinter, olive availability declined faster in super-intensive than in intensive orchards, becoming more similar to that of traditional orchards. Olive availability in late winter was at its lowest, albeit still higher in more intensive orchards, and virtually nil in traditional orchards. Olive availability on the ground was always

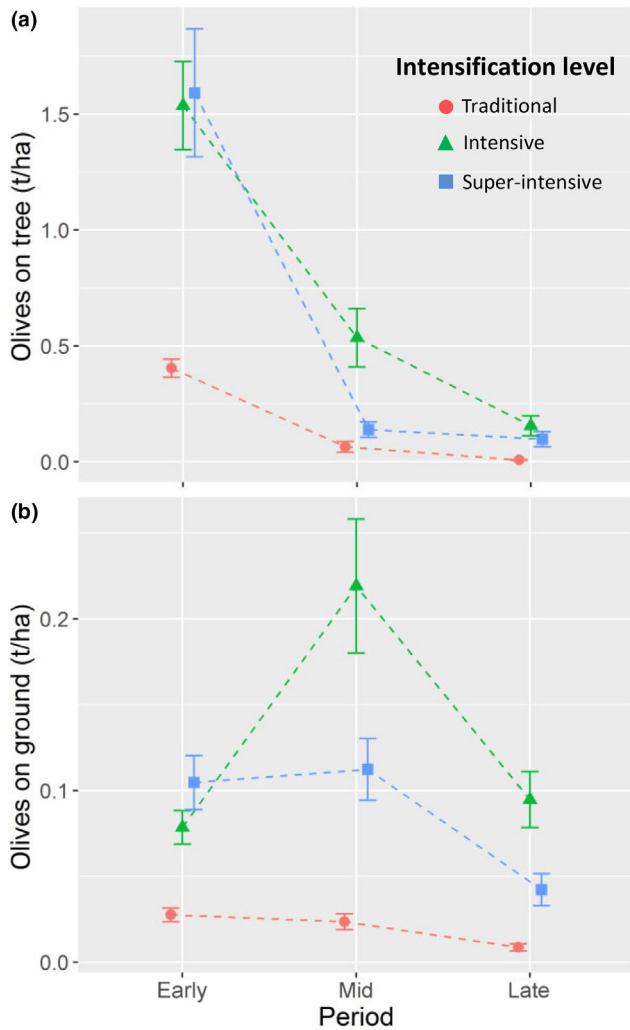


FIGURE 1 Variation in ripe olive availability (t/ha) on trees (a) and on ground (b) in traditional, intensive and super-intensive orchards between early (15–30 November), mid- (1–15 January) and late (15–28 February) winter of 2016–2017, estimated on 78 olive orchards in Portugal. Error bars show mean \pm SE. The position of intensification levels in each time period was slightly shifted to enhance readability. Olive harvest in our region occurs mainly (>50%) in December

higher in intensive and super-intensive than in traditional orchards, but while in early winter it was slightly higher in super-intensive orchards, in mid- and late winter it became higher in intensive orchards (Figure 1b; Table S5).

3.2 | Overall assemblage patterns

We recorded 11 frugivorous and 32 non-frugivorous bird species (Table S1). More species were recorded in traditional (39) than in intensive (35) and super-intensive (32) orchards, with five, one and one exclusive species in each respectively (Figure S5; Table S1). The three most widespread (frequency of occurrence >40%) species

(song thrush *Turdus philomelos*, blackcap *Sylvia atricapilla* and robin *Erithacus rubecula*) were frugivorous, and together accounted for nearly 50% of the birds counted (Table S1).

