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Threshold responses of birds to agricultural intensification in Mediterranean olive groves

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Abstract

Olive groves are the most representative crop of the Mediterranean basin. This agroforestry system is undergoing a strong transformation in recent decades as a result of the agricultural intensification process prevailing in the Northern Hemisphere. Although some authors have suggested that farmland biodiversity responds non-linearly to the complexity of agricultural landscapes, few studies have used community thresholds to identify potential tipping points. Here, we examined the existence of synchronous responses in bird abundance across a gradient of decreasing agricultural intensification in Spanish olive groves. Our study system comprised 25 sites, each consisting of a pair of farms: one with intensive management and the other one with extensive management of the herbaceous cover. We explored whether bird abundances exhibit non-linear threshold responses to ant abundance and tree density at a local (field) scale, plant diversity (both herbaceous and woody plants) at a local (farm) scale, and to proportion of natural habitat at a landscape scale using Threshold Indicator Taxa ANalysis (TITAN). We found a higher incidence of positive responses with decreasing levels of intensification, and these were not restricted to certain guilds or avian families. Few indicator species showed a significant negative response. Thresholds detected were not sharp but rather gradual changes along the environmental gradients. Although they do not necessarily support evidence of ecological thresholds characterized by rapid changes in species abundance or distribution, these patterns can help identify optimal change points for management decisions. Specifically, our results indicate that reaching a minimum threshold of ~85 and 15 species of herbaceous and woody plants, respectively, per unit of surface can entail a gain in terms of bird diversity for olive farms with virtually no detrimental effects. Overall, this study shows that the adoption of agri-environmental measures like the maintenance of ground cover and patches of natural habitat has a positive impact on different species inhabiting this woody crop, and this effect occurs at different spatial scales.

KEYWORDS
agri-environmental schemes, avian responses, community ecology, ecological gradients, ecological thresholds, extensive agriculture, farmland, *Olea europaea*, woody crop

INTRODUCTION

Olive groves (*Olea europaea*) constitute one of the most emblematic crops in the Mediterranean basin, a global biodiversity hotspot (Blondel et al., 2010). They have been an idiosyncratic feature of Mediterranean landscapes for millennia and, currently, they extend over more than 11 million ha across this region (FAO, 2023). Given their distribution across southern Europe, this woody crop represents an important refuge for wildlife, especially for frugivorous wintering birds like thrushes and warblers that find these "managed forests" a larder with which to face the harshest months (Rey, 2011). In addition to being a highly valuable agroecosystem for biodiversity and having a significant ecological role, olive groves are of high economic importance in the Iberian Peninsula and other zones of the Mediterranean basin such as Calabria, Lesbos, and Peloponnese (Loumou & Giourga, 2003). In Spain, olive groves are the most extensive permanent crop and constitute a large part of the gross domestic product in regions such as Jaén and Córdoba in Andalusia (Infante-Amate, 2012). Olive farming is well rooted in the cultural and social heritage of Southern Spain, and together with the *dehesas* (oak savannahs) constitutes a paradigmatic case of agrosystem that promotes biodiversity and, in turn, generates social externalities including the maintenance of population in rural areas and the preservation of tradition and local knowledge (de Graaf & Eppink, 1999; Rodríguez-Cohard et al., 2019).

Over the last 30 years, olive farming, like that of vines, has undergone a rapid transformation toward more productive and mechanized management in line with the intensification of agriculture in Europe (Emmerson et al., 2016). The global increase in olive oil consumption and the economic incentives of the Common Agricultural Policy (CAP) have contributed to the expansion of intensively managed olive orchards, which can negatively impact the biological communities inhabiting this woody crop (Carpio et al., 2017; de Paz et al., 2022). Intensive farming operates on two scales: local and landscape. At a local scale (i.e., individual farm), practices such as herb cover removal, use of pesticides and other chemical inputs, increase in tree density, and mechanization of the pruning and harvesting work are implemented to increase crop productivity (Kleijn et al., 2009). At the scale of the surrounding landscape, the expansion of monocultures and the eradication of steppe habitat, fallow land, hedgerows, ponds, and patches of natural vegetation have become common practices, which lead to smaller species pools and reduced species turnover among localities (Concepción et al., 2008; Tscharntke et al., 2005). Several studies have shown that this intensification process reduces the abundance and diversity of invertebrates (e.g., ants; Zumeaga et al., 2021) and leads to an impoverishment of vegetation (Carmona et al., 2020; Tarifa et al., 2021). This contributes to erode the taxonomic and functional diversity of birds that use olive groves as habitat (Castro-Caro et al., 2015; García-Navas, Martínez-Núñez, Tarifa, Manzaneda, Valera, Salido, Camacho, Isla, et al., 2022; Morgado et al., 2020; Pérez et al., 2023; Rey et al., 2019) and consequently, the ecological value of this agrosystem as a biodiversity refuge gets lost. However, studies providing practical recommendations for a more sustainable and biodiversity-friendly management of olive groves are scarce. This is crucial for local producers, managers, and other stakeholders to implement measures that make modern farming compatible with wildlife conservation. For instance, García-Navas, Martínez-Núñez, Tarifa, Manzaneda, Valera, Salido, Camacho, and Rey (2022) found that the surface covered by olive groves has a meaningful impact on the ecological uniqueness of farms. It means that extensive areas devoted to this crop (i.e., olive monocultures) can reduce the dissimilarity among localities and lead to a process of biotic homogenization. Specifically, they identified a threshold (around 25%–50%) from which local contribution to overall beta diversity declines with increasing area devoted to olive production (García-Navas, Martínez-Núñez, Tarifa, Manzaneda, Valera, Salido, Camacho, & Rey, 2022). In the same direction, some threshold of semi-natural habitats seems fundamental to avoid the collapse of some avian-delivered ecosystem services in olive landscapes. For example, 15%–20% of semi-natural woodland cover is needed to maintain some species of avian frugivores, enhancing the overall seed dispersal in these landscapes (Tarifa et al., 2024), particularly that provided by some summer migrants.

