



RESEARCH ARTICLE

Partitioning beta diversity to untangle mechanisms underlying the assembly of bird communities in Mediterranean olive groves

Vicente García-Navas^{1,2}  | Carlos Martínez-Núñez³ | Rubén Tarifa^{3,4} |
 José L. Molina-Pardo^{3,5}  | Francisco Valera⁶ | Teresa Salido³ | Francisco M. Camacho³ |
 Pedro J. Rey^{3,7}

¹Department of Integrative Ecology, Estación Biológica de Doñana EBD, CSIC, Seville, Spain

²Department of Evolutionary Biology and Environmental Studies, University of Zurich, Zurich, Switzerland

³Departamento de Biología Animal, Biología Vegetal y Ecología, Universidad de Jaén, Jaén, Spain

⁴Departamento de Biología Animal, IVAGRO, Universidad de Cádiz, Puerto Real, Cádiz, Spain

⁵Centro de Investigación de Colecciones Científicas de la Universidad de Almería, Almería, Spain

⁶Departamento de Ecología Funcional y Evolutiva, Estación Experimental de Zonas Áridas EEZA, CSIC, Almería, Spain

⁷Instituto Interuniversitario del Sistema Tierra de Andalucía, Universidad de Jaén, Jaén, Spain

Correspondence

Vicente García-Navas, Estación Biológica de Doñana EBD, CSIC, Avenida Américo Vespucio, 26, Isla de la Cartuja, E-41092 Sevilla, Spain.

Emails: vicente.garcianavas@gmail.com; vicente.garcianavas@ebd.csic.es

Funding information

V. García-Navas was supported by a 'Ramón y Cajal' contract (ref. RYC2019-026703-I) from the Spanish Ministry of Science and Innovation. This study was funded by the Life Program of the European Commission 'Oliveres Vivos' (ref. LIFE14 NAT/ES/001094) and the projects

Abstract

Aim: We investigated taxonomic and functional beta diversity of bird communities inhabiting Mediterranean olive groves subject to either intensive or low-intensity management of the ground cover and located in landscapes with different degrees of complexity.

Location: Andalusia, southern Spain.

Methods: We partitioned taxonomic and functional beta diversity into its two additive components, turnover and nestedness. We also explored the contributions of single sites to overall beta diversity (LCBD) and separated the effects of species replacement (turnover) and richness difference (nestedness) in order to identify ecologically unique sites—keystone communities—within the metacommunity. In a further step, we employed abundance- and functional-based indicator species analyses to characterize bird assemblages.

Results: Taxonomic beta diversity increased with landscape complexity. Although both taxonomic and functional differences among assemblages were driven mainly by species replacement (regardless of management or landscape type), the contribution of trait replacement to the total functional beta diversity was much lower, suggesting that species performing similar functions replace each other between sites. There were no differences in LCBD between management types or categories of landscape complexity, but the contributions of sites to beta diversity decreased as the percentage cover of olive groves increased. Species richness was also important in explaining variation in LCBD as species-poor sites tended to contribute the most to the local-to-regional beta diversity. However, some farms displayed high values of LCBD due to the existence of a high replacement component, indicating that some species recorded in these sites were scarce elsewhere. The indicator species analyses

AGRABIES and RECOVECOS (CGL2015-68963-C2 and PID2019-108332GB-I00, respectively, MINECO/MICIN, Gobierno de España and FEDER)

Editor: John Lambrinos

revealed that the woodchat shrike *Lanius senator* may constitute an excellent indicator of biodiversity in this agro-forestry system.

Main conclusions: Our results show that agricultural expansion promotes biotic homogenization and exemplify how the identification of both keystone species and communities can represent a powerful tool for the management of anthropized landscapes.

KEYWORDS

agriculture, community ecology, farmland birds, functional beta diversity, intensification, olive farms, woody crop

1 | INTRODUCTION

A major goal of ecology is to understand factors affecting the spatial variation of species diversity, which can be divided into alpha, beta and gamma components (Mittelbach & McGill, 2019). Beta (β) diversity can be viewed as a measure that bridges the gap between the local (alpha, α) and regional (gamma, γ) estimates of biodiversity. The concept of β diversity dates back to Whittaker (1960), who coined this term to define the amount of variation in species composition among sampling units. Studies of β diversity attempt to reveal the mechanisms that drive these differences (or lack of), which can be grouped into two broad categories: deterministic processes that lead to communities structured by species sorting, and neutral and stochastic processes such as ecological drift which generate random assemblages (Chase & Myers, 2011). Although species richness is a more common and intuitive measure of diversity, β diversity detects better changes in communities regarding environmental gradients. This is because richness is not sensitive to changes in composition and this might mask results when sensitive taxa are lost and generalist species become more common into the altered environments (Clavel et al., 2011). Consequently, β diversity has become a pervasive topic in community ecology, conservation and macroecology (Carlos-Júnior et al., 2019; Svenning et al., 2011).

In the last decade, the study of spatial changes in assemblage composition has sparked substantial interest due in part to the development of new methodologies that allow decomposing dissimilarity indices into two different antithetical components, turnover and nestedness (reviewed in Anderson et al., 2011; Legendre, 2014; Tuomisto, 2010). Turnover occurs when existing species are replaced by different ones at new sites, whereas nestedness patterns result when species loss or gain causes species-poor sites to resemble a strict subset of species-rich sites (Baselga, 2010, 2012). Thus, these two components imply distinct ecological processes determining biodiversity patterns. Generally, patterns of turnover are expected to be produced by factors that promote endemism at various spatial scales, whereas nestedness is a result of ordered extinctions (or colonizations) along gradients as a consequence of environmental filtering or spatial and historical constraints (Ulrich et al., 2009). In this context, unravelling the mechanisms underpinning the observed dissimilarities among biological communities has sound implications

for conservation management, as it facilitates the identification of unique characteristics in a given site in relation to the remaining localities (Socolar et al., 2016).

Understanding what promotes the 'uniqueness' of a local site across a broad geographic extent can give rise to important insights for better preservation of biodiversity. To accomplish this goal, Legendre and De Cáceres (2013) devised a method by which β diversity can be partitioned into contributions of single sites to total beta diversity (LCBD) or contributions of individual species to total beta diversity. Following this approach, some authors have shown that the ecological uniqueness of sites can be associated with certain environmental conditions (e.g. da Silva et al., 2018; Santos et al., 2021) or result from community characteristics such as species richness and abundance (e.g. Heino & Grönroos, 2017). Beyond species composition, a given community can also be distinct in terms of functional diversity. Community functional uniqueness represents how 'isolated' is a community in the functional space characterized by the entire set of sites. Consequently, this metric can inform us about the intrinsic conservation value and the resilience of communities (Cadotte et al., 2011).

The 'uniqueness' notion relies on the different role each species plays in the ecosystem. Some species are not only of great importance from a functional point of view but also for their diagnostic value. Due to their niche preferences, certain taxa can be used as ecological indicators of community types or habitat conditions. Following this rationale, Dufrêne and Legendre (1997) devised the indicator value (IndVal) method, which addresses the relationship between the species occurrence or abundance values from a set of sites and the classification of the same sites into clusters (e.g. community or habitat types). This method has been recently extended to combine species abundances and their functional attributes into a single composite index using fuzzy set theory (Ricotta et al., 2020). The dominant functional traits in biological communities should provide a much better ecological characterization of a group of sites, in terms of the local environmental conditions and ecosystem functioning, than the mere occurrence of species. In this way, it is now feasible to determine those functional attributes that better inform about the specific properties of certain sites along natural (e.g. successional stages) or human-induced environmental gradients (e.g. land-use intensity in farmland landscapes).

Agricultural intensification constitutes an important threat to wildlife diversity. Several authors have shown that intensive farming erodes taxonomic β diversity promoting biotic homogenization since the spatially uniform conditions arising from high-intensity agricultural practices are tolerable to only a reduced subset of abundant native species (e.g. Dormann et al., 2007; Ekroos et al., 2010; Karp et al., 2012; Tarifa et al., 2021). Consequently, this process leads to the selection of taxa ('winner' species) characterized by a specific set of functional attributes (Santana et al., 2017). Although it is increasingly recognized that a multi-faceted assessment of diversity is needed to improve our understanding of the mechanisms underlying biodiversity patterns and community assembly, few studies have examined the consequences of intensification in terms of both taxonomic and functional β diversity (but see Liu et al., 2016).

Here, we apply diversity partitioning to a dataset resulting from bird surveys conducted in low-intensity and intensive olive farms of Andalusia, southern Spain, in the framework of the LIFE-project 'Olivares Vivos' (www.olivaresvivos.com). Low-intensity farms were subject to traditional management of the herbaceous cover (which is maintained during most of the year and eventually removed by cattle grazing or machinery), whereas two factors characterize those farms with intensive management of the herbaceous cover: the use of pre- and/or post-emergence herbicides and/or recurrent ploughing to eliminate the weeds over the whole year. Ground cover removal is a long-lasting and widely extended major source of olive growing intensification, as it has been acknowledged by the European Common Agriculture Policy (CAP). Agri-environmental measures aimed to increase ground soil covers received special attention in this agroecosystem in past CAP and still is recommended for eco-schemes and agri-environmental and climate measures in ongoing proposals for the new CAP (Díaz et al., 2021). Ground cover can provide environmental and agronomic benefits by reducing soil loss and erosion (see table 1 in Sastre et al., 2017), which has been identified as one of the major environmental problems of Mediterranean agriculture (Infante-Amate et al., 2016; Panagos et al., 2015). In this vein, several studies have demonstrated the efficiency of cover crops in comparison with conventional tillage in olive groves to increase soil fertility and improve water storage and physical properties (see Gómez et al., 2014 and references therein). In addition, the presence of ground cover is known to benefit the biodiversity of some organisms, including bird communities (Castro-Caro et al., 2014; Martínez-Núñez et al., 2020; Rey et al., 2019). Similar results have been found in other woody crops (vineyards, coffee plantations) in which structural complexity and, more specifically, ground cover had a positive effect on diversity (e.g. Philpott et al., 2008). Our study farms are embedded in a gradient of different landscape complexity, from entirely agricultural landscapes to more heterogeneous landscapes composed of both agricultural and natural land covers (Rey et al., 2019). Landscape heterogeneity and configuration have been increasingly recognized to play an important role in structuring the composition of biological communities in agroecosystems and act synergistically with management practices or the farming system (e.g. Martins da Silva et al., 2017). Given their high dispersal capacity,

bird communities inhabiting olive groves are likely to be influenced by habitats directly adjacent to crop fields (functional 'spillover' from natural to managed habitats; Blitzer et al., 2012). In this study thus, we integrate two different aspects of agricultural intensification: land use (or management) intensification at the local scale and agriculture expansion (e.g. Medan et al., 2011).

Our main goal was to analyse the differences in bird total β diversity, turnover and nestedness in relation to local farming practices (i.e. the use of ground cover) and landscape complexity from a twofold perspective, taxonomic and functional. Specifically, we addressed the following questions: (i) how do β diversity and its components (turnover and nestedness) differ between intensive and low-intensity olive farms? (ii) Does the variability in landscape complexity affect β diversity? And (iii) do taxonomic and functional β diversity respond in a similar way to agricultural intensification? In a further step, we calculated the contributions of single sites to total β diversity to identify distinctive farms in terms of species spatial composition. We examined whether site contributions to β diversity differed between management types (low-intensity: with ground cover or intensive: bare ground) and among categories of landscape complexity. We also tested whether those farms harbouring more distinct communities were also characterized by a remarkable singularity ('uniqueness') from a functional perspective. Lastly, we also addressed the potential role of species as indicators of sites with certain environmental conditions in order to characterize ecologically each community type. By integrating species functional characteristics and species abundances, we examined whether these environmental conditions are associated with specific functional traits (e.g. diet or foraging strategy).