3.3 | Species prevalence and richness

The occurrence model had moderate to high discrimination ability as measured by AUC (0.87 ± 0.08 mean \pm SD; range = 0.64–1.00), while Tjur's R^2 was generally low but varied widely among species (0.09 ± 0.09 ; 0.00–0.45). The AUCs decreased ($r = -0.48$; $p < 0.01$) and Tjur's R^2 increased ($r = 0.70$; $p < 0.01$) with species prevalence (Figure S6). Model explained variation was mainly accounted for by intensification level ($13.2 \pm 7.7\%$ mean \pm SD; range = 2.1%–30.9%), period ($9.1 \pm 6.3\%$; 1.5%–36.3%) and to variation in species responses to intensification across periods ($14.6 \pm 7.1\%$; 2.6%–27.0%), with a high proportion also attributed to olive availability ($12.4 \pm 7.4\%$; 1.4%–25.6%) and landscape context ($9.7 \pm 8.5\%$; 0.8%–37.6%; Figure S7A). Species responses were affected by dietary preferences, albeit weakly (7.1% of variation) and phylogeny ($\rho = 0.87$; 95% credible interval = 0.68–0.99).

For 20 of 42 species modelled, all statistically supported main effects and/or interactions involving intensification level were negative, pointing out its generally negative effects after controlling for the influence of other variables (Figure 2). The only exceptions were the positive main effects of super-intensive orchards on chaffinch *Fringilla coelebs*, linnet *Linaria cannabina*, greenfinch *Chloris chloris* and Sardinian warbler *Sylvia melanocephala* (Figure 2). The prevalence of blackcap and song thrush increased with olive availability on trees, while blackcap and robin increased with olives on the ground (Figure 2; Figure S8). Landscape cover by olive orchards positively affected blackcap, song thrush, short-toed treecreeper *Certhia brachydactyla*, hoopoe *Upupa epops* and serin *Serinus serinus*, and negatively so six species (Figure 2; Figure S8). Considering the average values of olive availability and landscape cover within intensification–period categories, the model predicted higher prevalence of corn bunting *Emberiza calandra*, blue tit *Cyanistes caeruleus*, great tit *Parus major* and four relatively rare species in traditional orchards, while linnet, serin, blackcap and song thrush were more prevalent in more intensive orchards, at least in some periods (Figure S9).

There was no statistical support for species richness varying across intensification levels, except for the higher richness of non-frugivorous species in midwinter in traditional orchards (Figure 3). Frugivorous richness was positively affected by olive availability on ground and, particularly, by increasing landscape cover by olive orchards, while non-frugivorous richness declined with increasing orchard cover (Figure S10).

3.4 | Species abundances

The variation explained by the abundance model varied widely among species ($R^2 = 0.19 \pm 0.17$ mean \pm SD; range = 0.01–0.65), with higher