Ecological thresholds are useful tools for managers and ecologists as they allow us to identify tipping points beyond which ecological processes show a rapid, non-linear response to an incremental change in environmental pressures (Bestelmeyer et al., 2011; Brown et al., 2021; Gutzwiller et al., 2015). Hence, community thresholds represent asynchronous change in multiple taxa that are similarly influenced by an environmental gradient, which is of utmost interest for conservation purposes. For instance, assessing the response of individual bird species to vegetation change can thus help identify change points that mark noticeable declines in species descriptors along vegetation cover gradients (Macchi et al., 2019; Macchi & Grau, 2012). The identification of ecological thresholds based on community data along disturbance gradients is essential when implementing conservation measures in anthropogenized systems (Gutzwiller et al., 2015). In turn, this allows us to test the existence of segregation in the response of species in relation to their ecological guild (e.g., Brown et al., 2021). To our knowledge, few studies have adopted this approach to identify patterns of community change and to improve our understanding of how agroecosystem management can be optimized to achieve biodiversity conservation goals (but see Pardo et al., 2018; Salgueiro et al., 2018). This is striking since it has been shown that farmland biodiversity responds non-linearly to the complexity of agricultural landscapes (Concepción et al., 2012; Vallé et al., 2023).

Here, we examined the existence of change points in bird abundance across a gradient of agricultural intensification in Spanish olive groves. We tested if birds exhibit non-linear threshold responses to ant abundance, plant diversity (both herbaceous and woody plants), and tree density at a local scale, and to the proportion of natural habitat within 1-km radius landscapes surrounding olive farms. In this way, by examining the response of bird communities to agricultural stressors (Figure 1a), we can infer at what level there is an impoverishment of the avifauna and establish the minimum threshold above which increased agricultural intensification does not compromise the preservation of biodiversity associated with this millenarian woody crop.

MATERIALS AND METHODS

Study system

The LIFE+ "Olivares Vivos" project (www.olivaresvivos.com), in which this research is framed, aims to promote the sustainable and integrated management of olive farms in the Mediterranean region by disseminating science-based actions (Rey et al., 2019). The main objective of this project is to define a model of viable olive growing from an agronomic, economic, and social point of view, and effective in halting the alarming loss of biodiversity observed in agricultural landscapes of the Northern Hemisphere (Rigal et al., 2023).

For this study, we chose 50 olive farms from the "Olivares Vivos" study system located in Andalusia ($n = 42$), Castilla-La Mancha ($n = 6$), and Extremadura ($n = 2$) (Figure 1b; Appendix S1: Table S1). We followed a paired design in which we selected two olive farms in each locality (i.e., 25 localities, 50 farms): a farm with intensive management that most frequently involved the use of pre- and/or post-emergence herbicides and/or recurrent plowing for herbaceous cover elimination over the whole year; and a farm with extensive management of the cover, implying its maintenance during most of the year and its eventual removal by mechanic mowing or cattle grazing in late spring (see Rey et al., 2019 for more details). Each farm includes non-productive (i.e., semi-natural) areas interspersed among or surrounding the productive olive grove field areas (infield areas) (see more below). Study sites were selected to encompass a wide gradient of olive grove and semi-natural habitat cover at the landscape scale (see details in *Predictors of olive grove intensification*). This study system represents a two-level gradient of olive-growing intensification, ranging from traditional olive groves with a well-developed ground herb cover and embedded within a matrix of natural habitat, to vast monoculture olive grove landscapes with bare soils and little to no natural habitat (Figure 1b).

Bird censuses

Avian communities at 50 farms were surveyed every 4 months by a team of three skilled ornithologists under favorable weather conditions. Forty farms were censused from April 2016 to March 2017 and the other 10 farms from April 2022 to March 2023. We do not expect the fact we conducted the censuses in two different periods to affect our results as the observer team was the same and variations between farms and sites in agricultural stressors (see *Predictors of olive grove intensification*) are thought to influence bird abundance, diversity, and assemblage composition much more than the stochastic (climatic, demographic) interannual variability. In each of these four bird surveys, we carried out 6 (in small olive farms; <25 ha) or 10 (in large olive farms; >50 ha) census stations using the point-count method (Bibby et al., 1992), with around 2/3 of the census stations placed in the olive field and 1/3 in semi-natural habitats (i.e., unproductive zones) of the farm. Each census lasted 5 min during which the presence of all birds seen or heard inside a 100-m radius was recorded. To avoid repeated counts between neighbor