2 | MATERIAL AND METHODS

2.1 | Study system

The study area consists of 40 olive farms (average size: 72.1 ± 107.2 ha, range: 4.5–424.8) scattered along the Guadalquivir basin in Andalusia, southern Spain ($37^{\circ}43'28.5''\text{N}$ $4^{\circ}10'18.4''\text{W}$; Figure 1a). The 40 farms are situated in 20 localities covering a cultivated area *circa* 35 km² and encompassing a distance of 310 km between the most distant farms (average distance among localities: 102.8 km, range: 74.5–166.3). Following a paired design, half of the olive farms are under intensive management (including use of pre-emergence and/or post-emergence herbicides and/or recurrent ploughing for herbaceous cover elimination over the whole year), whereas the other half is subject to low-intensity management of such cover (it is maintained during most of the year and eventually removed by cattle grazing). The olive trees in all the localities were more than 30 years old and were grown with a plantation frame of 7×8 m or higher (average tree density: 120.5 ± 55.2 trees per hectare; range: 57–288). Super-intensive hedge-like olive groves (Morgado et al., 2020) were not considered in this project since although quickly increasing in the region, this system still represents

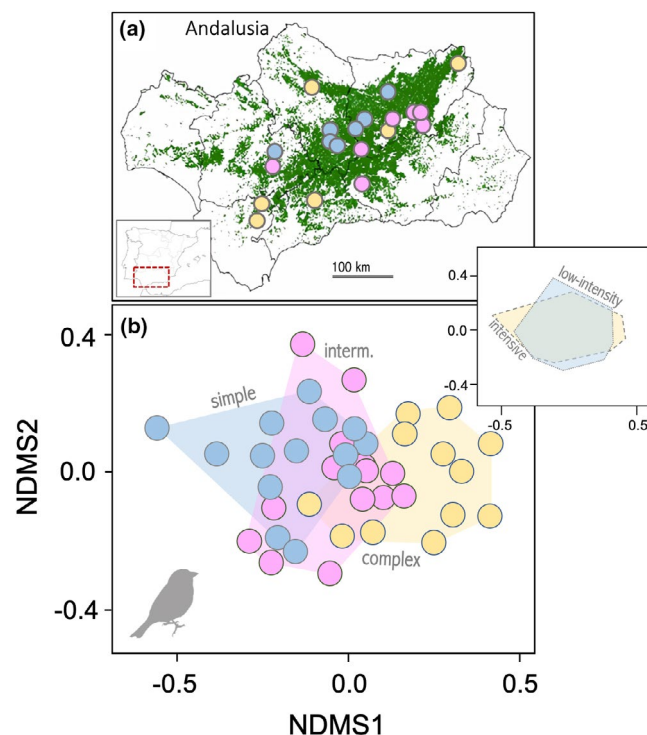


FIGURE 1 (a) Study area in the Guadalquivir basin (Southern Spain) with the location of the 40 farms in the 20 study sites. Following a paired design, each locality consists of two olive farms, one under intensive management (bare ground) and the second farm under low-intensity management (with herbaceous cover). Seven localities are surrounded by a relatively simple landscape (blue colour), seven localities are embedded within a landscape of intermediate complexity (pink colour) and six localities are in complex landscapes with a remarkable proportion of natural vegetation (yellow colour). The green-shaded area depicts the distribution of olive groves in Andalusia (data retrieved from REDIAM; <https://laboratorioriediam.cica.es>). (b) Non-metric multidimensional scaling, NDMDS, plot based on the Bray-Curtis dissimilarity matrix for assemblages of birds in simple ($n = 14$), intermediate ($n = 14$) and complex ($n = 12$) landscapes. The insets show a NDMDS plot for assemblages under intensive ($n = 20$, terrain colour) and low-intensity ($n = 20$, light-blue colour) olive grove management

less than 3% of land devoted to olive farming in Andalusia (Vilar & Pereira, 2018).

Landscape surrounding the two farms in each locality varies across the study area and can be classified into three broad categories of complexity: (i) simple landscapes, in which olive groves predominate while remnants of natural habitat are scarce; (ii) intermediate landscapes, with olive groves interspersed with other crops (mostly cereals) and with some natural or semi-natural habitat remnants; and (iii) complex landscapes where olive groves, which may not be the major land use, co-occur with a diverse representation of natural habitats (woodlands, scrublands and grasslands). This classification was based on different compositional and configurational heterogeneity metrics (e.g. percentage of natural/semi-natural habitat cover, 'cobnat'; percentage of olive groves in the landscape; land-use

diversity; mean patch size; edge density; distance between nearest neighbour patches of similar use, NND) obtained for each locality in a circular buffer of 2 km radius that encapsulates the corresponding pair of farms (Table S1). Landscape metrics were derived from recent land-use cover cartography of the region (SIOSE 2013; <http://www.siose.es>) and managed with QGIS v.2.14 (QGIS Development Team, 2018) and FRAGSTAT (McGarigal et al., 2012). We also estimated some of these metrics at 1 km circular buffers around the centroid of each olive farm to be used as environmental descriptors of each individual farm (see below). The ascription of each locality to a given landscape complexity category was further validated using classification and regression tree analysis (CART; Urban, 2002). The main advantages of this method over other classification techniques are that it does not make any assumptions on error distribution or linearity and that it defines cut-off points in metrics that optimize the discrimination among levels of landscape complexity. CART analysis showed that 'cobnat', NND and mean patch size correctly classified 100% of the study localities into the three categories of landscape complexity originally defined, confirming that, overall, our perceptual classification of the landscape can be translated into quantitative (objective) metrics. Simple landscapes were characterized by low representation of natural habitat ('cobnat' <9%), intermediate landscapes by 'cobnat' >9% and NND higher than 85 m, and complex landscapes were those with 'cobnat' >9% and a mosaic of uses with NND less than 85 m. This reflects a more coarse-grained mosaic of land use in intermediate than in complex landscapes. More details about this study system, including differences in species richness and herb cover between intensive and low-intensity farms, are given in Rey et al. (2019) and Martínez-Núñez et al. (2020).

2.2 | Bird surveys

We surveyed birds using point census stations. At each count point, all individuals detected—seen or heard—within a 100-m radius were identified and counted for 5 min. We set six stations in small olive farms (<25 ha) and 10 in large olive farms (≥25 ha). To avoid repeated counts between neighbour census stations, they were located at least 200 m apart in small olive groves and at least 300 m apart in large olive groves. Surveys were carried out monthly in two slots (from April to June 2016, and from September 2016 to March 2017) under favourable weather conditions by a team of skilled ornithologists.

Species from taxonomic groups with high dispersal capacity such as birds commonly show up in habitats in which they are not expected. Consequently, bird surveys often include accidental or transient species, which occur infrequently in a community over time and do not maintain viable local populations. The inclusion of these vagrant species can distort community-level analyses (Snell Taylor et al., 2018). To avoid this, Bray-Curtis similarity indices were calculated with only common species, that is species present in more than 10% of farms. Hence, our analyses included a total of 93 species accounting for 99% of records. The remaining 1%

comprises bird species with anecdotal presence (e.g. glossy ibis *Plegadis falcinellus*) that cannot be considered representative of olive crops.

2.3 | Functional data

We built a functional matrix (species-by-traits) with all bird species (rows) and their respective functional traits (columns), namely morphology (e.g. body size, tarsus length), ecology (e.g. lifespan, clutch size), diet (i.e. trophic guilds: insectivorous, granivorous and frugivorous), foraging strategy (e.g. grazing, gleaning), foraging substrate (e.g. canopy, understory), behaviour (e.g. nest location, migratory behaviour) and habitat preferences, totalling 53 trait states. Because some morphological variables were highly correlated, we first performed a phylogenetic principal component analysis, which yielded two principal components, PC1 and PC2, accounting for 98% (83% and 15%, respectively; see García-Navas et al. in press for more details) of the morphological variation. Our set of traits covered main niche dimensions and, therefore, portrayed species ability to respond to environmental conditions and their variation (Table S2). Data for the trait matrix were extracted from several sources (Myhrvold et al., 2015; Storchová & Hořák, 2018; Wilman et al., 2014). From this dataset, we computed a matrix of pairwise trait distances between species based on Gower distance coefficient using *ktab.list.df* and *dist.ktab* functions of 'ade4' package (Dray & Dufour, 2007). This species functional distance (dissimilarity) matrix was used to build a functional dendrogram using the unweighted pair group method with arithmetic mean (see Section 2.6).

2.4 | Environmental descriptors

We used two of the compositional heterogeneity indices obtained for each of the 40 olive groves at 1-km resolution (percentage of natural/semi-natural habitat cover and percentage of olive groves in the landscape) (see *Study area*) as environmental predictors. We hypothesize that these two variables affect the ecological singularity or distinctiveness of bird communities inhabiting olive farms. In addition, we computed the mean level of geographic (spatial) isolation of each farm by averaging pairwise Euclidean distances between farms.

2.5 | Composition of bird communities

To visualize the existence of differences in community composition between intensive and low-intensity farms, and among the different categories of landscape complexity, we used non-metric multi-dimensional scaling (NMDS), performed on a matrix of Bray–Curtis dissimilarities of abundance (square-root transformed) data using the 'vegan' package (Oksanen et al., 2020). Differences in community composition were tested using a permutational multivariate analysis of variance (PERMANOVA; Anderson, 2001) as implemented in

the *adonis* function. This method compares the variance between groups with the variance within groups in a dissimilarity matrix by means of the sum of squared distances. An *F*-ratio was computed, as in a one-way ANOVA model, and its *p*-value was obtained with 999 permutations.

2.6 | Taxonomic and functional beta diversity

Taxonomic β diversity was computed using the Bray–Curtis dissimilarity index, which quantifies differences in species composition between sites (Baselga & Orme, 2012). Following the Baselga's additive partitioning approach, abundance-based Bray–Curtis dissimilarity was decomposed into two additive components: (1) balanced variation in abundance (β_{bal}), by which individuals of some species in one site are substituted by the same number of individuals of different species in another site; and (2) abundance gradients (β_{gra}), whereby some individuals are lost from one site to the other and abundances vary between the sites (Baselga, 2012). β_{gra} can be estimated by subtracting the replacement component (β_{bal}) from the total β dissimilarity, which ranges from 0 to 1. Thus, the sum of (β_{gra}) and (β_{bal}) equals β for each community. We calculated multiple-site dissimilarities and components (β_{gra} , β_{bal}) for all farms together ($n = 40$ farms) and for each management type (intensive $n = 20$ farms; low-intensity $n = 20$ farms) and landscape complexity category (simple $n = 14$, intermediate $n = 14$ and complex $n = 12$) separately using the *beta.multi.abund* function of the 'betapart' package (Baselga et al., 2021). Since these estimates can be influenced by α diversity, which differs among subsets, we repeated analyses of β diversity using Raup–Crick dissimilarity (β_{RC} ; Raup & Crick, 1979), an incidence-based, probabilistic metric that is not influenced by differences in species richness (Chase et al., 2011; Vellend et al., 2007). That is, this metric quantifies β diversity associated exclusively with species turnover, while controlling for differences in nestedness (Baeten et al., 2012). β_{RC} oscillates between 0 (identical sampling units) and 1 (sampling units with no shared species). Therefore, it allowed us to assess whether the observed variation in the measured dissimilarity among groups results from differences in the compositional variation rather than differences in taxonomic richness.

