



Contents lists available at ScienceDirect

Agriculture, Ecosystems and Environment

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

Agricultural extensification enhances functional diversity but not phylogenetic diversity in Mediterranean olive groves: A case study with ant and bird communities

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ARTICLE INFO

Keywords:

Agri-environment schemes (AES)
Agricultural intensification
Biodiversity
Farming
Farmland birds
Functional traits
Landscape complexity
Multi-faceted
Woody crop

ABSTRACT

Agroforests are of well-known importance for biodiversity conservation, especially in the tropics, because they are structurally stable and may resemble natural forests. Previous studies have characterized jointly taxonomic, functional and phylogenetic diversity in these agro-ecosystems to comprehensively examine the mechanisms by which agriculture impacts on biodiversity. However, this approach has been barely applied to other woody crops of economic importance, such as olive grove, which is a remarkable overwintering habitat for frugivorous/insectivorous birds from central and northern Europe, and whose original distribution overlaps with the Mediterranean biodiversity hotspot. We examined the effects of landscape complexity and intensive management practices at a local scale (recurrent plowing and pesticides use) on the functional and phylogenetic diversity of animal communities inhabiting olive groves. Since the response of functional traits or clades may vary across different taxonomic groups, we conducted our study at two levels: ants, which are considered semi-sessile organisms, and birds, which exhibit a high dispersal capacity. In birds, neither management type nor landscape complexity had an effect on phylogenetic diversity (PD) indices. Extensively managed farms harbored bird communities with higher values of functional diversity (FD), but this effect only was evident when considering cultivated (productive) zones within the farm (i.e., infield diversity). Ant assemblages on intensively managed farms exhibited a lower level of phylogenetic clustering than those located in extensive farms, but this effect vanished when excluding non-cultivated zones. Ant functional diversity increased with landscape complexity. Our results indicate that PD and FD exhibit different responses to farming intensification in olive groves. Although intensive management does not erode PD due to the existence of phylogenetic redundancy, the loss of species associated to modern farming leads to a reduction in FD being this indicative of functional complementarity. This study provides evidence that land-use extensification (extensive farming and landscape diversification) promotes more functionally rich assemblages than modern intensive practices in olive groves. Our findings also show the need to set apart the effect of non-cultivated zones (e.g., hedgerows, margins) when evaluating the effectiveness of agri-environment schemes as the joint consideration of non-cultivated and cultivated areas may obscure the benefits of local extensification on infield biodiversity.

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<https://doi.org/10.1016/j.agee.2021.107708>

Received 31 May 2021; Received in revised form 2 October 2021; Accepted 5 October 2021

Available online 19 October 2021

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1. Introduction

Agricultural intensification constitutes an important threat for organisms inhabiting farmland landscapes, whose populations have suffered a severe decline in the last decades, especially in Southern Europe (Green et al., 2005; Hendershot et al., 2020). The massive use of pesticides and the loss of heterogeneity due, for instance, to the rise of monocultures, the loss of fallow lands and the removal of non-cultivated elements (e.g., hedgerows, field margins, isolated trees, dry-stone walls) have been identified as the main drivers of the observed species loss (Donald et al., 2006). To mitigate this harmful effect of modern agriculture on biodiversity, agri-environment schemes (AES) were introduced in the framework of the European Common Agricultural Policy (CAP) almost two decades ago (Kleijn and Sutherland, 2003; Batáry et al., 2015). However, the adoption of less intensive farming practices (e.g., organic farming, crop rotation, reducing inputs of fertilizers and/or pesticides) does not always guarantee a positive impact in terms of conservation, and its effectiveness may be limited (see Emmerson et al., 2016; Tscharrntke et al., 2021 and references therein). In fact, several studies found non-significant or even negative effects, which has been attributed to the overriding influence of landscape complexity (Bengtsson et al., 2005). Landscape heterogeneity and field-scale species richness may interact with local management effects, leading to non-linear effects (landscape-dependence hypothesis, LDH; Tscharrntke et al., 2005). Accordingly, the relative benefits of AES have been found to be higher in landscapes of intermediate complexity, where populations inhabiting non-crop habitats can colonize these environmentally friendly plots (Concepción et al., 2008). Although a large number of studies have examined the effectiveness of AES and its interaction with landscape complexity in annual crops (mostly cereal systems; Concepción et al., 2012; reviewed in Scheper et al., 2013; Tuck et al., 2014), perennial systems like olive groves and other woody crops -vineyards, fruit orchards- have attracted less attention so far, especially in Europe.