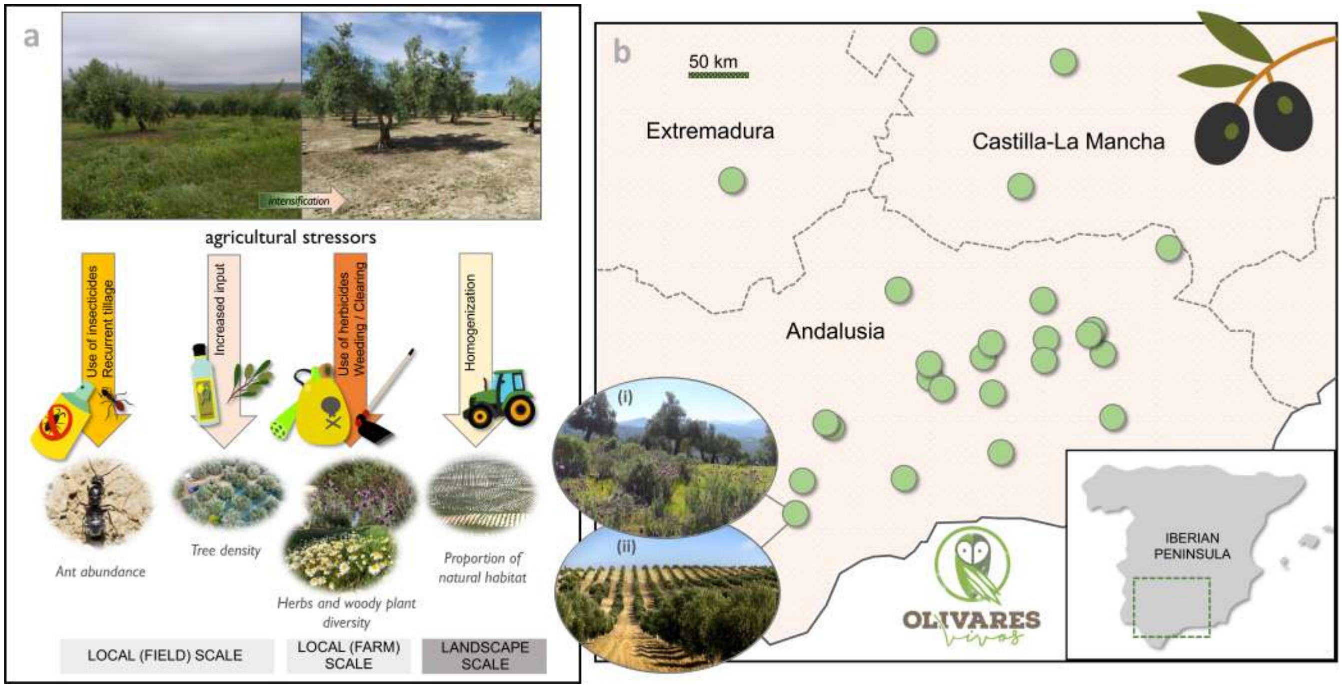

FIGURE 1 (a) Diagram showing the different environmental variables considered in the present study. These variables are affected by different stressors that define a gradient of agriculture intensification at different scales: local and landscape. Within the local scale, we define two levels: field-level (which only comprises the productive zone), and farm-level (which comprises both productive and non-productive zones, i.e., the whole farm). (b) Map of the study region in Southern Spain with the location of the 25 "Olivares Vivos" sites, each consisting of two olive farms, one extensively managed (*i*) and one intensively managed (*ii*). See www.olivaresvivos.com for further details about the study system. Illustrations: Alba Martín del Campo. Logo and photographs: "Olivares Vivos" team (reused under a Creative Commons Attribution License: https://creativecommons.org/licenses/by/4.0/).

census stations, they were located at least 200 m apart in small farms and at least 300 m apart in large olive farms. A total of 82 bird species were recorded in at least five farms (see *Analyses*). Large and nocturnal raptors and waterbirds were not considered because these taxa cannot be correctly monitored using this methodology. All bird species were characterized in terms of diet (frugivorous, granivorous, insectivorous, vertebrate-eating/scavenger, and omnivorous) and foraging strategy (aerial-hawker, canopy-gleaner, trunk-gleaner, shrub-gleaner, perch-and-pounce, ground-dweller, and generalist) according to López and Martín (2025), Tobias et al. (2022), Wilman et al. (2014), and personal observations.

Predictors of olive grove intensification

We characterized the level of agricultural intensification of each olive farm and its landscape context using five continuous environmental variables, four at a local scale (with two levels; field-level, which only includes the productive zone; and farm-level, which includes both productive and non-productive zones, i.e., the whole farm) and one at the landscape (1 km radius circular buffer around each farm) scale. At a local scale, we estimated ant abundance, olive tree density, and herb and woody species richness. At the landscape scale, we measured the percentage of semi-natural habitat (see below).

Ant abundance was censused within the productive zone (infield) using pitfall traps in the same sampling stations used for bird censuses. Many bird species consume formicids on a daily basis as part of their diet, and thus the abundance of these insects can be used as a proxy for food availability susceptible to decrease by intensification of soil management agricultural practices within the cultivated fields (Cabodevilla et al., 2021; Hódar, 1998; Wilson et al., 1999). Specifically, in southern Spain, it has been reported that ant-eating behavior is widespread among avian species during certain periods of the annual cycle; for instance, Herrera (1983) and Jordano (1981) reported that some species rely heavily on this prey type during the autumn period (see Appendix S1: Table S2). During the breeding period, ants constitute an important source of proteins for nestlings and adult birds because of their ready availability and abundance, and their presence and that of other insects can be severely reduced due to the use of pesticides and recurrent soil tillage (e.g., Herranz et al., 1997; Rocher et al., 2022; Rueda et al., 1993). Consequently, ant abundance can be considered a proxy for food availability in this region. Additionally, it has been suggested that ants serve as valuable indicators of biodiversity and ecosystem function in natural systems (i.e., ecosystem engineers). Ants respond quickly to habitat disturbances, pesticide use, and soil modifications, making them useful for detecting changes in land management and informing about soil quality (e.g., Andersen et al., 2002; Lobry de Bruyn, 1999). Ant sensitivity to olive growing and landscape use intensification has also been documented in the "Olivares Vivos" study system (García-Navas, Martínez-Núñez, Tarifa, Manzaneda, Valera, Salido, Camacho, & Rey, 2022; Martínez-Núñez et al., 2021; Rey et al., 2019).

We set between 8 and 12 pitfall traps (7 cm diameter, 12 cm depth) in each farm depending on its size (12 traps in large farms and eight traps in small farms). Traps were filled with a 1:1 mixture of water and propylene glycol (and some soap drops) and set up at three dates, corresponding to spring, summer, and autumn surveys, remaining active approximately 1 month in each survey (see also Rey et al., 2019). We estimated the abundance of ants per trap in each olive farm. Because some pitfalls were not retrieved at some surveys and the exact number of days was not exactly the same in each locality due to weather conditions at the collecting dates, ant abundance is standardized in terms of per 7 days of exposition by dividing the ants collected in each pitfall by the number of total days of pitfall exposure per survey. We also estimated olive tree density per hectare within the productive zone of each farm using Google Earth images (www.earth.google.com). This was done by counting manually on these images the total number of olive trees within each of the 100-m radius bird census stations that were GPS-located in the field and mapped in Google Earth. Note the number of trees within a farm, or within large sections of each farm, is usually the same, as they are under regular tree planting frames within the farm. The study farms comprise olive groves with low (<100 trees ha^{-1}) and medium or moderately high (<300 trees ha^{-1}) tree density.