It was not computationally feasible to adopt Baselga's method when decomposing functional beta diversity due to the size of our dataset. This method follows a convex hull approach (the standard Baselga functional metric) and is only suitable when the number of communities is low due to its computational demands. Consequently, we followed Carvalho et al. (2012) to calculate functional β diversity and its components. In this method, the functional representation is based on functional clustering trees rather than on a functional ordination. Similar to the taxonomic β diversity, the total functional β diversity considered as the Jaccard dissimilarity between two communities can be partitioned into variation through species replacement (turnover; $\beta_{\text{replacement}}$) and variation due to species richness (nestedness; β_{richness}) (Cardoso et al., 2014). $\beta_{\text{replacement}}$ and β_{richness} are the functional analogues of β_{gra} and β_{bal} . Functional β

diversity estimates were calculated using the *beta.multi* function of the 'BAT' package in R (Cardoso et al., 2020).

Complementarily, we visualized differences in functional β diversity and its components between management types and among landscape complexity categories using n -dimensional hypervolumes (Mammola & Cardoso, 2020). This method is based on the framework recently proposed by Carvalho and Cardoso (2020), which computes a pairwise decomposition of the overall differentiation among kernel hypervolumes (total β diversity) into two components: the replacement of space between hypervolumes (replacement) and gain/loss of space enclosed by each hypervolume (richness). Each component oscillates between 0 (when hypervolumes are identical) and 1 (fully disjunct hypervolumes), and $\beta_{\text{total}} = \beta_{\text{replacement}} + \beta_{\text{richness}}$.

2.7 | Identifying ecologically distinctive sites: Local contribution to beta diversity and community functional uniqueness

We calculated the LCBD using the *beta.div* function in 'adespatial' R package (Dray et al., 2018) based on Legendre and De Cáceres (2013). This method calculates the total β diversity from the total variance of the site-by-species community matrix. The LCBD is derived by partitioning the total β diversity into the local contributions (Legendre & De Cáceres, 2013). We ran the analysis using both abundance and presence-absence data to examine whether there were differences between quantitative and qualitative data.

In a preliminary step, the abundance matrix was Hellinger-transformed to reduce the asymmetry in the species distribution. Since we obtained quite similar results, and for the sake of brevity, we only report results for presence-absence data in the main text. High LCBD values indicate great importance of the given site to the observed total variation in species composition across sites (Anderson et al., 2011). That is, from an ecological point of view, LCBD values represent the degree of uniqueness of the sampling units in terms of metacommunity. The local contributions of species replacement ($\text{LCBD}_{\text{repl}}$) and richness difference ($\text{LCBD}_{\text{rich}}$) to total beta diversity (based on Baselga family, Jaccard-based indices) were calculated using the function *beta.div.comp* (Legendre, 2014). Both $\text{LCBD}_{\text{repl}}$ and $\text{LCBD}_{\text{rich}}$ values allow inquiring if sites with unique species composition show more changes related to spatial substitution or gain/loss of species.

We subsequently computed the average functional uniqueness of the study sites. First, we obtained the 'uniqueness' score for each species using the library 'funrar' (Grenié et al., 2017) based on the species functional distance matrix. Uniqueness estimates the extent to which a species has no functional equivalent in the species pool (see equation III in Violle et al., 2017). We then computed the community-level weighted means (CWM) using the uniqueness scores of the species weighted according to their frequencies in the different communities. By using CWM values, we scaled up trait information to the metacommunity level, allowing the estimation of

the average functional singularity of the 40 farms. We investigated the relationship between LCBD and community functional uniqueness, community richness and community abundance using beta regressions with logit link function as implemented in the R package 'betareg' (Cribari-Neto & Zeileis, 2010). Beta regression is typically used to model variables that assume values in the standard unit interval (0, 1) and, therefore, is suitable for this type of data. We also employed this approach to examine the relationship between LCBD and three environmental variables: (i) percentage of natural/semi-natural habitat cover, (ii) percentage of olive groves in the landscape and (iii) degree of spatial isolation. Lastly, we investigated how LCBD and community functional uniqueness differ among landscape categories, and between management types using a Kruskal-Wallis test. In this way, we determined whether the ecological uniqueness of sites is based on environmental conditions.

2.8 | Identifying diagnostic species: Indicator species analyses

To determine whether any particular bird species was significantly more abundant in intensive or low-intensity farms or particularly common in a certain landscape context, we performed a species indicator analysis following two approaches: the traditional abundance-based analysis (Dufrêne & Legendre, 1997) and a functional variant of this method recently developed by Ricotta et al. (2020).

The traditional IndVal analysis assesses the association between species and farm groups. The IndVal analysis is based on two components: (i) 'specificity', the conditional probability of a positive predictive value of a given species as an indicator of the target farm group (component 'A'), and (ii) 'sensitivity' (or fidelity), the conditional probability that the given species will be found in a newly surveyed farm belonging to the same group (component 'B'). A good indicator species should be both ecologically restricted to the target farm group and frequent within it. Analyses were run using the *multipatt* function of the 'indicspecies' R package (De Cáceres et al., 2010). Besides considering individual species, we also explored the IndVal of combinations of species since two or three species, when found together, bear more ecological information than a single one (De Cáceres et al., 2012).

Ricotta et al. (2015, 2020) recently proposed to include the functional traits of species, in addition to their occurrence and abundance, for the determination of indicator species. We followed this approach, which consists of (i) the indicator species that best characterize a given group of farms are identified with the standard statistical tools based on the species abundance data and (ii) the functional association between the traditional (abundance-based) indicator species and the target group of farms is tested by calculating the functional distance between the indicator species and the functional centroids of all farms in that group. A species is considered diagnostic of a given group if its mean functional distance from the plot (farm) centroids of the target group is significantly lower than expected by chance (see Ricotta et al., 2015). p -values of positive

functional association (ϕ) between a given species j and each group of farms k were calculated as the proportion of permutation-derived values of ϕ_{jk} that were as high or higher than the actual value (999 permutations, two-tailed test). All calculations were done with a R script provided in Ricotta et al. (2020).

3 | RESULTS

3.1 | Composition of bird communities

The NMDS analysis (non-metric fit: $R^2 = 0.95$) revealed that the composition of bird communities differed among olive farms belonging to different landscape complexity categories (PERMANOVA $F = 2.76$, $p = 0.001$, $R^2 = 0.13$; Figure 1b). However, the composition of communities in intensive and low-intensity farms did not differ significantly ($F = 0.46$, $p = 0.95$; Figure 1b).

3.2 | Taxonomic and functional beta diversity

Taxonomic β diversity among low-intensity olive farms was quite similar to the observed one among the intensive farms (Table 1). Multiple-site differences in taxonomic β diversity increased with landscape complexity; we found higher dissimilarities among farms embedded within a complex landscape. However, it was only evident when correcting for the effect of species richness by means of the Raup–Crick method (Table 1). Raup–Crick values were generally low ($\beta_{RC} < 0.2$), indicating high similarity in community composition between farms. In terms of functional β diversity, there were

no differences between management types or among categories of landscape complexity (Figure 2; Table 1).

The partitioning of taxonomic β diversity revealed that the turnover component was the major reason for bird dissimilarity among sites for all the data subsets (Table 1). Yet, the contribution of the nestedness component was higher when comparing farms located in complex landscapes (15.0%) than when examining the dissimilarity among farms within intermediate or within simple landscapes (13.7% and 11.4%, respectively; Table 1). Concerning functional diversity, the effect of the trait loss/gain component was almost equal (46%–49%) to that of the trait replacement component in all the analysed data subsets indicating that replacement of species is not coupled with a corresponding replacement of functions (Figure 2; Table 1).

3.3 | Local contribution to beta diversity and community functional uniqueness

The values of LCBD ranged between 0.018 and 0.033; four farms had a significant contribution to beta diversity (Figure 3a; Table 3). Half of farms that contributed most to total beta diversity were characterized by high replacement (LCBD_{repl}), whereas the other half represented the highest richness difference values (LCBD_{rich}) (Table 2). LCBD did not differ significantly between management types (Kruskal–Wallis, chi-square = 0.01, $p = 0.91$) or among landscape complexity categories (chi-square = 0.58, $p = 0.75$; Figure 3a). LCBD correlated negatively with the proportion of land covered by olive groves (estimate: -0.002 ± 0.001 , $z = -2.82$, $p < 0.01$, pseudo- $R^2 = 0.17$; Figure 3b), but not with the proportion of natural or semi-natural habitat ($z = 1.38$, $p = 0.17$) or geographic

TABLE 1 Taxonomic and functional β diversity (and its components) computed considering all sites ($n = 40$) and reduced subsets. For taxonomic β diversity, we employed the Baselga's Bray–Curtis index, in which the abundance-based Bray–Curtis similarity index (β_{sim}) is decomposed into two components: the replacement component (balanced variation in abundance; β_{hal}) and the nestedness component (abundance gradients; β_{gra}). For functional β diversity, total beta diversity was partitioned into β_{repl} (replacement) and β_{rich} (trait loss/gain) using a functional cladogram and quantitative site \times spp matrices. The Raup–Crick index (Chase et al., 2011), a measure of dissimilarity that is independent of α diversity, is also provided

	N	SR	Facet	Beta total β	Turnover	Nestedness-trait loss/gain	% β_{tur}	Raup–Crick β_{RC}
All farms	40	51.1	Taxonomic	0.909	0.859	0.051	94.5	0.071
			Functional	0.550	0.295	0.255	53.6	
Only intensive farms	20	50.4	Taxonomic	0.838	0.755	0.083	90.1	0.084
			Functional	0.554	0.291	0.262	52.5	
Only low-intensity farms	20	51.7	Taxonomic	0.848	0.773	0.077	91.1	0.081
			Functional	0.557	0.302	0.254	54.2	
Only farms in complex landscapes	12	54.7	Taxonomic	0.778	0.661	0.117	85.0	0.121
			Functional	0.555	0.285	0.270	51.3	
Only farms in intermediate landscapes	14	52.5	Taxonomic	0.762	0.658	0.103	86.3	0.097
			Functional	0.508	0.262	0.246	51.5	
Only farms in simple landscapes	14	46.5	Taxonomic	0.780	0.708	0.091	88.6	0.077
			Functional	0.555	0.297	0.258	53.5	

Abbreviations: SR, average species richness; % β_{tur} , relative contribution of the turnover component.