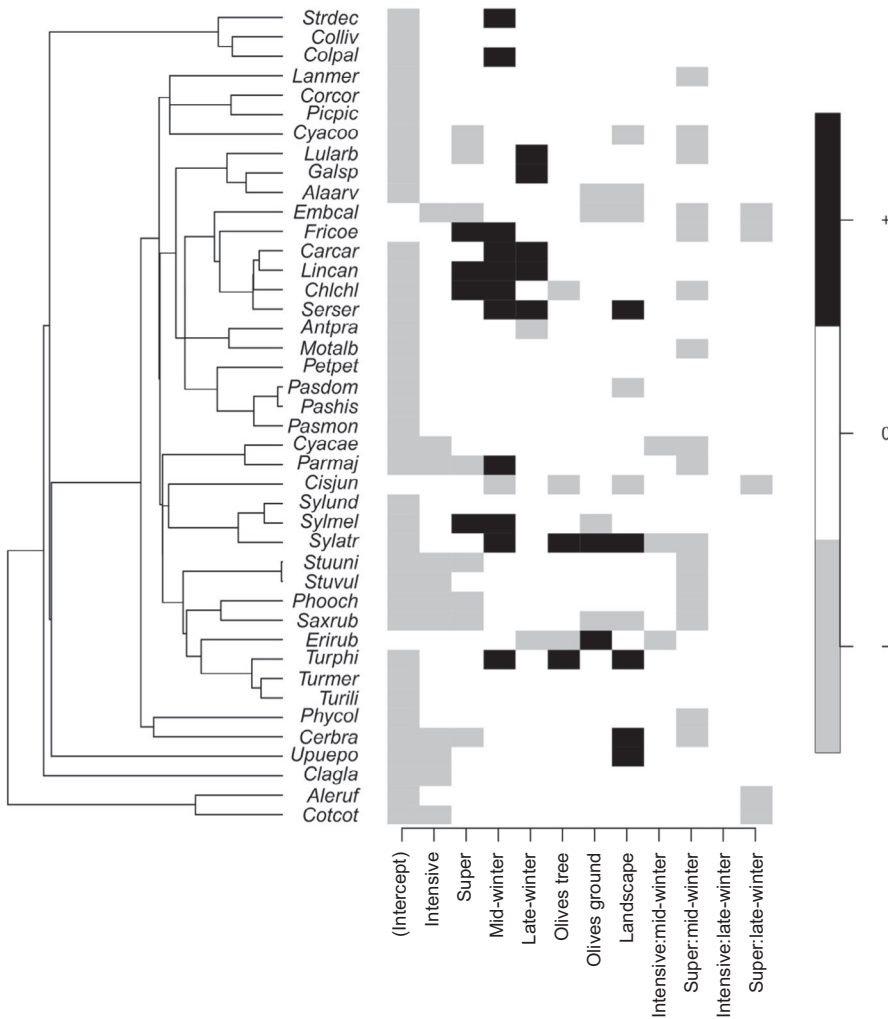


FIGURE 2 Heat map showing statistically supported coefficients (95% credible intervals not intersecting zero) of linear predictors estimated by the HMSC, relating the prevalence of 42 bird species to intensification level and period (and their interaction), olive availability (trees and ground) and landscape cover by olive orchards. Black and grey colours represent positive and negative coefficients respectively. Reference levels for intensification and period categories are traditional orchards and early winter. Species codes in Table S1

values for more abundant species ($r = 0.84$; $p < 0.001$; Figure S6C). The explained variation was largely accounted for by intensification level ($11.9 \pm 7.9\%$ mean \pm SD; range = 1.7%–28.0%), period ($11.2 \pm 7.6\%$; 2.3%–21.7%) and their interaction ($15.4 \pm 9.6\%$; 2.2%–35.9%), but was also attributed to olive availability ($8.1 \pm 7.1\%$; 1.5%–24.2%) and landscape context ($5.7 \pm 6.9\%$; 1.1%–29.0%; Figure S7B). Species responses were affected by dietary preferences (21.6% of variation) and phylogeny ($\rho = 0.90$; 95% credible interval: 0.52–1.00).

From 16 species modelled, all statistically supported main effects and/or interactions involving intensification level were negative for greenfinch, corn bunting, white wagtail *Motacilla alba*, great and blue tits and robin, and positive for chaffinch, goldfinch *Carduelis carduelis*, linnet, serin and song thrush (Figure 4). For Sardinian warbler and blackcap, there were both positive and negative coefficients, indicating contrasting effects of intensification in different periods (Figure 4). Blackcap and song thrush abundances increased with olive availability on both trees and the ground, whereas robin only responded positively to the latter. Blackcap, robin and song thrush abundances increased with landscape cover by olive orchards, while corn bunting showed the opposite response (Figure 4; Figure S11). At average levels of the other variables within intensification and period categories, there was much higher abundance in intensive

and/or super-intensive orchards, at least in some winter periods, of linnet, serin, blackcap and song thrush, while the reverse was found for corn bunting, and great and blue tits (Figure S12).

There was statistical support for higher total bird abundance in intensive and/or super-intensive orchards in early and late winter, and for higher abundance of frugivorous birds in more intensive orchards throughout the winter (Figure 5a,b). Non-frugivorous abundance was higher in traditional than in intensive and super-intensive orchards in early and midwinter respectively (Figure 5c). Total and frugivorous bird abundance increased with olive availability, particularly on the ground, and with landscape cover by olive orchards, while non-frugivorous species tended to decline with increasing orchard cover (Figure S13).