Herbaceous species richness was surveyed only in spring coinciding with the dates on which the bird surveys were conducted at each farm; that is, monthly during the 2016 and 2022 campaigns. Surveys were conducted in non-permanent 1-m^2 quadrats ($n = 18$ and 30 in small and large farms, respectively, considering both olive field and semi-natural habitat) placed randomly close (<10 m) in the same sampling stations used for bird censuses (Tarifa et al., 2021). It has been shown that a greater diversity of herbaceous plants positively influences avian communities inhabiting oil palm and rubber plantations (Azhar et al., 2013; Warren-Thomas et al., 2020). The classification of herbs was conducted in the field when possible; yet, material was also collected for taxonomic corroboration in the lab if needed. Herb richness was significantly correlated with herbaceous cover ($n = 50$, $\rho = 0.43$, $p = 0.002$).

Woody plant richness was estimated once in a buffer of a 50-m radius around each of the sampling points set in each farm for bird censuses (including both productive and non-productive zones) during the autumn-winter period of 2016 ($n = 40$ farms) and 2022 ($n = 10$ farms). In each sampling point, we set nine squares of 100 m^2, evenly distributed across the entire 50-m radius area. The presence of woody elements can positively affect species that rely on dense vegetation for foraging and/or nesting, which commonly leads to high bird diversity in agroforestry systems (Edo et al., 2024; Godinho & Rabaça, 2011).

Next, we applied rarefaction based on sample coverage using *iNEXT* 3.0.0. (Chao et al., 2014; Hsieh et al., 2016) to produce unbiased estimations of species richness. We obtained separate indices of rarified species richness for herbs and woody plant species at the local (farm-level) scale, pooling information on species occurrence from all the periodic surveys for each sampling station in each olive farm. Following Chao et al. (2014) and Colwell et al. (2012), we considered as an unbiased estimate (projection) of species richness the point of the species accumulation curve corresponding to an extrapolation of twice the number of independent sampling stations across surveys (S36 and S12 for herbs and woody plants, respectively). The minimum species coverage on the species accumulation curve across olive groves was mostly around 0.9, both for herbs and woody plants (Appendix S1: Table S1), which indicates that our estimates were overall close to the asymptote.

We quantified the percentage of natural habitat cover (including woodlands, scrublands, semi-natural grasslands, and hedgerows) as an estimate of landscape compositional heterogeneity (Martin et al., 2019). The percentage of natural cover was measured at a 1-km-radius buffer around the centroid of each farm using the most updated land-use cartography of the study region (SIOSE, 2014) in QGIS v. 2.14 (QGIS Development Team, 2018). The cover of natural habitat informs about the extent of agricultural landscape homogenization in a given locality and tends to increase bird diversity within plantations, as shown in previous studies (see e.g., Bretagnolle et al., 2018; Sekercioglu, 2012 and references therein). This landscape metric was negatively correlated with the proportion of surface devoted to olive growing ($n = 50$, $\rho = -0.67$, $p < 0.001$).

These five variables characterize the two-scale gradient of agricultural intensification or wildness described in *Study system*. At the landscape scale, the expansion of olive monocultures and the loss of natural habitat represent intensification, leading to habitat degradation and reduced resources for birds. Meanwhile, at the local (farm) scale, intensive farming is characterized by the removal of ground herb cover and/or increased olive tree density within olive fields. This intensive management, including the recurrent use of insecticides and herbicides, depletes the vascular flora and associated arthropod fauna, while altering olive tree density and structure, potentially affecting food availability and nesting sites for birds (Martínez-Núñez et al., 2021; Morgado et al., 2020; Rey et al., 2019; Tarifa et al., 2021; Vasconcelos et al., 2022).

Analyses

We adopted the Threshold Indicator Taxa ANalysis (TITAN) method devised by Baker and King (2010) to identify abrupt changes in the abundance of individual bird species along environmental gradients in: field-level (1) ant abundance and (2) olive tree density per hectare; farm-level (3) herbaceous richness and (4) woody plant richness; and landscape-level (5) percentage of natural habitat within a 1-km radius. This approach combines change point analysis (King & Richardson, 2003) and indicator species analysis (IndVal) (Dufrêne & Legendre, 1997). Indicator species are organisms associated with a specific environmental condition, where a change in the occurrence or abundance of that species indicates a change in the environment. TITAN uses taxon-specific indicator value scores (normalized on a scale from 0% to 100%) to assess the strength of association between each species and the environmental gradient. The relative strength of indicator value scores on either side of candidate change points indicates whether each species shows a positive ($z+$) or negative response ($z-$) to the analyzed environmental gradient. Species classified as $z-$ are lower in abundance above the change point (cp) value along the gradient, whereas $z+$ species are greater in abundance. Evidence for community-level thresholds among negative and positive responding groups of species (communities) was assessed separately by summing all $z-$ and $z+$ scores for each candidate cp value (only considering indicator species; see below) and identifying the cp with the maximum summed values (sum(z)). Large values of sum(z) scores occur when several indicator species have strong responses at a similar point of the environmental gradient (Baker & King, 2010). TITAN computes the probability (p) of randomly obtaining indicator value scores equal to or greater than observed values, using 500 permutations. Uncertainty around change points is estimated by bootstrapping the original data (500 iterations) and expressed as quartiles, where narrow intervals between upper and lower change point quantiles (5%–95%) reflect sharp, non-linear responses in taxon abundance, whereas broader intervals indicate linear or more gradual responses. From bootstrap resampling, TITAN yields two diagnostic parameters of indicator response quality: reliability and purity. Reliability is the percent of bootstrapped change point indicator value scores that consistently have p-values <0.05. Purity is the percent of bootstrap replicates with the same change point response directions (positive or negative) as the observed response. We only considered taxa as indicators when their reliability and purity values were >95%. As input data, TITAN requires a minimum of five presences across all sites to consider a species. Thus, we excluded species with less than five presences from our analyses. TITAN analyses were implemented using the "TITAN2" package (Baker et al., 2015) in R 4.3.3 (R Core Team, 2025).

RESULTS

We detected 82 bird species with presence in more than four farms (Appendix S1: Table S3). The most common species were *Curruca melanocephala*, *Fringilla coelebs*, *Carduelis carduelis*, and *Chloris chloris*, whereas the less common among the species considered were *Emberiza cia*, *Lophophanes cristatus*, and *Caprimulgus ruficollis*.