Olive groves constitute an emblematic and worldwide-recognized feature of the Mediterranean culture. The cultivated olive tree *Olea europaea* var. *europaea* evolved over millennia by human selection of the wild olive *Olea europaea* var. *sylvestris* and its history is deeply rooted in the very origin of farming by civilizations that have inhabited the Mediterranean basin (Rey, 1993, 2011; Sánchez-Martínez and Cabrera, 2015). This crop occupies 2,5 million hectares in Spain, the main olive oil producer and exporter. In 2019, Spain produced 1,2 million tons of olive oil, of which approximately 75% came from the region of Andalusia (COI, Consejo Oleícola Internacional, 2019). Olive oil is an essential piece of the Mediterranean diet and its consumption has almost doubled in the last 30 years, reaching a record high in 2020 (Sánchez-Hernández et al., 2020; Guzmán et al., 2020). The amount of land devoted to this crop has increased markedly during the last decades, and this has been accompanied by an intensification of olive plantations (Weissteiner et al., 2011). Although intensive olive farming (with increasing tree densities, irrigation systems, recurrent plowing and higher levels of mechanization and agrochemical inputs) is currently the most extended production system in Spain, some farmers are increasingly adopting environmentally sustainable practices in accordance with the new “greening measures” introduced by the EU rural development policy, which encourages non-productive investments in agriculture (European Commission, 2010). The CAP of the olive sector makes especial emphasis in the maintenance of the herbaceous cover and this has become the most common agri-environmental measure in olive groves. Previous studies have shown that organic and traditionally managed (extensive) olive groves harbor more wildlife than those with an intensive mode of production. Specifically, it has been shown that herbaceous ground cover has a positive effect on the abundance and richness of songbirds (Castro-Caro et al., 2014), soil

nematodes (Sánchez-Moreno et al., 2015), insect pollinators (Martínez-Núñez et al., 2020) and other arthropods (Ruano et al., 2004; Paredes et al., 2013; Carpio et al., 2019; Sánchez-Fernández et al., 2020). However, few studies have addressed how the surrounding landscape modulates the effect of agricultural management on species richness in different taxonomic groups inhabiting olive crops (Rey et al., 2019; Morgado et al., 2021).

Beyond species diversity, modern farming practices may affect other facets of biodiversity that, despite being important for the functioning and stability of ecosystems, have been barely explored (Meynard et al., 2011; Barbaro et al., 2021; Tarifa et al., 2021). For instance, functional diversity (FD) indices provide information above and beyond what species richness can explain. Functional traits capture different aspects of species’ resource use and ecological requirements and thus, they inform about several aspects of ecosystem functioning (e.g., pollination, seed dispersal, etc.) and about the capacity of the biological communities to respond to disturbances (Mouillot et al., 2013). Consequently, examining the functional trait composition of species assemblages can help to better understand the processes affecting community assemblage, which would not be apparent by focusing on taxonomic diversity alone (Flynn et al., 2009; Perović et al., 2015). On the other hand, the phylogenetic diversity (PD) reflects the adaptive potential of the community. By considering the evolutionary history of species, PD broadly summarizes the trait space within a community. It is frequently assumed that, by maximizing PD, we ensure that a wide variety of forms and functions are present within a species set and thus, the chance of losing unique phenotypic and ecological traits decreases (Faith, 2018). However, some authors argue that preserving PD can be a poor strategy for conserving FD and that, ideally, both facets should be considered jointly (Mazel et al., 2017).