4 | DISCUSSION

Our study confirmed marked effects of intensification on olive availability and on birds wintering in olive orchards. Olive availability was always higher in more intensive orchards, mainly in trees in early winter, and then on the ground later in the season. Local abundances of frugivorous birds were higher in more intensive orchards, and

FIGURE 3 Variation in total (a), frugivorous (b) and non-frugivorous (c) bird species richness predicted by the HMSC model, in early, mid- and late winter, in traditional, intensive and super-intensive olive orchards. Boxes show posterior median \pm interquartile range, and whiskers show 84% credible intervals

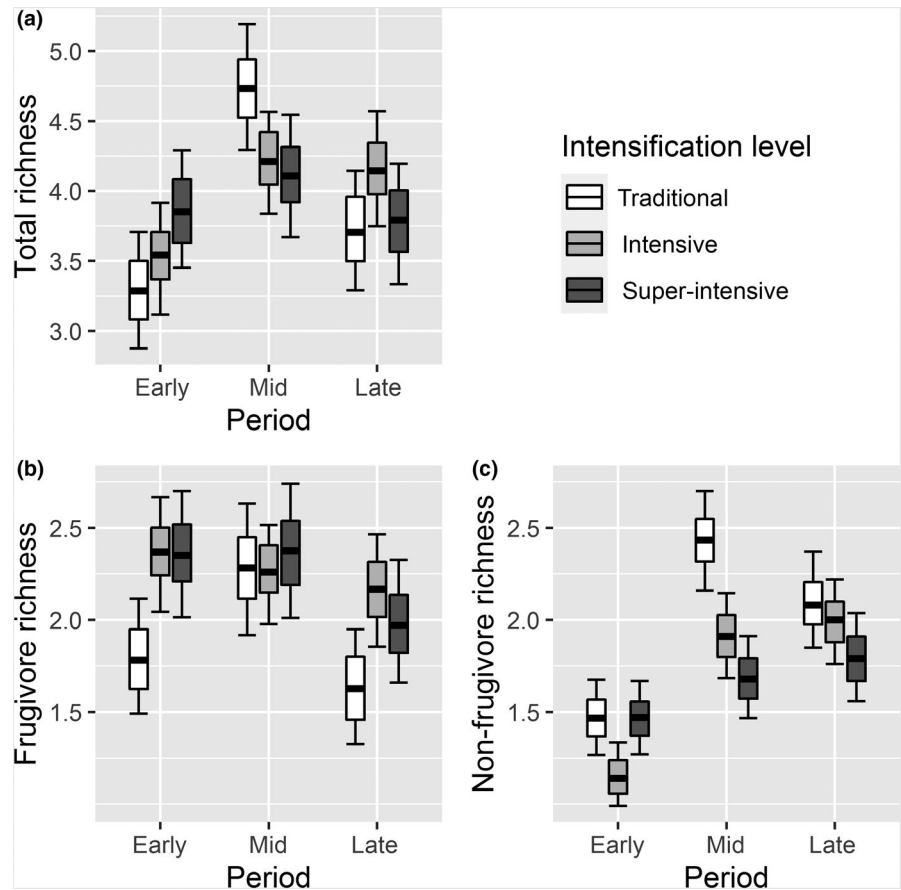
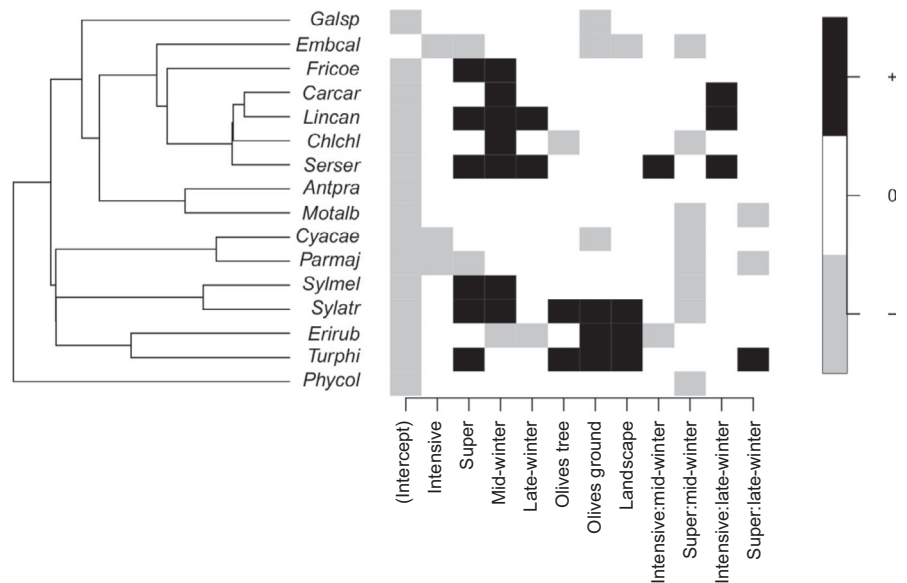