Thirty-six bird species out of 82 examined presented significant indicator value scores in some of the five environmental gradients considered. None of the thresholds identified were sharp or rapid declines, but rather gradual changes along the environmental gradients, as shown in Figure 2.

At a local (field) scale, several bird species exhibited positive responses ($z+$) to infield ant (Formicidae) abundance, whereas only one species (*Hippolais polyglotta*) showed a negative response. Most species that increased in abundance as the availability of ants increased were ground-foragers like *Galerida theklae*, *Coturnix coturnix*, or *Alectoris rufa*. These two latter phasianid species (together with *Lanius meridionalis*) showed a synchronous response (Figure 2a). Interestingly, two corvid species (*Pica pica* and *Corvus corone*) also coincided at their change point. The overall avian community increased above a threshold of 25 ants/trap^{-1} week^{-1} (Table 1; Figure 2a). The tree density gradient yielded a low number of pure and reliable taxa ($z+ = 2$ species; $z- = 4$ species), preventing the interpretation of results in a reliable manner (Appendix S1: Figure S1).

At the local (farm) level, we observed positive threshold responses to woody plant and herb diversity (Table 1; Figure 2b,c). Four bird species (*Emberiza cirlus*, *Turdus merula*, *C. melanocephala*, and *F. coelebs*) responded

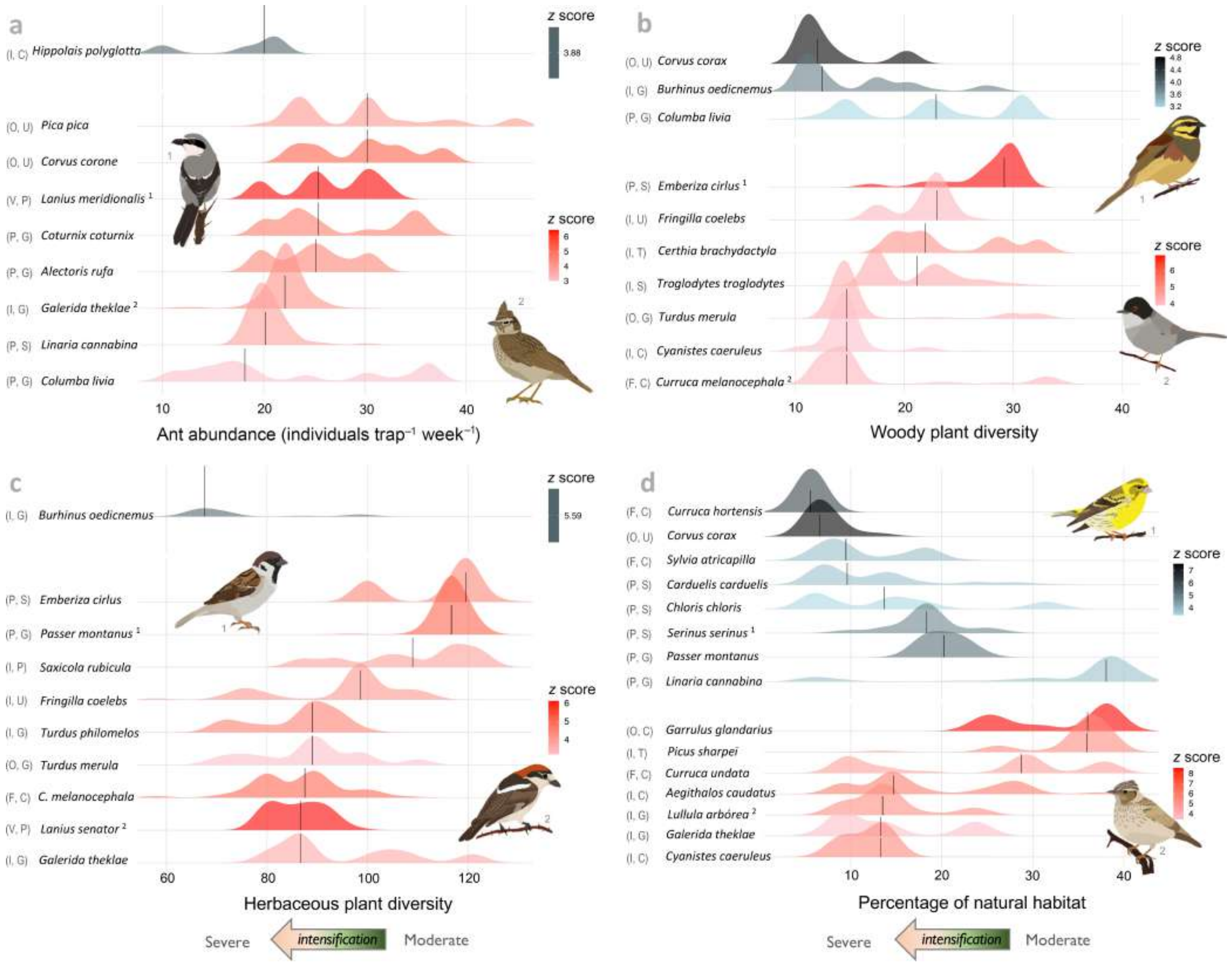

FIGURE 2 Individual response plots of significant ($p < 0.05$) and reliable (purity and reliability ≥0.95) indicator bird species to agriculture intensification in relation to (a) ant abundance, (b) woody plant diversity, (c) herbaceous plant diversity, and (d) percentage of natural habitat in olive groves. Taxa that responded positively (increased in abundance) to the gradient of decreasing intensification are shown in red, while negative responders (i.e., species that increase with intensification) are shown with blue. Taxa change points (across 500 bootstrapped replicates) are visualized as a probability density function with color intensity scaled according to the magnitude of the response (i.e., its standardized z score). Sharp ridges indicate nonlinear response, whereas flat ridges represent linear or more gradual response. The vertical black line indicates the position of the candidate change point. The two letters accompanying each scientific name (listed under the scientific names in panels [a], [b], [c], and to the left of scientific names in panel [d]) indicate the diet (F, fruits; I, invertebrates; O, omnivory; P, plants and seeds; V, vertebrates and carrion) and foraging technique (A, aerial-hawker; C, canopy-gleaner; G, ground-dweller; P, perch-and-pounce; S, Shrub-gleaner; T, trunk-gleaner; U, generalist) of the species according to Tobias et al. (2022), Wilman et al. (2014), and personal observations. Illustrations by Alba Martín del Campo.