FIGURE 2 Density of functional beta diversity values for pairwise comparison of (a–c) bird communities in low-intensity and intensive olive farms, and (d–f) bird communities located in complex, intermediate and simple landscapes. Total functional diversity β_{total} (a, d) is split into two components: $\beta_{\text{replacement}}$ (b, e) is the turnover in functional composition explained by replacement of space between hypervolumes, and β_{richness} (c, f) is the turnover in functional composition explained by species loss/gain of space enclosed by each hypervolume

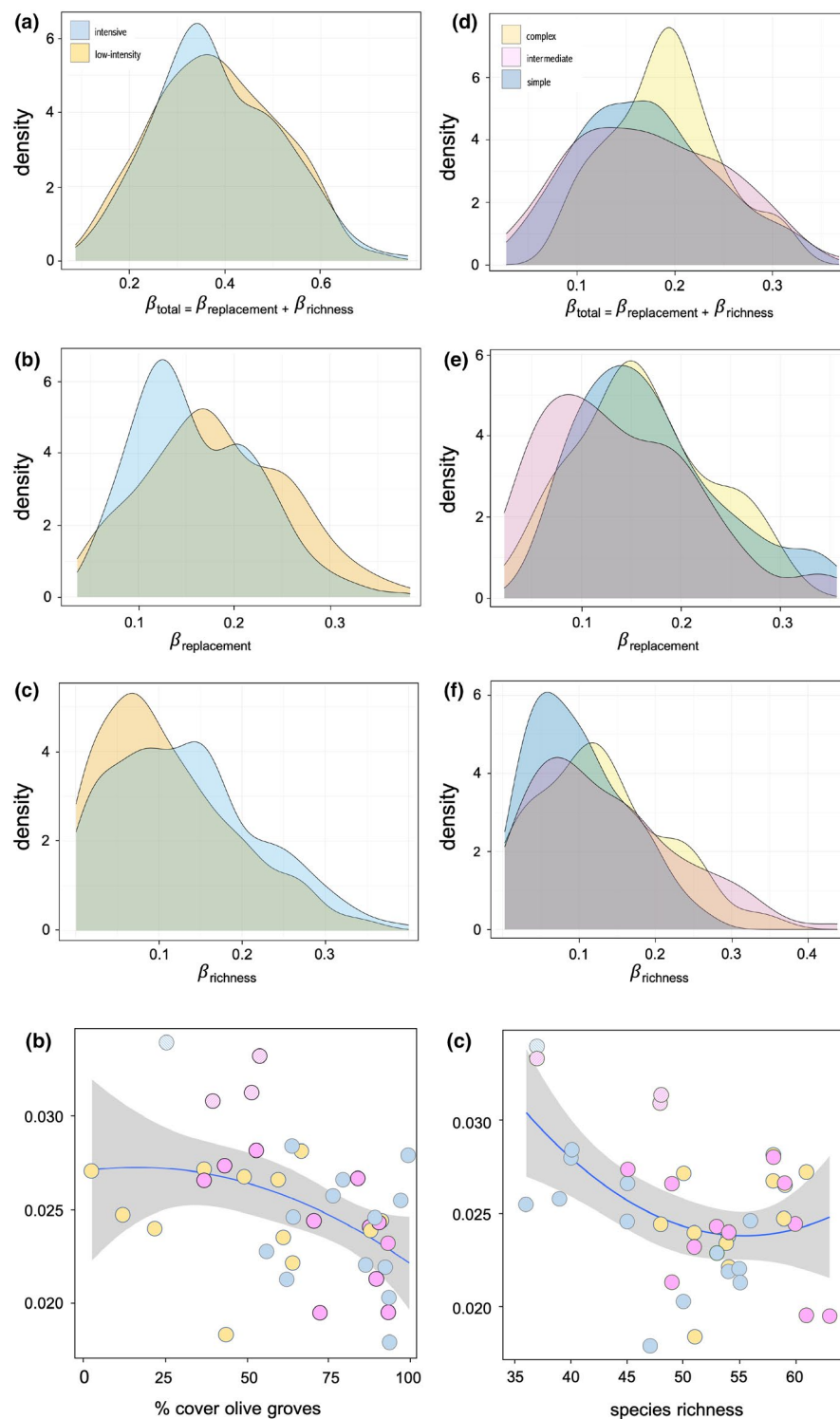


FIGURE 3 (a) Differences in local contribution to beta diversity (LCBD) among categories of landscape complexity. (b) Relationship between LCBD and percentage (%) of land devoted to olive crops within each locality (1 km-radius). (c) Relationship between LCBD and species richness. The curves in blue were fitted using a quadratic model (%olive: $z = 1.29$, $p = 0.20$, %olive²: $z = -2.39$, $p = 0.02$; pseudo- $R^2 = 0.4$; richness: $z = -2.00$, $p = 0.045$, richness²: $z = 1.77$, $p = 0.076$, pseudo- $R^2 = 0.2$) as implemented in the *betareg* function. The striped dots indicate sites with a significant contribution ($p < 0.05$) to beta diversity

distance ($z = 1.05$, $p = 0.29$). LCBD was significantly related to community richness (and marginally with its quadratic term) (richness: estimate: -0.073 ± 0.036 , $z = -2.00$, $p = 0.04$; richness²: estimate: 0.001 ± 0.000 , $z = -1.77$, $p = 0.076$), but not with community

abundance ($z = -1.30$, $p = 0.19$). We obtained quite similar results when running the analyses using abundance data (see Figure S1).

Open-habitat specialists such as the stone curlew, *Burhinus oedipnemus*, the common quail *Coturnix coturnix*, the red-legged

TABLE 2 List with the seven top-ranked olive farms in terms of local contribution to beta diversity (sites with a significant contribution are indicated with an asterisk). LCB_D was partitioned into species replacement (turnover: LCB_D_{repl}) and richness difference (nestedness: LCB_D_{rich}). Those farms whose LCB_D_{repl} or LCB_D_{rich} values were among the top five for all farms ($n = 40$) are in bold. For each of the most ecologically unique farms, the following variables are provided: average functional uniqueness (function. uniq.), elevation (elevat), mean annual temperature (temp), percentage of olive groves in the landscape (% olive crop), percentage of natural/semi-natural habitat cover (% cobnat) in a 1-km radius, distance to the nearest urban area (DNU) and average distance between each farm and the remaining localities (i.e. degree of isolation; isolat). Variables were obtained from SIOSE (<http://www.siose.es>) and REDIAM (<http://www.juntadeandalucia.es/medioambiente/site/rediam>) using GIS

Olive farm	Province	Local management	Landscape complexity	LCBD	LCBD _{repl}	LCBD _{rich}	Function. uniq.	elevat (m)	temp (°C)	% olive crop	% cobnat	DNU (km)	isolat (m)
QUI-L	Jaen	Low-intensity	Simple	0.034*	0.321	0.164	0.304	420	16.8	25.4	8	0.3	92.9
OLI-I	Jaen	Intensive	Intermediate	0.033*	0.311	0.171	0.310	447	16.6	54.0	44	0.3	106.0
MOR-I	Granada	Intensive	Intermediate	0.031*	0.397	0.064	0.308	575	16.3	51.5	13	1.6	91.8
MOR-L	Granada	Low-intensity	Intermediate	0.030*	0.393	0.065	0.310	579	16.3	39.4	13	1.2	91.5
QUI-I	Jaen	Intensive	Simple	0.028	0.310	0.137	0.307	414	16.8	63.9	8	0.1	92.9
OJU-L	Seville	Low-intensity	Intermediate	0.028	0.358	0.082	0.318	143	17.6	52.7	3	2.9	113.4
ARD-I	Jaen	Intensive	Complex	0.028	0.365	0.075	0.285	656	15.0	25.1	40	2.9	162.1
Average values across sites ($n = 40$)													
				0.025	0.330	0.091	0.300	451	16.4	65.8	20.1	3.9	100.2
Max				0.033	0.397	0.217	0.318	1000	17.8	99.5	68	9.1	162.1
Min				0.018	0.220	0.062	0.285	120	13.9	2.4	2	0.1	72.6

partridge *Alectoris rufa*, the European bee-eater *Merops apiaster*, or the lesser kestrel *Falco naumanni* were among the species with the highest functional uniqueness values (Table S3). From these values, we computed an average value for each farm ('community functional uniqueness'). We did not find a significant relationship between community functional uniqueness and LCB_D ($z = 1.04$, $p = 0.29$) despite four of the seven top-ranked farms in terms of LCB_D also exhibited high values (i.e. within the top-seven rank) of functional uniqueness (Table 2). There were no statistically significant differences between management types (Kruskal-Wallis, chi-squared = 0.06, $p = 0.81$) or landscape complexity categories (chi-squared = 4.50, $p = 0.10$) in terms of community functional uniqueness.

3.4 | Indicator species analyses

According to the traditional (abundance-based) indicator species analysis, two bird species (the common quail and the Dartford warbler *Curruca undata*) were marginally associated with the presence of ground cover (i.e. low-intensity farms). Six bird species (including the woodlark *Lullula arborea* and the Eurasian jay *Garrulus glandarius*) were indicators of high landscape complexity, the Eurasian tree sparrow *Passer montanus* was positively associated with intermediate landscapes, and the European roller *Coracias garrulus* and the rufous-tailed scrub robin *Erythropygia galactotes* were characteristic of simpler landscapes (Table 3). When exploring the IndVal of species combinations, we found that the woodchat shrike *Lanius sena-*tor was included in more than 70% of pair combinations associated with farms with a low-intensity management of the ground cover (see Table S4).

When applying a functional-based indicator species analysis, the number of indicator species increased. The largest number of diagnostic species is associated with complex landscapes (23 species), whereas for intermediate and simple landscapes, the number of diagnostic species was similar (seven species; Figure 4). The woodchat shrike, the European pied flycatcher *Ficedula hypoleuca* and the common swift *Apus apus* were diagnostic of low-intensity farms, whereas the Cetti's warbler *Cettia cetti* and the common whitethroat *Curruca communis* were significantly associated with olive groves under intensive management (Figure 4). These last two species appear exclusively associated with hedges and riparian vegetation in these olive groves.

4 | DISCUSSION

In the present study, we analysed taxonomic and functional β diversity of bird communities inhabiting olive groves subject to a different management of the ground herb cover (intensive vs. low-intensity) and embedded in a landscape matrix whose degree of complexity varies markedly among sites. By adopting a metacommunity approach, we examined the relative contribution of taxonomic and functional β diversity components (species replacement and richness

TABLE 3 Bird species with significant ($p < 0.005$) diagnostic power in terms of species abundances (traditional IndVal analysis) for the three landscape complexity categories (complex, intermediate and simple) and the two soil management types (low-intensity and intensive) considered in this study. Component 'A' indicates the probability that the surveyed site belongs to the target site group given the fact that the species has been found (i.e. specificity). Component 'B' indicates the probability of finding the species in sites belonging to the site group. This second conditional probability is called the fidelity or sensitivity of the species as indicator of the target site group. Asterisks indicate a marginally significant power

	Specificity ('A')	Fidelity ('B')	Stat.	p-value
I: Landscape complexity				
(1) Complex landscape				
<i>Lullula arborea</i>	0.812	0.833	0.822	0.003
<i>Garrulus glandarius</i>	1.000	0.583	0.764	0.001
<i>Ptyonoprogne rupestris</i>	0.763	0.667	0.713	0.001
<i>Troglodytes troglodytes</i>	0.738	0.583	0.656	0.012
<i>Coccothraustes coccothraustes</i>	0.750	0.500	0.612	0.009
<i>Loxia curvirostra</i>	0.858	0.417	0.598	0.019
(2) Intermediate landscape				
<i>Passer montanus</i>	0.959	0.428	0.641	0.004
(3) Simple landscape				
<i>Coracias garrulus</i>	1.000	0.357	0.598	0.010
<i>Erythropgia galactotes</i>	0.917	0.357	0.572	0.019
(1+2) Complex+intermediate				
<i>Cyanistes caeruleus</i>	0.936	0.885	0.910	0.006
<i>Emberiza cirrus</i>	0.924	0.731	0.822	0.008
<i>Aegithalos caudatus</i>	0.939	0.615	0.760	0.001
<i>Dendrocopos major</i>	1.000	0.538	0.734	0.004
<i>Picus sharpei</i>	0.879	0.577	0.712	0.050
<i>Accipiter nisus</i>	0.934	0.385	0.599	0.034
(2+3) Intermediate+simple				
<i>Buteo buteo</i>	0.9263	0.786	0.853	0.005
II: Management type				
(1) Low intensity (with ground cover)				
<i>Curruca undata</i>	0.826	0.368	0.545	0.069*
<i>Coturnix coturnix</i>	0.890	0.316	0.513	0.067*
(2) Intensive (bare ground)				
None	–	–	–	–

differences) to shed light on the ecological processes underlying community assembly. We also employed two different methods that allowed us to flag sites that make a significant contribution to β diversity (i.e. ecologically unique farms) and those species with a diagnostic value, which can be helpful to guide conservation strategies.