FIGURE 4 Heat map showing statistically supported coefficients (95% credible intervals not intersecting zero) of the linear predictors estimated by the HMSC, relating the abundance of 16 bird species to intensification level and period (and their interaction), olive availability (trees and ground) and landscape cover by olive orchards. Black and grey colours represent positive and negative coefficients respectively. Reference levels for intensification and period categories are traditional orchards and early-winter. Species codes in Table S1



increased with olive availability and landscape cover by olive orchards. Except for some generalist finches, there were clearly negative effects of intensification on most non-frugivorous birds, which also responded negatively to increasing landscape cover by olive orchards. Overall, our findings point out the need to find management solutions to promote potential benefits of olive farming intensification on wintering frugivorous birds, while mitigating strongly negative impacts on other components of biodiversity (Moreira et al., 2019).

4.1 | Intensification favours frugivorous birds through increased olive availability

The higher availability of olives in more intensive orchards was probably due to their much higher productivity (IOC, 2015). Availability on trees peaked in early winter, and was much lower in mid- and late winter, probably because of olive harvest between the first and the second sampling periods. This is supported by the timing of

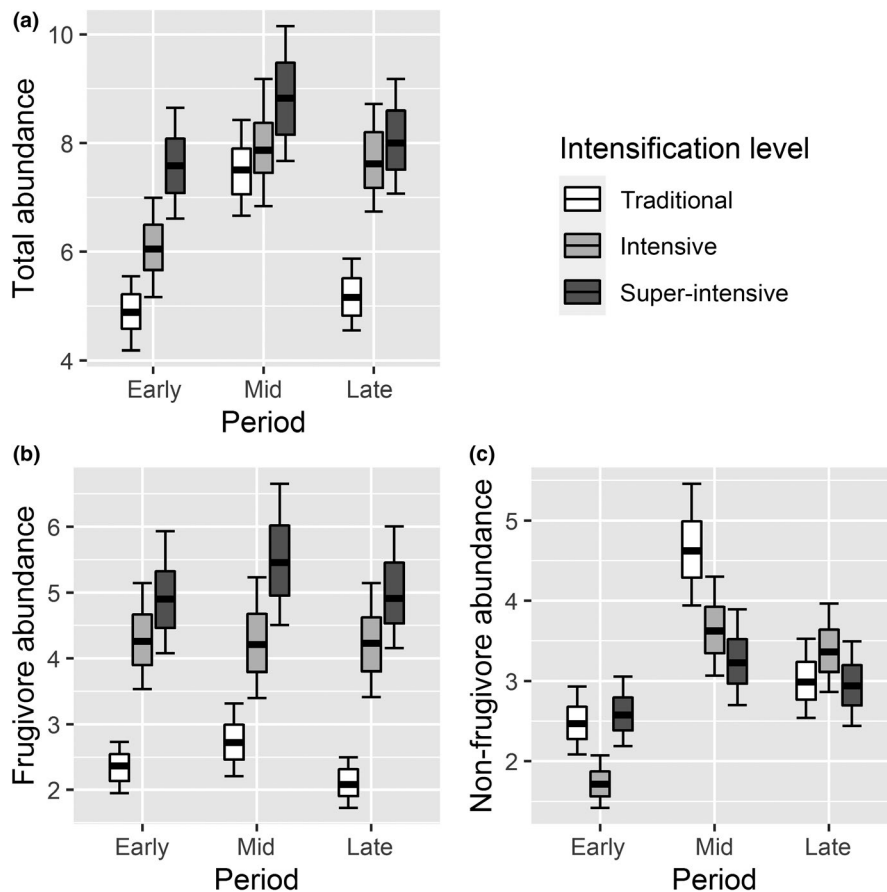


FIGURE 5 Variation in total (a), frugivorous (b) and non-frugivorous (c) bird abundance predicted by the HMSC model, in early, mid- and late winter, in traditional, intensive and super-intensive olive orchards. Boxes show posterior median \pm interquartile range, and whiskers show 84% credible intervals