positively to these two environmental variables, whereas *Burhinus oedicnemus* presented a negative response in both cases (Figure 2b,c). In relation to herb diversity, indicator species increased in abundance beyond a threshold of ~85 herbaceous plant species, with a relatively broad quantile interval that indicates a gradual response. Remarkably, five bird species showed a synchronous response and increased in abundance with a richer herb layer above the same threshold (Table 1; Figure 2c). In terms of woody plant diversity, birds presented a positive community threshold response to woody plant diversity at a mean richness of 15 woody plant species and few significant negative effects among species (Table 1). Three bird species with broad ecological tolerance (*Cyanistes caeruleus*, *C. melanocephala*, *T. merula*) exhibited a similar response and coincided at the change point, whereas three forest interior species (*Troglodytes troglodytes*, *F. coelebs*, and *Certhia*

TABLE 1 Community-level threshold values (cp: change point) for decreasing agriculture intensification gradients in Mediterranean olive groves.

Environmental variable	Trend	cp	Quantile 0.05	Quantile 0.95
Ant abundance (individuals trap^{-1} week^{-1}) (average: 22.6; range: 5–79)	(−)	21.07[a]	9.54	21.58
	(+)	25.43	19.68	32.44
Woody plant diversity (rarefied richness) (average: 22.3; range: 0–48)	(−)	12.02[a]	10.21	29.78
	(+)	14.73	13.58	32.28
Herbs plant diversity (rarefied richness) (average: 94.7; range: 37–162)	(−)	66.86[a]	58.09	100.47
	(+)	86.61	79.67	101.91
Olive tree density (per ha) (average: 123.6; range: 51–288)	(−)	126.79[a]	96.87	146.07
	(+)	153.93[a]	138.15	161.28
Percentage of natural habitat (%) (average: 18.5; range: 0–81)	(−)	18.31	5.68	20.21
	(+)	14.71	8.81	38.05

Note: Observed change points correspond to the value of the candidate change point resulting in the largest sum of indicator value (IndVal) z scores among all negative (sum(z−)) and positive (sum(z+)) indicator species (i.e., responses are filtered using only indicator taxa with purity and reliability ≥95%). Quantiles (5% and 95%) correspond to change points from 500 bootstrap replicates.

[a]Results must be interpreted cautiously due to the low number of indicator species ($n \leq 5$).

brachydactyla) required a higher diversity (Figure 2b). *E. cirlus*, a thicket-dwelling species with a preference for tangled hedgerows, had the highest IndVal score.

Landscape-level variation in natural habitat cover yielded the highest number of birds with significant indicator values. At this level, we observed an almost similar number of decreasers (z– taxa) and increasers (z+ taxa) in response to percentage cover of natural habitat (Figure 2d). Granivorous species that feed on thistles and weeds and tend to occupy wasteland were the most negatively affected as the proportion of farmland habitat (productive and unproductive zones) decreased, while some bird species increased in abundance above 15% of natural habitat. Two forest species (*Picus sharpei* and *Garrulus glandarius*) showed threshold responses at a higher proportion of natural habitat, suggesting that close habitat species benefit from a more heterogeneous surrounding landscape (Figure 2d).

DISCUSSION

In order to improve food security and human development, agricultural intensification has widely expanded in the Northern Hemisphere during the last decades. Nowadays agriculture is the single largest contributor to biodiversity decline (Dudley & Alexander, 2017) and is considered one of the main drivers of potential biodiversity loss in the near future (IPBES, 2019). The impact of agricultural intensification is particularly relevant in Europe, where approximately 40% of land is farmed (Eurostat, 2021) and where roughly 50% of plant and animal species depend on agricultural habitats (EEA, 2024). In Southern Europe, agroforestry systems traditionally considered biodiversity-friendly or biodiversity-promoting crops have also been affected by this dynamic (Martínez-Nuñez et al., 2024). Olive groves, the flagship crop of the Mediterranean basin, are shifting toward intensification, which translates into increased production, higher requirements in inputs, increased irrigation, and a higher level of mechanization compared to traditional management (Rey et al., 2019). As a result of this transformation, the once-considered "cultivated forest" has seen a decrease in the diversity of plants it harbors, giving rise to olive groves that are increasingly simple and homogeneous in structure, taking on the appearance of tree-lined desert (Infante-Amate et al., 2016). In fact, it has been estimated that since 1980, only some olive groves in Andalusia have lost more soil than in the previous two centuries due to erosion (Gómez et al., 2014). Here, we examined whether birds exhibited non-linear threshold responses to agricultural intensification in the olive groves of Southern Spain. The establishment and determination of ecological thresholds based on community data in modified systems is essential when implementing conservation measures as these allow us to identify those points beyond which certain species increase or others decrease more or less abruptly and thus, manage the trade-offs between production and biodiversity conservation (Huggett, 2005; Spake et al., 2022). Our results suggest that intensification threshold responses were typically gradual rather than sharply non-linear, since the obtained quantile intervals for such thresholds were moderately broad among indicator species. Overall, we found positive responses of birds to decreasing intensification; only a few taxa (mainly early successional and synanthropic species) showed the opposite trend.