4.1 | Composition of bird communities

We observed that the influence of landscape complexity on the composition of bird communities is greater than the one of management type (Figure 1b). This finding adds to the growing body of evidence that other environmental factors (mainly landscape heterogeneity and local features like hedgerows), besides management practices play a key role in influencing community composition of agroecosystems (e.g. Zumeaga et al., 2021). In this sense, the presence of patches of natural vegetation within the cultivated land can lessen the effect of local agro-environmental practices mostly in simple landscapes (Castro-Caro et al., 2015; García-Navas et al., in press).

4.2 | Taxonomic and functional beta diversity

We found that compositional dissimilarity among sites increased with landscape complexity when the number of shared species between farms was evaluated against a community null model. The type of management seems to have less influence than landscape complexity in explaining between-site variation in species composition suggesting that large-scale factors are more important than local ones (i.e. farming practices) in a metacommunity context (see also Clough et al., 2007). None of the two analysed categorical variables reflecting agricultural intensification (local management; landscape complexity) affected functional total β diversity, which remained almost constant. This result agrees with the one found by Si et al. (2015) for island bird assemblages, where taxonomic nestedness-resultant and turnover components increased and decreased with difference in island area, respectively, but functional counterparts did not (Si et al., 2015).

Both taxonomic and functional differences in bird assemblages among farms were mostly due to a turnover effect and not to

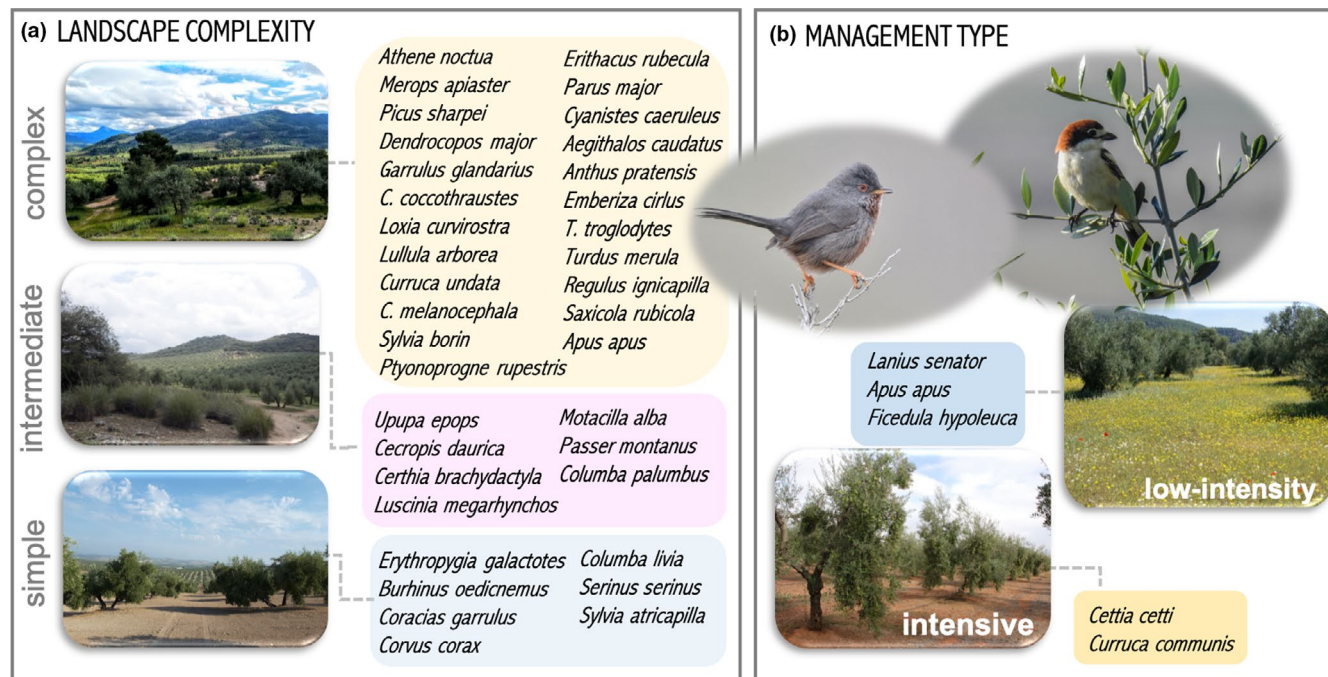


FIGURE 4 Bird species with significant diagnostic power in terms of functional association values φ_{jk} ($p < 0.05$; 999 iterations; two-tailed test) for (a) the three categories of landscape complexity, and (b) both types of olive farming. The functional association values were obtained by combining the species abundances with their functional traits following the approach detailed in Ricotta et al. (2020). Two of the species associated with low-intensity olive groves according to the traditional (abundance-based) and the functional approach are represented: *Curruca undata* and *Lanius senator* (photo credits: Eduardo Gómez, Daniel Alfonso and Pedro J. Rey)

species richness differences. This result reflects the predominance of species selection by environmental or spatial filters over other processes. However, the relative contribution of the trait replacement component was much lower (about half) in comparison with that of species replacement. It suggests that this agroforestry system favours a moderate turnover of species—as it allows the coexistence of forest and farmland species—and, in turn, tends to create a nested pattern of species traits. Thus, although bird species are replaced among farms, their functional attributes are not replaced to the same extent, because species in one site are substituted by functionally redundant species from another site. This pattern is also common in natural systems (see Branco et al., 2020; Carvalho et al., 2020).

The existence of a higher contribution of the nestedness component when comparing farms located in complex landscapes in relation to what was observed when examining the dissimilarity among farms within intermediate or within simple landscapes suggests that among-farm differences are more accentuated as the level of landscape complexity increases. That is, there is a steeper gradient of habitat quality within olive farms surrounded by natural habitats (woodlands, scrublands and grasslands), which would favour an ordered (non-random) colonization/extinction of species (e.g. Si et al., 2015). It means that assemblages occupying degraded or early-successional stages would be a derivative of the original species pool that can be found in old-grown Mediterranean forests. While, among-farm heterogeneity and thus, habitat nestedness (i.e.

hierarchical habitat distributions) is expected to decline as landscape complexity decreases making it more difficult to detect a nested structure in bird assemblages inhabiting olive groves embedded within a transformed habitat matrix.

4.3 | Local contribution to beta diversity and community functional uniqueness

Olive farms with a greater contribution to overall beta diversity (LCBD) were not associated with a particular landscape category or management type. Our analysis identified four unique sites (half of which were low-intensity farms) located in both intermediate (three farms) and simple (one farm) landscapes. Within the seven top-ranked farms in terms of ecological uniqueness (Table 3), three were characterized by high replacement (LCBD_{repl}) values indicating that there were high numbers of bird taxa recorded in these farms that were not recorded in the other ones (i.e. unique species). Two of them are located near cool mountain areas (Sierra Nevada in Granada and Sierra de Segura in Jaen), whereas the other one is close to a wetland (Lantejuela lagoons in Seville) catalogued as Important Bird Area. Thus, these olive farms are enriched with the contribution of distinctive elements—montane (e.g. brambling *Fringilla montifringilla*, mistle thrush *Turdus viscivorus*) and marsh species (e.g. fantailed warbler *Cisticola juncidis*, ciril bunting *Emberiza cirrus*), respectively—relatively scarce elsewhere. In contrast, two farms located in the surroundings

(<3 km apart) of urbanized areas ('OLI' and 'QUI'; Table 3) were more dissimilar and contributed substantially to β diversity due to their high richness difference (nestedness; $\text{LCBD}_{\text{rich}}$) values. Thus, these farms constitute impoverished sets of taxa largely composed of generalists and a few taxa associated with human settlements (e.g. red-rumped swallow *Cecropis daurica*; jackdaw *Corvus monedula*). Accordingly, and in agreement with previous studies (da Silva et al., 2020; Landeiro et al., 2018; López-Delgado et al., 2020), we found that LCBD was negatively related to species richness, although the relationship was also slightly curvilinear (Heino & Grönroos, 2017). It means that species-poor sites tend to contribute the most to the local-to-regional β diversity. Both components of LCBD were associated with taxonomic species richness, although displayed opposing trends (Figure S2). $\text{LCBD}_{\text{repl}}$ values were highest at intermediate richness values, while $\text{LCBD}_{\text{rich}}$ values were lowest at intermediate richness values since farms with the highest and lowest taxonomic diversity represent sites with a substantial gain or loss (respectively) of species (Hill et al., 2021).

Although we did not find differences in LCBD among categories of landscape complexity, it seems that the amount of land covered by olive groves has a meaningful impact on the ecological uniqueness of sites. It may be due to the fact that the expansion of monocultures reduces the presence of wastelands, fallows and grasslands, which negatively affects shrubland (e.g. common stonechat *Saxicola rubicola*) and steppe-land birds (e.g. red-legged partridge, lesser kestrel). Our results suggest a threshold (around 25%–50%; Figure 3b; Figure S1) from which both presence-absence and abundance-based LCBD decline with increasing area devoted to olive production. It means that olive monocultures (>50% of the total surface devoted to this crop) can reduce the dissimilarity among sites and lead to a process of biotic homogenization regardless of the surrounding landscape (Figure 3b). Consequently, hedges, riversides and other live fences play a key role in diversifying communities in which generalists and forest species (e.g. sparrows and tits) predominate as they favour birds of edge, scrubby and early-successional habitats (e.g. spotted flycatcher *Muscicapa striata*). Sites with high LCBD values were not only associated with a distinctive species composition, but also with idiosyncratic communities in terms of functional uniqueness. This finding suggests that the preservation of ecologically unique sites can also be relevant for ecosystem functioning as these may comprise species with unique attributes and whose loss may eventually lead to destabilizing effects (Bracken & Low, 2012; O'Gorman et al., 2011).