harvesting in our region, which is mainly conducted in November and, particularly, in December (GPP, 2021). Olive availability in midwinter was highest in intensive orchards, particularly on the ground, probably because highly efficient mechanical harvest in super-intensive orchards resulted in less olives remaining on trees and spilled on the ground (Tous et al., 2010), while very low availability in traditional orchards reflected their low productivity. Olive availability in late winter was at its lowest, but still higher in more intensive orchards.

As expected from fruit-tracking behaviour (Rey, 1995; Tellería & Pérez-Tris, 2003), frugivorous bird abundances were positively associated with olive availability. This effect was particularly evident for widespread and abundant species feeding heavily on olives during winter, such as blackcap, song thrush and robin (e.g. Rey, 1993, 2011). There were some differential effects of olive availability in trees versus on the ground, with for instance the ground-feeding robin only associating positively with the latter (Snow & Snow, 1988). Conversely, blackcap and song thrush were positively influenced by olive availability both in trees and on ground, possibly reflecting foraging flexibility by species that are primarily tree and ground foragers respectively (Snow & Snow, 1988). The strongly positive responses of blackcap and song thrush to cover by olive orchards possibly reflect their concentration in large numbers in landscapes with high fruit availability.

Structural orchard changes across intensification levels showed relatively limited effects on frugivorous birds after controlling for olive availability. The most consistent exception was Sardinian

warbler, a resident species associated throughout the year to shrubland-like super-intensive orchards mimicking their natural habitats (Morgado et al., 2020), which often produce relatively small olives (<2 g; Tous et al., 1999) that can be swallowed by small warblers (Rey et al., 1997). Song thrush and blackcap abundances were higher in super-intensive orchards after accounting for olive abundance. The effect on song thrush was stronger in late winter despite the lower olive availability in super-intensive than intensive orchards, probably because they use the former mainly for night roosting at this time of year (R. Morgado unpubl. data). Overall, our results suggest that frugivorous bird responses to intensification were mainly driven by olive availability at orchard and landscape scales, with structural orchard features playing a secondary role.

4.2 | Negative impacts of intensification on non-frugivorous birds

The consequences of olive farming intensification on non-frugivorous species were mainly negative. Exceptions were chaffinch, greenfinch, linnet and serin, which showed largely positive responses to super-intensive orchards and/or increased cover by olive orchards. This is probably because these are generalist species that often occupy highly modified landscapes (Billerman et al., 2021), including intensive olive orchards in spring (Morgado et al., 2020) and other intensive permanent crops (Assandri et al., 2017; Genghini et al., 2006).

Most other species responded negatively to intensive and, particularly, super-intensive orchards after controlling for other variables, including game birds (quail *Coturnix coturnix*), corvids (Iberian magpie *Cyanopica cooki*) and woodland (e.g. treecreeper, great and blue tits) and open farmland (e.g. corn bunting) birds. Broadly similar responses were observed during the breeding season, probably reflecting marked changes in orchard structure along the intensification gradient, from large and old trees planted at low density, in traditional orchards, to young and small trees planted at very high densities, in super-intensive orchards (Morgado et al., 2020). Other factors correlated with structural changes may also be at play, including disturbance through mechanised operations, and higher application of agro-chemicals (Infante-Amate et al., 2016; Tous et al., 2010) potentially reducing food availability (Ruano et al., 2004; Solomou & Sfougaris, 2011). Many species also reacted negatively to increasing cover by olive orchards, particularly open farmland species such as skylark *Alauda arvensis*, corn bunting, zitting cisticola *Cisticola junco* and stonechat *Saxicola rubicola*, which tend to decline with increasing landscape cover by woody habitats (Morgado et al., 2020; Rey et al., 2019; Santos & Cabral, 2004). These results suggest that apart from frugivorous birds and a few generalist finches, intensification of olive cultivation has generally negative impacts on wintering bird assemblages (Muñoz-Cobo et al., 2001).