Regarding the first agricultural stressor (use of insecticides and recurrent tillage), the narrow distribution of change points along the gradient for ant abundance suggests a consistent positive response of birds to increased food availability. Both small and medium-sized species benefit from this resource (or they respond positively to other variables not considered in this study and related to lower pesticide use and higher insect abundance; i.e., indirect effects), which constitutes a significant part of the diet of a large number of passerines (Herranz et al., 1997; Herrera, 1983; Jordano, 1981) and non-passerines (e.g., *C. coturnix* and *A. rufa*: Cabodevilla et al., 2021; *P. pica*: Díaz-Ruiz et al., 2015; *C. corone*: Soler & Soler, 1991) in Spain. One of the species that showed a positive response was *L. meridionalis*, listed as "Endangered" in Spain (Giralt & Infante, 2021). Shrikes (*L. meridionalis* and *Lanius senator*) seem to constitute excellent indicators of biodiversity in this agro-forestry system since they are typically associated with traditional farms with a low-intensity management of the ground cover (García-Navas, Martínez-Núñez, Tarifa, Manzaneda, Valera, Salido, Camacho, & Rey, 2022; see also Brambilla et al., 2007; Yosef & Lohrer, 1995).

Clearing and weeding (by hand, with machinery or by using herbicides) constitutes another agricultural stressor and defines a gradient of herbaceous plant richness. In relation to this gradient, the number of bird species that responded positively to herb diversity was greater than the number of species that showed the opposite trend. A well-developed herbaceous layer can provide food resources (seeds, insects) and nesting habitat for a wide range of birds. For instance, several granivorous species feed their chicks seeds from arvense and ruderal vegetation (*Diplotaxis virgata*, *Erodium* sp., *Chenopodium* sp.) (e.g., McHugh et al., 2016; Valera et al., 2005), whereas ground-feeding insectivorous birds like *Upupa epops* or *Phoenicurus ochruros* show a preference for sparse and short vegetation patches where different prey items are available and the risk of predation is reduced (e.g., Martínez et al., 2010). Our results revealed that edge or sparse woodland species like *L. senator*, *Passer montanus*, or *Saxicola rubicula* increased in abundance in olive groves with a rich (>80 spp.) herbaceous cover, whereas only *B. oedicnemus*—a species that relies on early detection of predators and thus avoids areas with dense understory (Green & Griffiths, 1994)—was identified as a negative indicator species. Hence, a moderately rich herbaceous cover benefits not only granivorous species but also insectivorous or generalist bird species that forage on the ground and avoid large patches of bare soil. Our results agree with those reported by Castro-Caro et al. (2014) in Andalusian olive groves, who showed that the presence of ground cover had a positive effect on the abundance and richness of passerine communities regardless of landscape heterogeneity, although it was not addressed quantitatively. It also aligns with the findings of Rey et al. (2019), who reported correlated responses of infield bird and herb species richness to intensification in olive groves of the "Olivares Vivos" study system.

Regarding woody plant diversity, we found that species known to forage, breed, or display in hedgerows and brambles (e.g., *C. melanocephala*, *T. merula*) showed similar positive threshold responses to this environmental variable. Permanent vegetation such as trees and shrubs can provide complementary food resources (fruits, berries) and shelter for birds in agricultural landscapes. Small woody features can also serve as nesting habitat, perches for singing or foraging, or larders for shrikes. In addition, hedgerows contribute to farmland connectivity as dispersal corridors for woodland species (Davies & Pullin, 2007). Consequently, several woodland and ecotone bird species can benefit from these features that increase landscape heterogeneity and lead to greater resource diversity (Tschumi et al., 2020; Vallé et al., 2023). Yet, on the other hand, hedgerows may reduce habitat suitability for openland birds. Hence, some studies have suggested that the presence of woody plants can negatively affect grassland specialists and ground-nesters like *Alauda arvensis*, which suffer higher predation close to vertical elements that act as sources of ground predators or provide perches from which raptors can hunt (Besnard & Secondi, 2014; Concepción et al., 2020; Morris & Gilroy, 2008). *Corvus corax* and *Columba livia*, which also showed negative threshold responses to woody plant diversity with high purity and reliability values, are eclectic generalists that often thrive in highly modified and poor landscapes. The only grassland bird that showed a negative response was *B. oedicnemus*. This means that, overall, the presence of hedgerows and woody elements within olive farms does not entail a detrimental effect on steppe birds, a guild of high conservation value in the Iberian Peninsula (De Juana et al., 1988). In line with this, Castro-Caro et al. (2015) reported that olive groves with hedges sustain a higher abundance and richness of birds (particularly insectivorous species) than olive groves without edges.

The gradient of tree density did not yield conclusive results. We obtained a low number of indicator species, which may be because the extent of our density gradient is not large enough to elicit ecologically significant responses from bird species. Our study system does not include super-intensive farms whose density oscillates between 800 and 2000 trees ha^{-1} and which are characterized by younger trees and permanent drip irrigation (Guerrero-Casado et al., 2021). Consequently, it is likely that our gradient (average tree density = 123 ha^{-1}) does not encompass densities above which species are impaired, a phenomenon that has been reported in studies conducted in irrigated and super-intensive plantations, mostly affecting negatively open farmland and cavity-nesting species (Morgado, 2022). The negative response of some insectivorous hole-nesters, such as flycatchers or *Parus major*, to this variable may be related to the fact that a higher tree density results in smaller trees with reduced crown size and fewer available natural cavities (Grüebler et al., 2013).

Lastly, birds exhibited both positive and negative responses to the increasing proportion of natural habitat within olive farms. Canopy- or bark-gleaners associated with forested areas like *P. sharpei*, *G. glandarius*, or *C. caeruleus* increased in frequency and abundance as the proportion of natural habitat increased, which indicates that olive groves embedded within a matrix of heterogeneous landscape can sustain ecologically more singular communities due to across-habitat spillover effects (García-Navas, Martínez-Núñez, Tarifa, Manzaneda, Valera, Salido, Camacho, & Rey, 2022; see also García et al., 2023). The overall avian community increased in abundance beyond a threshold of 15% of natural habitat; this means that the maintenance of a minimum proportion of natural habitat can make a significant contribution to the diversity of species assemblages inhabiting this crop (see also Tarifa et al., 2024). On the other hand, the negative response to decreasing intensification was mainly driven by finches and can be interpreted as positive responses to increasing anthropogenic disturbance and availability of non-forest habitat. It may seem counterintuitive that two sylviid warblers were also favored by low cover of natural habitat in the surrounding landscape. On the one hand, *Sylvia atricapilla* is a woodland-dwelling bird but has adopted the large extension of circum-Mediterranean olive orchards as one of its main winter quarters (Rey, 1993). To this, it has developed the plastic behavior of fruit pecking to maintain its typically highly frugivorous winter diet based primarily on olives in these landscapes (Rey & Gutiérrez, 1996). On the other hand, *Curruca hortensis* is a typical breeder in savanna-like Mediterranean oak woodlands; thereby, the semi-open structure of the traditional olive groves likely favors its settlement as a breeder, with preference over scrublands and grasslands (Rey et al., 1997).