The main goal of this study was to characterize the functional and phylogenetic diversity of ant and bird communities inhabiting olive groves subject to different management practices (maintenance or removal of the herbaceous cover; Fig. 1) in Andalusia, Spain. Ants are key members of terrestrial animal communities and play an important role in plant community dynamics, acting as seed harvesters, dispersal agents and influencing soil nutrient status and plant growth (Tiede et al., 2017). This taxonomic group is particularly sensitive to soil management and agrochemicals. Birds act as vital links in many food webs and are reliable biological indicators of ecosystem health. Recent studies warn that breeding bird communities inhabiting olive groves in the Iberian Peninsula are becoming increasingly homogeneous (Morgado et al., 2020), which is in line with the detrimental impact of farming intensification on birds reported across the continent (e.g., Donald et al., 2006). By exploring patterns of FD and PD at both spatial scales, we gain insight into the underlying mechanisms such as environmental filtering (resulting in phylogenetic and/or functional clustering) or competitive interactions among species (leading to phylogenetic and/or functional overdispersion) and the scale at which these operate (Cadotte et al., 2009). In this context, we hypothesize that agricultural intensification should constrain the communities to assemblages of species that are more tolerant to harder and more stressful conditions (i.e., reduced FD and PD). Specifically, in this study, we aimed to answer the following questions: i) do intensive agricultural practices (recurrent plowing, fumigation) act as an environmental filter leading to phylogenetic and/or functional clustering? ii) does landscape complexity constrain the effectiveness of AES in olive groves as predicted by the LDH when considering functional and phylogenetic facets of biodiversity? iii) do ant and bird communities exhibit a similar pattern, from both functional and phylogenetic perspectives, in response to intensive farming practices and landscape simplification despite their divergent dispersal capacities? iv) to what extent does functional and phylogenetic diversities differ in response to extensification at infield and the farm (cultivated and non-cultivated areas) levels?

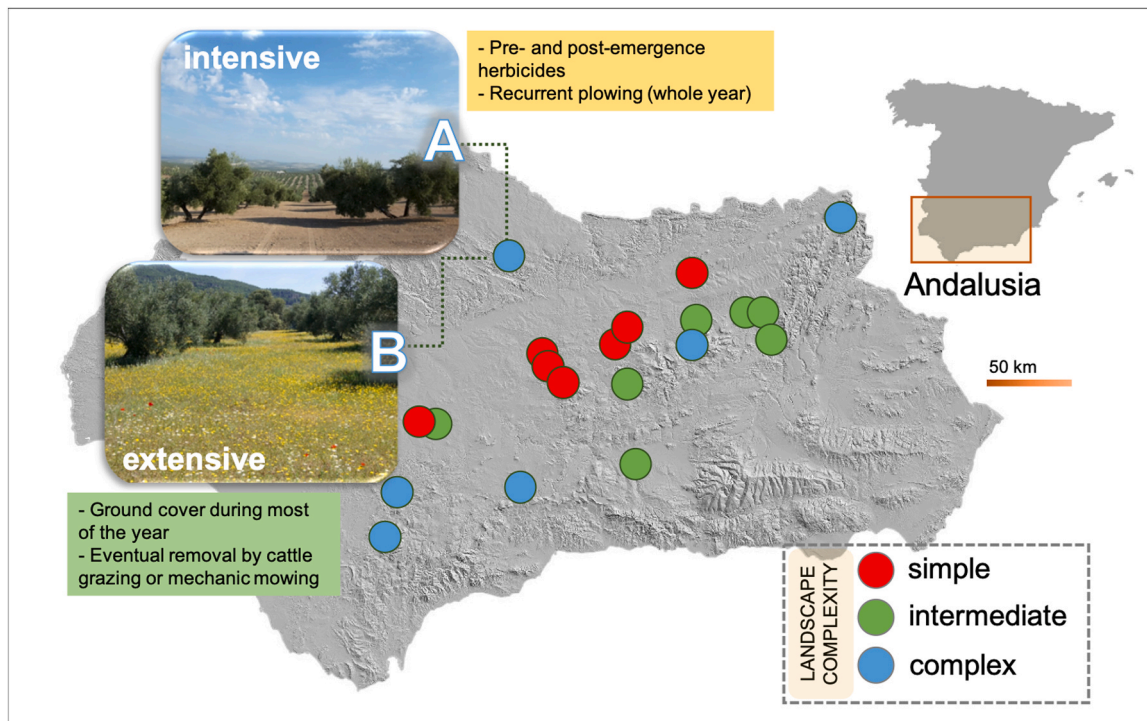


Fig. 1. Map of the study area in Andalusia, Southern Spain, with the location of the 40 farms in the 20 study localities. Following a paired design, each locality consists of two farms, one under intensive management (bare ground) (A) and the second farm under extensive management (with herbaceous cover) (B). Seven localities are surrounded by a relatively simple landscape, seven localities are embedded within a landscape of moderate complexity, and six localities are in complex landscapes with a remarkable proportion of natural vegetation.