4.3 | Conservation and management implications

Several studies have documented major negative effects of olive farming intensification on biodiversity, mainly due to the conversion into intensive and super-intensive orchards of other agricultural land uses (Ribeiro et al., 2014), including species-rich traditional olive orchards (Costa et al., 2020; Herrera et al., 2015; Morgado et al., 2020), and open farmland providing habitat for globally threatened steppe birds (Moreira et al., 2012; Santana et al., 2017). Our study showed similar negative effects of intensive olive farming on wintering non-frugivorous birds, thus supporting calls for halting or reducing its expansion, through the use of agri-environmental subsidy schemes and market mechanisms (e.g. certification) to maintain traditional groves and other crops with higher biodiversity value, as well as legal restrictions to new plantations in high nature value farmland (Moreira et al., 2019; Santana et al., 2017). Our results also support the need to avoid homogenisation resulting from the overly dominance of olive orchards at the landscape scale, which would require mechanisms promoting mosaics of semi-natural habitats and different agricultural land uses, including for instance a mix of different olive orchard types that were found to be favoured by different bird species in different periods of the winter.

Despite their wider negative effects, more intensive orchards appeared favourable for frugivorous birds, at least at the local scale. However, the population-level implications of this result require further investigation. On the one hand, olive availability in highly productive orchards may increase the carrying capacity of Mediterranean agro-ecosystems for frugivorous birds, and thus

favour their populations at the continental scale. Also, high olive availability may increase winter survival and body condition, which in turn might enhance migration survival and fecundity. On the other hand, birds in more intensive orchards are exposed to risks, due in particular to high mortality associated with mechanical night harvest (INIAV, 2020; Silva & Mata, 2019). Also, heavy use of agro-chemicals, together with landscape homogenisation, may reduce the availability of alternative foods (Bergmeier & Strid, 2014; Cárdenas et al., 2006; Rey, 2011; Ruano et al., 2004; Solomou & Sfougaris, 2011), which may be problematic in late winter when olive availability is low. Finally, olives may be contaminated with pesticide residues (Cabras et al., 1997), with poorly known but potentially serious consequences for birds (Schabacker et al., 2020). Overall, our results are encouraging regarding the ability of intensive olive farming to sustain frugivorous birds, but we recommend that exposure to risks should be reduced by stopping night harvest (Silva & Mata, 2019), increasing heterogeneity at local (woody hedges, herbaceous cover) and landscape (semi-natural habitats and diverse land uses, including different olive orchard types) scales to promote alternative food sources (Assandri et al., 2017; Bouvier et al., 2020; Castro-Caro et al., 2015; Rey et al., 2019) and reducing agro-chemical use to avoid negative effects on birds and their foods (Rey, 2011).

5 | CONCLUSIONS

The intensive production of olives and other fleshy fruits has strongly negative impacts on biodiversity, and should thus be restricted in high nature value farmland. However, some intensive fruit crops may be compatible with frugivorous bird conservation, though requiring management targeted at reducing direct mortality, undernourishment in certain periods and pesticide contamination. While favouring frugivorous birds within fruit crops may be impossible where they cause significant economic damages, there may be opportunities in olive orchards and other systems where such damages are marginal, and their conservation may be an environmental added value. Agricultural policy instruments should promote these benefits, thereby supporting calls to withdraw the current exemption of the olive sector from environmental requirements in the European post-2020 Common Agricultural Policy (CAP) proposal (Moreira et al., 2019).

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CONFLICT OF INTEREST

The authors declare they have no conflicts of interest.

AUTHORS' CONTRIBUTIONS

R.M., F.M. and P.B. conceived the ideas and designed methodology; R.M. and R.P. collected the data; R.M. and M.P. analysed the data; R.M., F.M. and P.B. led the writing of the manuscript. All authors contributed to the drafts and gave final approval for publication.

DATA AVAILABILITY STATEMENT

Data available from the Dryad Digital Repository <https://doi.org/10.5061/dryad.80gb5mkrh> (Morgado et al., 2021).

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