4.4 | Indicator species analyses

Our abundance-based indicator analysis revealed that some bird species showed high specificity and fidelity values in relation to landscape composition. For instance, the woodlark is ecologically restricted to olive groves embedded within complex landscapes and frequent within this habitat type. Other eminently forest species such as the Eurasian jay, the crossbill *Loxia curvirostra*,

the hawfinch *Coccothraustes coccothraustes* or the Eurasian wren *Troglodytes troglodytes* were also associated with landscapes with high heterogeneity, whereas open-woodland species like the European roller *C. garrulus* and species linked to cereal crops and steppe-like habitats (e.g. stone-curlew) were diagnostic of simple landscapes. This analysis identified a few species associated with low-intensity management, whereas no indicator species of intensive farming was found. The Dartford warbler (typical of homogeneous habitats that appear as degraded successional stages of former Mediterranean forest types) and the common quail (requiring dense vegetation for breeding; Németh et al., 2019) were marginally associated with the presence of herbaceous cover. In addition, when using species combinations as indicators, we found that the woodchat shrike accounted for most (73%) of the double-combinations associated with low-intensity management. The woodchat shrike shows a marked preference for high maquis vegetation surrounded by low vegetation (Lefranc & Worfolk, 1997; Papageorgiou et al., 2017). Shrikes create temporary caches (larders) by impaling prey on thorns or in forked branches throughout their territory, which can be used as a cue by heterospecifics to rapidly assess habitat quality (Chiatante, 2019; Hromada et al., 2008). In fact, this and other shrike species breed in association with warbler species, which it has been suggested to be an antipredator-oriented mutualism (*L. senator* and *Sylvia hortensis*; Isenmann & Fradet, 1995; *L. collurio* and *S. nisoria*; Polak, 2012, 2014). Thus, the woodchat shrike constitutes an excellent indicator of biodiversity in this ecosystem.

The high diagnostic value of *L. senator* was corroborated when applying a functional approach. The woodchat shrike was one of the three species functionally associated with low-intensity farms. Curiously, the two other species—the common swift and the European pied flycatcher—are aerial foragers, which may indicate that olive groves with low-intensity management harbour a substantial number of flying insects (Heteroptera, Hymenoptera, Diptera) that these species feed on. Using the functional-based indicator analysis, we found 47 bird species showing significant association ($p < 0.05$, two-tailed test) with one of the three landscape categories. According to these results as well as the examples provided in Ricotta et al. (2020), the functional indicator species analysis enables to highlight the diagnostic value of a larger pool of species.

5 | CONCLUSIONS

From a mechanistic point of view, the observed Raup–Crick values indicate that bird community assembly in olive farms is driven mainly by neutral, stochastic processes, rather than by niche-based, deterministic processes, which could be due to the high dispersal capacity of this group compared to that of other organisms (e.g. Wendt et al., 2021; Rego et al., 2019) or to the higher resemblance among sites in our study system in comparison with more heterogeneous environments (e.g. Si et al., 2016). The lower contribution of the trait

replacement component in relation to species replacement suggests that some sites vary in taxonomic composition but exhibit similar functional trait combinations. That is, some farms acted as functional subsets to the others (impoverished sites, see below), despite different species compositions.

Although we did not find significant differences between management types nor among landscape complexity categories in terms of contribution to total β diversity, we observed that an environmental variable indicative of intensification (proportion of land devoted to olive crop) predicts the level of compositional uniqueness. Moreover, we detected a threshold (% of land devoted to olive crop >50) over which biotic homogenization increase drastically. Since species replacement (turnover) broadly measures the same phenomenon as total β diversity (both measures are often highly correlated; Soininen et al., 2018), it is not surprising that we also found a significant relationship between $\text{LCBD}_{\text{repl}}$ and percentage cover of olive groves (Figure S3). Thus, our results suggest that olive monocultures erode community diversity and promote biotic homogenization (see also Rey et al., 2019). This process could be reversed by intermixing olive farms with other crops (e.g. cereals) and remnants of natural habitat, which would foster habitat diversification and reduce species sorting.

Local contribution to beta diversity approaches can be useful for bioassessment and conservation purposes, as several studies focused on freshwater communities have revealed (e.g. Gavioli et al., 2019; Heino et al., 2017; Li et al., 2020). However, it should be noted that sites having high LCBD values are often rather species-poor sites (Heino & Grönroos, 2017). Our results show that by partitioning LCBD into richness differences and species replacement, it is feasible to discern between (i) divergent assemblages that reflect degraded or highly perturbed habitats that may be candidates for ecological restoration (i.e. impoverished sites) and (ii) sites with distinctive elements or unique features particularly important for biodiversity conservation because they sustain relatively unique species (i.e. species with restricted distribution along the study area). Yet, this approach has been barely applied (but see Hill et al., 2021). Finally, as shown, the presence of certain indicator species can also be helpful when assessing the impact of a given site in the metacommunity and provides relevant information for landowners and managers. Overall, our study shows that by examining different diversity dimensions separately and partitioning beta diversity into different components, it is possible to obtain a better understanding of biological phenomena that generate the observed spatial patterns, which is essential for conservation purposes.

ACKNOWLEDGEMENTS

We are indebted to all the owners and farmers of the olive groves in which this study was conducted for allowing and facilitating our work.

CONFLICT OF INTEREST

The authors have no conflicts of interest to declare.

PEER REVIEW

The peer review history for this article is available at <https://publons.com/publon/10.1111/ddi.13445>.

DATA AVAILABILITY STATEMENT

Data are archived at the Dryad digital data repository: <https://doi.org/10.5061/dryad.7wm37pvtr>.

ORCID

Vicente García-Navas  <https://orcid.org/0000-0002-9362-2663>

José L. Molina-Pardo  <https://orcid.org/0000-0001-7270-366X>

REFERENCES

- Anderson, M. J. (2001). A new method for non-parametric multivariate analysis of variance. *Austral Ecology*, 26, 32–46.
- Anderson, M. J., Crist, T. O., Chase, J. M., Vellend, M., Inouye, B. D., Freestone, A. L., Sanders, N. J., Cornell, H. V., Comita, L. S., Davies, K. F., Harrison, S. P., Kraft, N. J. B., Stegen, J. C., & Swenson, N. G. (2011). Navigating the multiple meanings of β diversity: A roadmap for the practicing ecologist. *Ecology Letters*, 14, 19–28. <https://doi.org/10.1111/j.1461-0248.2010.01552.x>
- Baeten, L., Vangansbeke, P., Hermy, M., Peterken, G., Vanhuyse, K., & Verheyen, K. (2012). Distinguishing between turnover and nestedness in the quantification of biotic homogenization. *Biodiversity and Conservation*, 21, 1399–1409. <https://doi.org/10.1007/s10531-012-0251-0>
- Baselga, A. (2010). Partitioning the turnover and nestedness components of beta diversity. *Global Ecology and Biogeography*, 19, 134–143.
- Baselga, A. (2012). The relationship between species replacement, dissimilarity derived from nestedness, and nestedness. *Global Ecology and Biogeography*, 21, 1223–1232. <https://doi.org/10.1111/j.1466-8238.2011.00756.x>
- Baselga, A., & Orme, C. D. L. (2012). *betapart*: An R package for the study of beta diversity. *Methods in Ecology and Evolution*, 3, 808–812.
- Baselga, A., Orme, C. D. L., Villéger, S., De Bortoli, J., Leprieux, F., & Logez, M. (2021). *betapart*: Partitioning beta diversity into turnover and nestedness components. R package version 1.5.3. <http://CRAN.R-project.org/package=betapart>
- Blitzer, E. J., Dormann, C. F., Holzschuh, A., Klein, A. M., Rand, T. A., & Tscharntke, T. (2012). Spillover of functionally important organisms between managed and natural habitats. *Agriculture, Ecosystems & Environment*, 146, 34–43. <https://doi.org/10.1016/j.agee.2011.09.005>
- Bracken, M. E. S., & Low, N. H. N. (2012). Realistic losses of rare species disproportionately impact higher trophic levels. *Ecology Letters*, 15, 461–467.
- Branco, C. C. Z., Bispo, P. C., Peres, C. K., Tonetto, A. F., Krupek, R. A., Barfield, M., & Holt, R. D. (2020). Partitioning multiple facets of beta diversity in a tropical stream macroalgal metacommunity. *Journal of Biogeography*, 47, 1765–1780. <https://doi.org/10.1111/jbi.13879>
- Cadotte, M. W., Carscadden, K., & Mirotchnick, N. (2011). Beyond species: Functional diversity and the maintenance of ecological processes and services. *Journal of Applied Ecology*, 48, 1079–1087. <https://doi.org/10.1111/j.1365-2664.2011.02048.x>
- Cardoso, P., Mammola, S., Rigal, F., & Carvalho, J. C. (2020). BAT: Biodiversity assessment tools. <https://cran.r-project.org/package=BAT>
- Cardoso, P., Rigal, F., Carvalho, J. C., Fortelius, M., Borges, P. A. V., Podani, J., & Schmera, D. (2014). Partitioning taxon, phylogenetic and functional beta diversity into replacement and richness difference components. *Journal of Biogeography*, 41, 749–761. <https://doi.org/10.1111/jbi.12239>