2. Material and methods

2.1. Study system

The study area was located in Andalusia, southern Spain, and consisted of 40 olive farms (average size: 72.1 ± 107.2 ha, range; 4.5–424.8) scattered through six provinces (Jaen, Cordoba, Granada, Malaga, Seville, and Cadiz), that covered altogether a cultivated area of 35 km². 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). Half of the selected olive farms had intensive management of the herbaceous cover (using of pre- and/or post-emergence herbicides and/or recurrent plowing to eliminate the weeds over the whole year), whereas the other half was subject to extensive management of the herbaceous cover. Thus, each locality consisted of a pair of olive groves each one subject to a different management type (see Fig. 1). The two farms conforming each locality were within a circle of 2 km radius which was the scale used to characterize a common landscape (average distance between paired farms: 1946 ± 112 m) (Rey et al., 2019). This pairwise design allowed testing the effect of ground herb cover (i.e., intensive vs. extensive management) without the confounding effect of spatial location. The landscape surrounding the two farms in each locality varied across the study area and can be classified into three broad categories of complexity: (i) simple landscapes (seven localities, 14 farms), dominated by olive groves, with some other crops (frequently cereals) intercalated and with scarce remnants of natural habitat; (ii) intermediate landscapes (seven localities, 14 farms), in which olive groves are interspersed with other crops and with some natural or semi-natural habitat remnants (often semi-natural forests, afforestations, scrublands or grasslands); and (iii) complex landscapes (six localities, 12 farms) where olive groves (which may not be the major land use) co-occur with a diverse representation of natural habitats (woodlands, scrublands and grasslands). Assignment of each locality to these landscape categories was based on landscape

compositional and configurational heterogeneity metrics and following a well-balanced design (see Rey et al., 2019; Martínez-Núñez et al., 2020) (Table S1; Fig. S1). Consequently, this design is suitable to test the effects of agri-environmental practices on biodiversity and the interplay between management type and landscape complexity. This study system is part of the LIFE project 'Olivares Vivos'. More details about the study system can be found at: <https://olivaresvivos.com/en/interested/>.

2.2. Biodiversity sampling

Birds – We surveyed birds using point census stations. At each count point, birds within a 100 m radius were identified and counted for 5 min early in the morning (within the four hours after sunrise). We set six stations (2 in non-cultivated areas and 4 in cultivated areas) in small olive farms (<25 ha) and 10 (4 in non-cultivated areas and 6 in cultivated areas) in large olive farms (≥ 25 ha). We refer to uncultivated areas as those consisting of spots of semi-natural vegetation like woodland patches or hedgerows (i.e., non-productive zones). Census stations were located at least 200 m apart in small olive groves and at least 300 m apart in large olive groves. As far as possible sampling stations were separated at least 150–200 m of the orchard edges. Surveys were carried out monthly in two slots (from April to June 2016, and from September 2016 to March 2017) under favorable weather conditions (i.e., avoiding hot weather, heavy rain or strong wind conditions) by a team of skilled ornithologists. Monthly data (abundances) were merged into a single plot (farm) \times species quantitative matrix. Waterbirds and raptors with large home ranges (eagles, vultures) were excluded from the analyses, as these species are not properly censused with this methodology. Only bird species detected in at least five olive farms were considered, thus discarding rare and anecdotal species. Consequently, a total of 93 common species accounting for 99% of records were used in subsequent analyses.

Ants – Ants were collected by pitfall trapping. In each olive farm, we established twelve sampling stations (4 in non-cultivated areas and 8 in

cultivated ones) in some cases concurring with the ones used for bird monitoring. In each station, we set a pitfall trap (7 cm in diameter and 12 cm deep) filled with a 1:1 mixture of water and propylene glycol and 5–10 soap drops. Ants were also collected every month in two slots (from April to July 2016, and from September to December 2016) and determined in the laboratory by using a $10 \times -45 \times$ stereo-microscope. Most individuals were identified to the species level except for a few exceptions (*Solenopsis* spp.) whose taxonomy remains contentious. Data for each farm were obtained by pooling data for all (year-round) counts. We considered the number of active traps in each plot (some were found inoperative during the surveys and were not included in the monthly count) to compute the relative abundance (i.e., sampling effort-corrected abundance) of each species.