Thresholds in ecological responses to anthropogenic drivers are an appealing concept, primarily because they provide generic figures that can serve as specific targets. For example, a recent review of landscape ecology studies suggested that forest cover needs to be maintained on at least 40% of land area in order to preserve biodiversity and ecosystem services (Arroyo-Rodríguez et al., 2020). Similarly, Macchi et al. (2019) emphasized the importance of maintaining woody cover above approximately 40% to support bird diversity in certain silvopastoral systems such as those in the South American Dry Chaco. In addition to offering policy makers clear guidelines for conservation-oriented actions (relying on empirical evidence rather than expert opinions or rules of thumb), ecological thresholds help improve our understanding of ecological processes and address questions related to species sensitivity and distribution changes. For instance, they can provide insights into whether the adoption of agri-environmental schemes negatively impacts steppe and open-land birds and at what points these effects become significant. In this sense, although a large number of studies have addressed the effects of agricultural intensification in agricultural systems and landscapes such as those shown here (e.g., Emmerson et al., 2016; Tscharntke et al., 2005), thresholds of anthropogenic environmental change critical to species abundance and diversity have rarely been demonstrated. Our results suggest the existence of gradual shifts rather than abrupt changes, which are seldom detected in natural systems due to noise and the complex interactions of multiple pressures and responses (see e.g., García-Navas et al., 2025; Hillebrand et al., 2020). When examining the species response, it is also worth mentioning that the positive effects of adopting traditional (extensive) management in olive groves are not restricted to a specific ecological guild. Our findings show that bird species with different foraging strategies (canopy-gleaners, shrub-dwellers, ground-dwellers, aerial-hawkers) and dietary preferences (granivorous, insectivorous, frugivorous, scavengers, and omnivorous) responded positively to increasing levels of woody and herbaceous plant diversity (Figure 2). This indicates that the benefits associated with extensive farm management—such as enhanced plant diversity—translate into a greater availability of resources for species with disparate ecological traits and requirements.

CONSERVATION IMPLICATIONS AND CONCLUSION

In the last two decades, the area devoted to woody crops (olive, almond, avocado, and pistachio trees) has increased dramatically in Southern Europe. Specifically, the reconversion of arable land into new olive groves was one of the most frequent land-use changes in Europe in the early 2000s (Büttner & Kosztra, 2011). In Spain, the surface devoted to this crop increased by 125,000 ha during the period 2010–2019 (MAPA, 2020), mainly due to the expansion of intensive olive groves characterized by younger trees and a lower amount of vegetation cover (Guerrero-Casado et al., 2021). In this scenario, the implementation of some actions associated to traditional agriculture such as maintaining a ground cover or keeping some isolated old olive trees, thorny hedges, dry-stone walls, and singular point elements (e.g., poles: Pustkowiak et al., 2021) should be encouraged to promote biological diversity in this crop and avoid turning it into an "ecological trap" (e.g., Rotem et al., 2013). In this sense, there is mounting evidence that complex landscapes significantly increase species richness, abundance, and evenness (see Estrada-Carmona et al., 2022; Priyadarshana et al., 2024, and references therein). Enhancing the heterogeneity and structural complexity of the agricultural landscape allows for the coexistence of a greater number of bird species with different niche requirements (Vikery & Arlettaz, 2012). This is because some farmland species require several types of landscape elements to have access to different resources, which may involve regular movement for concurrent use of different parts of the landscape (e.g., for foraging and nesting).

The present study underlines the importance of keeping a moderate-high diversity of herbs and woody plants, which favor granivorous and ground-nesting species and also impact positively on species that rely on shrubby patches, brambles, and gorse for feeding or nesting. Reaching a minimum threshold of ~85 and 15 species of herbaceous and woody plants (respectively) per unit of surface can entail a gain in terms of biodiversity for farms with virtually no detrimental effects (with the exception of *B. oedicnemus* and some generalists). Interestingly, species with different ecological strategies (canopy-gleaners, bark-gleaners, ground-foragers) showed a considerable overlap in change points, indicating a positive response to agriculture extensification from moderate thresholds (that is, below or around the average values observed in our study area). On the other hand, *E. cirlus*, one of the few species for which it has been shown benefits of agri-environment schemes at the population level and thus, considered a target species of agri-environment management (Kleijn et al., 2011), exhibited the highest IndVal score for both herbs and woody plants gradients. Overall, our findings show that the adoption of agri-environmental measures and biodiversity-friendly practices (e.g., maintenance of the herb cover and suppression of pesticides; provision of grass margins and weedy winter stubbles) has a positive impact on different bird species inhabiting olive groves, and this effect occurs at different scales (local [field- and farm-level] and landscape). Thus, actions aimed at preserving biodiversity in this woody crop should not be limited to the productive zone but should also consider the surrounding area and landscape as far as possible since semi-natural patches attract and sustain a considerable variety of bird species. We hope that our study can help identify optimal change points for management decisions concerning an agro-forestry system of paramount importance in southern Europe. The current Spanish Strategic Plan of the CAP for the period 2023–2027 allows farmers to voluntarily request funding for the promotion and maintenance of herbaceous cover in olive groves in order to mitigate the effects of climate change and preserve biodiversity. In this context, establishing clear guidelines or incentives on the minimum number of plant species per unit area to be maintained could enhance the effectiveness of this strategy as a conservation-oriented measure in agricultural landscapes (Díaz & Concepción, 2016; Pérez-Pozuelo et al., 2025).

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

Data (García-Navas et al., 2025) are available in Figshare at https://doi.org/10.6084/m9.figshare.28908080.v1.

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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