- Carlos-Júnior, L. A., Spencer, M., Neves, D. M., Moulton, T. P., Pires, D. D. O., e Castro, C. B., Ventura, C. R. R., Ferreira, C. E. L., Serejo, C. S., Oigman-Pszczol, S., Casares, F. A., Mantelatto, M. C., & Creed, J. C. (2019). Rarity and beta diversity assessment as tools for guiding conservation strategies in marine tropical subtidal communities. *Diversity and Distributions*, 25, 743–757. <https://doi.org/10.1111/ddi.12896>
- Carvalho, J. C., Cardoso, P., & Gomes, P. (2012). Determining the relative roles of species replacement and species richness differences in generating beta-diversity patterns. *Global Ecology and Biogeography*, 21, 760–771. <https://doi.org/10.1111/j.1466-8238.2011.00694.x>
- Carvalho, J. C., Malumbres-Olarte, J., Arnedo, M. A., Crespo, L. C., Domenech, M., & Cardoso, P. (2020). Decomposing the causes for niche differentiation between species using hypervolumes. *Frontiers in Ecology and Evolution*, 8, 243. <https://doi.org/10.1111/jbi.13722>
- Castro-Caro, J. C., Barrio, I. C., & Tortosa, F. S. (2014). Is the effect of farming practices on songbird communities landscape dependent? A case study of olive groves in southern Spain. *Journal of Ornithology*, 155, 357–365. <https://doi.org/10.1007/s10336-013-1010-z>
- Castro-Caro, J. C., Barrio, I. C., & Tortosa, F. S. (2015). Effects of hedges and herbaceous cover on passerine communities in Mediterranean olive groves. *Acta Ornithologica*, 50, 180–192. <https://doi.org/10.3161/00016454AO2015.50.2.006>
- Chase, J. M., Kraft, N. J. B., Smith, K. G., Vellend, M., & Inouye, B. D. (2011). Using null models to disentangle variation in community dissimilarity from variation in α -diversity. *Ecosphere*, 2, art24. <https://doi.org/10.1890/ES10-00117.1>
- Chase, J. M., & Myers, J. A. (2011). Disentangling the importance of ecological niches from stochastic processes across scales. *Philosophical Transactions of the Royal Society of London: Biological Sciences*, 366, 2351–2363. <https://doi.org/10.1098/rstb.2011.0063>
- Chiatante, G. (2019). Heterospecific social attraction in migrant birds: Habitat niche overlap between two threatened shrikes. *Wildlife Research*, 45, 25–36. <https://doi.org/10.1071/WR18031>
- Clavel, J., Julliard, R., & Devictor, V. (2011). Worldwide decline of specialist species: Toward a global functional homogenization? *Frontiers in Ecology and the Environment*, 9, 222–228. <https://doi.org/10.1890/080216>
- Clough, Y., Holzschuh, A., Gabriel, D., Purtauf, T., Kleijn, D., Kruess, A., Steffan-dewenter, I., & Tscharrntke, T. (2007). Alpha and beta diversity of arthropods and plants in organically and conventionally managed wheat fields. *Journal of Applied Ecology*, 44, 804–812. <https://doi.org/10.1111/j.1365-2664.2007.01294.x>
- Cribari-Neto, F., & Zeileis, A. (2010). Beta regression in R. *Journal of Statistical Software*, 34, 1–24.
- Da Silva, P. G., Bogoni, J. A., & Heino, J. (2020). Can taxonomic and functional metrics explain variation in the ecological uniqueness of ecologically-associated animal groups in a modified rainforest? *Science of the Total Environment*, 708, 135171. <https://doi.org/10.1016/j.scitotenv.2019.135171>
- Da Silva, P. G., Hernández, M. I. M., & Heino, J. (2018). Disentangling the correlates of species and site contributions to beta diversity in dung beetle assemblages. *Diversity and Distributions*, 24, 1674–1686. <https://doi.org/10.1111/ddi.12785>
- De Cáceres, M., Legendre, P., & Moretti, M. (2010). Improving indicator species analysis by combining groups of sites. *Oikos*, 119, 1674–1684. <https://doi.org/10.1111/j.1600-0706.2010.18334.x>
- De Cáceres, M., Legendre, P., Wiser, S. K., & Brotons, L. (2012). Using species combinations in indicator value analyses. *Methods in Ecology and Evolution*, 3, 973–982. <https://doi.org/10.1111/j.2041-210X.2012.00246.x>
- Díaz, M., Concepción, E. D., Morales, M. B., Alonso, J. C., Azcárate, F. M., Bartomeus, I., Bota, G., Brotons, L., García, D., Giral, D., Gutiérrez, J. E., López-Bao, J. V., Mañosa, S., Milla, R., Miñarro, M., Navarro, A., Olea, P. P., Palacín, C., Peco, B., ... Velado-Alonso, E. (2021). Environmental objectives of Spanish agriculture: Scientific guidelines for their effective implementation under the Common Agricultural Policy 2023–2030. *Ardeola*, 68, 445–460. <https://doi.org/10.13157/arla.68.2.2021.fo1>
- Dormann, C. F., Schweiger, O., Augenstein, I., Bailey, D., Billeter, R., de Blust, G., DeFilippi, R., Frenzel, M., Hendrickx, F., Herzog, F., Klotz, S., Liira, J., Maelfait, J.-P., Schmidt, T., Speelmans, M., van Wingerden, W. K. R. E., & Zobel, M. (2007). Effects of landscape structure and land-use intensity on similarity of plant and animal communities. *Global Ecology and Biogeography*, 16, 774–787. <https://doi.org/10.1111/j.1466-8238.2007.00344.x>
- Dray, S., Bauman, D., Blanchet, G., Borcard, D., Clappe, S., Guenard, G., Jombart, T., Larocque, G., Legendre, P., Madi, N., & Wagner, H. H. (2018). *adespatial*: Multivariate multiscale spatial analysis. R package version 0.2-0. <https://cran.r-project.org/web/packages/adespatial/index.html>
- Dray, S., & Dufour, A. B. (2007). The *ade4* package: Implementing the duality diagram for ecologists. *Journal of Statistical Software*, 22, 1–20.
- Dufrene, M., & Legendre, P. (1997). Species assemblages and indicator species: The need for a flexible asymmetrical approach. *Ecological Monographs*, 67, 345–366. <https://doi.org/10.2307/2963459>
- Ekkroos, J., Heliölä, J., & Kuussaari, M. (2010). Homogenization of lepidopteran communities in intensively cultivated agricultural landscapes. *Journal of Applied Ecology*, 47, 459–467.
- Frasconi Wendt, C., Ceia-Hasse, A., Nunes, A., Verble, R., Santini, G., Boieiro, M., & Branquinho, C. (2021). Local environmental variables are key drivers of ant taxonomic and functional beta-diversity in a Mediterranean dryland. *Scientific Reports*, 11, 2292. <https://doi.org/10.1038/s41598-021-82059-w>
- García-Navas, V., Martínez-Núñez, C., Tarifa, R., Manzaneda, A. J., Francisco-Valera, T. S., Camacho, F. M., Isla, J., & Rey, P. J. (in press). Agricultural extensification enhances functional diversity but not phylogenetic diversity in Mediterranean olive groves: A case study with ant and bird communities. *Agriculture, Ecosystems & Environment*, 324. <https://doi.org/10.1016/j.agee.2021.107708>
- Gavioli, A., Milardi, M., Castaldelli, G., Fano, E. A., & Soininen, J. (2019). Diversity patterns of native and exotic fish species suggest homogenization processes, but partly fail to highlight extinction threats. *Diversity and Distributions*, 25, 983–994. <https://doi.org/10.1111/ddi.12904>
- Gómez, J. A., Infante-Amate, J., González de Molina, M., Vanwalleghe, T., Taguas, E. V., & Lorite, I. (2014). Olive cultivation, its impact on soil erosion and its progression into yield impacts in Southern Spain in the past as a key to a future of increasing climate uncertainty. *Agriculture*, 4, 170–198. <https://doi.org/10.3390/agriculture4020170>
- Grenié, M., Denelle, P., Tucker, C. M., Munoz, F., & Violle, C. (2017). *funrar*: An R package to characterize functional rarity. *Diversity and Distributions*, 23, 1365–1371. <https://doi.org/10.1111/ddi.12629>
- Heino, J., Bini, L. M., Andersson, J., Bergsten, J., Bjelke, U., & Johansson, F. (2017). Unravelling the correlates of species richness and ecological uniqueness in a metacommunity of urban pond insects. *Ecological Indicators*, 73, 422–431. <https://doi.org/10.1016/j.ecoli.2016.10.006>
- Heino, J., & Grönroos, M. (2017). Exploring species and site contributions to beta diversity in stream insect assemblages. *Oecologia*, 183, 151–160. <https://doi.org/10.1007/s00442-016-3754-7>
- Hill, M. J., White, J. C., Biggs, J., Briers, R. A., Gledhill, D., Ledger, M. E., Thornhill, I., Wood, P. J., & Hassall, C. (2021). Local contributions to beta diversity in urban pond networks: Implications for biodiversity conservation and management. *Diversity and Distributions*, 27, 887–900. <https://doi.org/10.1111/ddi.13239>
- Hromada, M., Antczak, M., Valone, T. J., & Tryjanowski, P. (2008). Settling decisions and heterospecific social information use in shrikes. *PLoS One*, 3(10), e3930. <https://doi.org/10.1371/journal.pone.0003930>

- Infante-Amate, J., Villa, I., Aguilera, E., Torremocha, E., Guzmán, G., & Cid, A. (2016). The making of olive landscapes in the South of Spain. A history of continuous expansion and intensification. In: M. Agnoletti & F. Emanuelli (Eds.), *Biocultural diversity in Europe. Environmental history*, Vol. 5, (157–179). Springer.
- Isenmann, P., & Fradet, G. (1995). Is the nesting association between the orphean warbler (*Sylvia hortensis*) and the woodchat shrike (*Lanius senator*) an anti-predator oriented mutualism? *Journal für Ornithologie*, 136, 288–291. <https://doi.org/10.1007/BF01651297>
- Karp, D., Rominger, A. J., Zook, J., Ranganathan, J., Ehrlich, P. R., & Daily, G. C. (2012). Intensive agriculture erodes β -diversity at large scales. *Ecology Letters*, 15, 963–970. <https://doi.org/10.1111/j.1461-0248.2012.01815.x>
- Landeiro, V. L., Franz, B., Heino, J., Siqueira, T., & Bini, L. M. (2018). Species-poor and low-lying sites are more ecologically unique in a hyperdiverse Amazon region: Evidence from multiple taxonomic groups. *Diversity and Distributions*, 24, 966–977. <https://doi.org/10.1111/ddi.12734>
- Lefranc, N., & Worfolk, T. (1997) *Shrikes. A guide to the shrikes of the world*. Pica Press.
- Legendre, P. (2014). Interpreting the replacement and richness difference components. *Global Ecology and Biogeography*, 23, 1324–1334.
- Legendre, P., & De Cáceres, M. (2013). Beta diversity as the variance of community data: Dissimilarity coefficients and partitioning. *Ecology Letters*, 16, 951–963. <https://doi.org/10.1111/ele.12141>
- Li, F., Tonkin, J. D., & Haase, P. (2020). Local contribution to beta diversity is negatively linked with community-wide dispersal capacity in stream invertebrate communities. *Ecological Indicators*, 18, 105715. <https://doi.org/10.1016/j.ecolind.2019.105715>
- Liu, C., Guénard, B., Lanchard, B., Peng, Y.-Q., & Economo, E. (2016). Reorganization of taxonomic, functional, and phylogenetic ant biodiversity after conversion to rubber plantation. *Ecological Monographs*, 86, 215–227. <https://doi.org/10.1890/15-1464.1>
- López-Delgado, E. O., Winemiller, K. O., & Villa-Navarro, F. A. (2020). Local environmental factors influence beta-diversity patterns of tropical fish assemblages more than spatial factors. *Ecology*, 101, e02940. <https://doi.org/10.1002/ecy.2940>
- Mammola, S., & Cardoso, P. (2020). Functional diversity metrics using kernel density n -dimensional hypervolumes. *Methods in Ecology and Evolution*, 11, 986–995.
- Martínez-Núñez, C., Manzaneda, A. J., Isla, J., Tarifa, R., Calvo, G., Molina, J. L., Salido, T., Ruiz, C., Gutiérrez, J. E., & Rey, P. J. (2020). Low-intensity management benefits solitary bees in olive groves. *Journal of Applied Ecology*, 57, 111–120. <https://doi.org/10.1111/1365-2664.13511>
- Martínez-Núñez, C., Rey, P. J., Manzaneda, A. J., Tarifa, R., Salido, T., Isla, J., Pérez, A. J., Camacho, F. M., & Molina, J. L. (2020). Direct and indirect effects of agricultural practices, landscape complexity and climate on insectivorous birds, pest abundance and damage in olive groves. *Agriculture, Ecosystems & Environment*, 304, 107145. <https://doi.org/10.1016/j.agee.2020.107145>
- Martins da Silva, P., Oliveira, J., Ferreira, A., Fonseca, F., Pereira, J. A., Aguiar, C. A. S., Serrano, A. R. M., Sousa, J. P., & Santos, S. A. P. (2017). Habitat structure and neighbor linear features influence more carabid functional diversity in olive groves than the farming system. *Ecological Indicators*, 79, 128–138. <https://doi.org/10.1016/j.ecolind.2017.04.022>
- McGarigal, K., Cushman, S. A., & Ene, E. (2012). *FRAGSTATS v4: Spatial pattern analysis program for categorical and continuous maps*. University of Massachusetts.
- Medan, D., Torretta, J. P., Hodara, K., Fuente, E. B., & Montaldo, N. H. (2011). Effects of agriculture expansion and intensification on the vertebrate and invertebrate diversity in the Pampas of Argentina. *Biodiversity and Conservation*, 20, 3077–3100. <https://doi.org/10.1007/s10531-011-0118-9>
- Mittelbach, G. G., & McGill, B. G. (2019). *Community ecology* (2nd ed.). Oxford University Press.
- Morgado, R., Santana, J., Porto, M., Sánchez-Oliver, J. S., Reino, L., Herrera, J. M., Rego, F., Beja, P., & Moreira, F. (2020). A Mediterranean silent spring? The effects of olive farming intensification on breeding bird communities. *Agriculture, Ecosystems & Environment*, 288, 10669. <https://doi.org/10.1016/j.agee.2019.106694>
- Myhrvold, N. P., Baldridge, E., Chan, B., Sivam, D., Freeman, D. L., & Ernest, S. K. M. (2015). An amniote life-history database to perform comparative analyses with birds, mammals, and reptiles. *Ecology*, 96, 3109. <https://doi.org/10.1890/15-0846R.1>
- Németh, T. M., Kelemen, P., Csiszár, Á., Kovács, G., Faragó, S., & Winkler, D. (2019). Habitat selection of the Common Quail in an intensively managed agricultural environment. *Ornis Hungarica*, 27, 99–109.
- O'Gorman, E. J., Yearsley, J. M., Crowe, T. P., Emmerson, M. C., Jacob, U., & Petchey, O. L. (2011). Loss of functionally unique species may gradually undermine ecosystems. *Proceedings of the Royal Society of London: Biological Sciences*, 278, 1886–1893.
- Oksanen, J., Blanchet, F. G., Friendly, M., Kindt, R., Legendre, P., McGlinn, D., Minchin, P. R., O'Hara, R. B., Simpson, G. L., Peter Solymos, M., Stevens, H. H., Szoecs, E., & Wagner, H. (2020). *vegan: Community ecology package* (version 2.5-5). <https://cran.r-project.org/web/packages/vegan/index.html>
- Panagos, P., Ballabio, C., Borrelli, P., Meusburger, K., Klik, A., Rousseva, S., Tadić, M. P., Michaelides, S., Hrabalíková, M., Olsen, P., Aalto, J., Lakatos, M., Rymaszewicz, A., Dumitrescu, A., Beguería, S., & Alewell, C. (2015). Rainfall erosivity in Europe. *Science of the Total Environment*, 511, 801–814. <https://doi.org/10.1016/j.scitotenv.2015.01.008>
- Papageorgiou, D., Barboutis, C., Kassara, C., & Giokas, S. (2017). Habitat selection of woodchat shrikes *Lanius senator* during spring stopover is related to foraging strategy. *Current Zoology*, 63, 139–149.
- Philpott, S. M., Arendt, W. J., Armbricht, I., Bichier, P., Diestch, T. V., Gordon, C., Greenberg, R., Perfecto, I., Reynoso-santos, R., Soto-pinto, L., Tejeda-cruz, C., Williams-linera, G., Valenzuela, J., & Zolotoff, J. M. (2008). Biodiversity loss in Latin American coffee landscapes: Review of the evidence on ants, birds, and trees. *Conservation Biology*, 22, 1093–1105. <https://doi.org/10.1111/j.1523-1739.2008.01029.x>
- Polak, M. (2012). Habitat preferences of the sympatric barred warbler (*Sylvia nisoria*) and the red-backed shrike (*Lanius collurio*) breeding in central Poland. *Annales Zoologici Fennici*, 49, 355–363.
- Polak, M. (2014). Protective nesting association between the Barred Warbler *Sylvia nisoria* and the Red-backed Shrike *Lanius collurio*: An experiment using artificial and nests. *Ecological Research*, 29, 949–957.
- QGIS Development Team. (2018). *QGIS geographic information system*. Open Source Geospatial Foundation Project. <http://qgis.osgeo.org>
- Raup, D. M., & Crick, R. E. (1979). Measurement of faunal similarity in paleontology. *Journal of Paleontology*, 53, 1213–1227.
- Rego, C., Boieiro, M., Rigal, F., Ribeiro, S. P., Cardoso, P., & Borges, P. A. V. (2019). Taxonomic and functional diversity of insect herbivore assemblages associated with the canopy-dominant trees of the Azorean native forest. *PLoS One*, 14, e0219493. <https://doi.org/10.1371/journal.pone.0219493>
- Rey, P. J., Manzaneda, A. J., Valera, F., Alcántara, J. M., Tarifa, R., Isla, J., Molina-Pardo, J. L., Calvo, G., Salido, T., Gutiérrez, J. E., & Ruiz, C. (2019). Landscape-moderated bio-diversity effects of ground herb cover in olive groves: Implications for regional biodiversity conservation. *Agriculture Ecosystems & Environment*, 277, 61–73. <https://doi.org/10.1016/j.agee.2019.03.007>
- Ricotta, C., Acosta, A. T. R., Caccianiga, M., Cerabolini, B. E. L., Godefroid, S., & Carboni, M. (2020). From abundance-based to functional-based indicator species. *Ecological Indicators*, 118, 106761. <https://doi.org/10.1016/j.ecolind.2020.106761>

- Ricotta, C., Carboni, M., & Acosta, A. T. R. (2015). Let the concept of indicator species be functional! *Journal of Vegetation Science*, 26, 839–847. <https://doi.org/10.1111/jvs.12291>
- Santana, J., Porto, M., Reino, L., Moreira, F., Ribeiro, P. F., Santos, J. L., Rotenberry, J. T., & Beja, P. (2017). Using beta diversity to inform agricultural policies and conservation actions on Mediterranean farmland. *Journal of Applied Ecology*, 54, 1825–1835. <https://doi.org/10.1111/1365-2664.12898>
- Santos, F., Lima, M. G. M., Espinosa, S., Ahumada, J. A., Jansen, P. A., Spironello, W. R., Hurtado, J., Juen, L., & Peres, C. A. (2021). Site and species contribution to β -diversity in terrestrial mammal communities: Evidence from multiple Neotropical forest sites. *Science of the Total Environment*, 789, 147946. <https://doi.org/10.1016/j.scitotenv.2021.147946>
- Sastre, B., Barbero-Sierra, C., Bienes, R., Marques, M. J., & García-Díaz, A. (2017). Soil loss in an olive grove in Central Spain under cover crops and tillage treatments, and farmer perceptions. *Journal of Soils Sediments*, 17, 873–888. <https://doi.org/10.1007/s11368-016-1589-9>
- Si, X., Baselga, A., & Ding, P. (2015). Revealing beta-diversity patterns of breeding bird and lizard communities on inundated land-bridge islands by separating the turnover and nestedness components. *PLoS One*, 10, e0127692. <https://doi.org/10.1371/journal.pone.0127692>
- Si, X., Baselga, A., Leprieux, F., Song, X., & Ding, P. (2016). Selective extinction drives taxonomic and functional alpha and beta diversities in island bird assemblages. *Journal of Animal Ecology*, 85, 409–418.
- Snell Taylor, S. J., Evans, B. S., White, E. P., & Hurlbert, A. H. (2018). The prevalence and impact of transient species in ecological communities. *Ecology*, 99, 1825–1835. <https://doi.org/10.1002/ecy.2398>
- Socolar, J. B., Gilroy, J. J., Kunin, W. E., & Edwards, D. P. (2016). How should beta-diversity inform biodiversity conservation? *Trends in Ecology and Evolution*, 31, 67–80. <https://doi.org/10.1016/j.tree.2015.11.005>
- Soininen, J., Heino, J., & Wang, J. (2018). A meta-analysis of nestedness and turnover components of beta diversity across organisms and ecosystems. *Global Ecology and Biogeography*, 27, 96–109.
- Storchová, L., & Hořák, D. (2018). Life-history characteristics of European birds. *Global Ecology and Biogeography*, 27, 400–406. <https://doi.org/10.1111/geb.12709>
- Svenning, J. C., Fløjgaard, C., & Baselga, A. (2011). Climate, history and neutrality as drivers of mammal beta diversity in Europe: Insights from multiscale deconstruction. *Journal of Animal Ecology*, 80, 393–402. <https://doi.org/10.1111/j.1365-2656.2010.01771.x>
- Tarifa, R., Martínez-Núñez, C., Valera, F., González-Varo, J. P., Salido, T., & Rey, P. J. (2021). Agricultural intensification erodes taxonomic and functional diversity in Mediterranean olive groves by filtering out rare species. *Journal of Applied Ecology*, 58(10), 2266–2276. <https://doi.org/10.1111/1365-2664.13970>
- Tuomisto, H. (2010). A diversity of beta diversities: Straightening up a concept gone awry. Part 2. Quantifying beta diversity and related phenomena. *Ecography*, 33, 23–45.
- Ulrich, W., Almeida-Neto, M., & Gotelli, N. J. (2009). A consumer's guide to nestedness analysis. *Oikos*, 118, 3–17. <https://doi.org/10.1111/j.1600-0706.2008.17053.x>
- Urban, D. L. (2002). Classification and regression trees. In B. McCune & J. B. Grace (Eds.), *Analysis of ecological communities* (pp. 222–232). MjM Software Design.
- Vellend, M., Verheyen, K., Flinn, K. M., Jacquemyn, H., Kolb, A., Van calster, H., Peterken, G., Graae, B. J., Bellemare, J., Honnay, O., Brunet, J., Wulf, M., Gerhardt, F., & Hermy, M. (2007). Homogenization of forest plant communities and weakening of species-environment relationships via agricultural land use. *Journal of Ecology*, 95, 565–573. <https://doi.org/10.1111/j.1365-2745.2007.01233.x>
- Vilar, J., & Pereira, J. E. (2018). *International olive growing. Worldwide analysis and summary*. Fundación Caja Rural de Jaén.
- Violle, C., Thuiller, W., Mouquet, N., Munoz, F., Kraft, N. J. B., Cadotte, M. W., Livingstone, S. W., & Mouillot, D. (2017). Functional rarity: The ecology of outliers. *Trends in Ecology & Evolution*, 32, 356–367. <https://doi.org/10.1016/j.tree.2017.02.002>
- Whittaker, R. H. (1960). Vegetation of the Siskiyou Mountains, Oregon and California. *Ecological Monographs*, 30, 280–338. <https://doi.org/10.2307/1948435>
- Wilman, H., Belmaker, J., Simpson, J., de la Rosa, C., Rivadeneira, M. M., & Jetz, W. (2014). EltonTraits 1.0: Species-level foraging attributes of the world's birds and mammals. *Ecology*, 95, 2027. <https://doi.org/10.1890/13-1917.1>
- Zumeaga, H., Azcárate, F. M., Concepción, E. D., Hevia, V., & Díaz, M. (2021). Landscape and agri-environmental scheme effects on ant communities in cereal croplands of central Spain. *Ecological Indicators*, 79, 128–138.

BIOSKETCH

The authors do research in animal ecology and behaviour and biological conservation, with especial attention to the anthropogenic impact on biodiversity. The team is integrated both by senior (PJR, FVH and the main author VGN) and young researchers (most of them PhD students). They bring their interests together to address the recovery of biodiversity in olive groves through collaborating in the LIFE project 'Oliveres Vivos'. This paper is part of such attempt.

Authors' contributions: VGN and PJR developed the main ideas of this study. PJR and FV designed the fieldwork. RT, FMC, PJR and JLM conducted bird censuses and TS processed the information on environmental correlates and the GIS data and produced the landscape categorization. VGN analysed the data with feedback from CMN and RT and wrote a first draft of this paper. All authors commented previous drafts of this manuscript and gave their final approval for submission.

SUPPORTING INFORMATION

Additional supporting information may be found in the online version of the article at the publisher's website.

How to cite this article: García-Navas, V., Martínez-Núñez, C., Tarifa, R., Molina-Pardo, J. L., Valera, F., Salido, T., Camacho, F. M., & Rey, P. J. (2022). Partitioning beta diversity to untangle mechanisms underlying the assembly of bird communities in Mediterranean olive groves. *Diversity and Distributions*, 28, 112–127. <https://doi.org/10.1111/ddi.13445>