2.3. Phylogenetic data

Birds - We obtained a Maximum clade credibility (MCC) tree from a set of 500 phylogenetic trees generated in BirdTree (birdtree.org) using the Ericson backbone sample (Jetz et al., 2012) (Fig. S2).

Ants - We used a phylogenetic tree assembled by Xavier Arnan and Xim Cerdá based on the Moreau and Bell (2013) chronogram (5 nuclear genes, 311 taxa comprising 21 subfamilies, 45 fossil calibrations). Within genera, the position of each node (within-genus divergence events) was estimated from molecular and morphological data (Arnan et al., unpublished). Some ant species observed in our study area were missing from this tree and were added manually to its putative sister taxon (Fig. S3).

2.4. Functional data

Birds - We assembled data for 53 functional traits including information on morphology, ecology (e.g., lifespan), diet (e.g., % of diet composed of invertebrates), provisioning strategy, feeding niche (e.g., % time spent foraging on the ground), habitat preferences, and behavior (e.g., nest location) for each species. Data were retrieved from different sources (Wilman et al., 2014; Storchová and Hořák, 2018; Myhrvold et al., 2015). Some traits were coded as categorical binary variables, which allowed us to include plasticity in species traits (e.g., the red-legged partridge *Alectoris rufa* uses both browsing and grazing as provisioning strategy). Because some morphological variables were highly correlated, we first performed a phylogenetic Principal Component Analysis (phyl-PCA; Revell, 2009), which yielded two principal components (PC1 and PC2) accounting for 98% (83% and 15%, respectively; see Table S2 in Supplementary Material) of the morphological variation. Consequently, the original matrix was reduced to 49 variables (see Table S3 for definitions and more info).

Ants - We compiled a matrix of 15 functional traits for the 43 ant species included in the analyses. Data were mainly retrieved from Arnan et al. (2016) dataset, which includes life-history (e.g., colony size), morphological (e.g., worker size) and behavioral traits (e.g., diet), and the AntWeb database (antweb.org). Moreover, we used the functional classification proposed by Roig and Espadaler (2010). See Table S4 in Supplementary Material for further details.

2.5. Phylogenetic diversity measures

For both taxonomic groups, we first quantified the phylogenetic diversity (PD) of each farm by means of the Faith's PD index, which computes the sum of the lengths of all those branches on the tree that span the members of the set. We also computed the Mean pairwise Phylogenetic Distance (MPD) among all pairs of species within each assemblage, which informs about the phylogenetic relatedness (structure) of species (i.e., how closely related the average pair of species in each assemblage are). High values of MPD indicate phylogenetic overdispersion and low values indicate a trend towards phylogenetic clustering. For both metrics, we computed the "standardized effect sizes"

(SES) by comparing the observed values to the pattern expected under a null model ("independent swap" algorithm, 999 iterations) via the package 'picante' in R (Kembel et al., 2010).

2.6. Functional diversity measures

For both taxonomic groups, we computed a matrix of (multivariate) functional distances from the trait raw data. Since our trait dataset comprised different types of variables (continuous, categorical, binary, fuzzy-coded, and ordinal variables) both for birds and ants, we used the Gower's distance. This matrix was subsequently used as input in a Principal Coordinates Analysis (PCoA) and the first six resulting PCoA axes were used as new composite functional traits. We determined the quality of the functional space using the mean squared deviation (mSD), which was < 0.001 in both cases (Fig. S4). From these six axes (new traits), we computed the following functional diversity (FD) indices: functional richness (FRic), functional divergence (FDiv), functional evenness (FEve), and functional originality (FOri) (Villéger et al., 2008). FRic represents the multidimensional functional space (convex hull volume) occupied by a species assemblage. FDiv informs about the extent to which species abundances are on the limits of the functional space (high values indicate a high degree of niche differentiation, and thus low resource competition). FEve quantifies the regularity of interspecies distances and the homogeneity of species abundances within the niche space, which indicates whether resources are used evenly, or whether there are gaps in resource use. FOri indicates the average pairwise distance between a species and its nearest-neighbor and can be used as an indicator of an assemblage's functional redundancy (Schleuter et al., 2010). FRic and FDiv are not independent of the number of species and thus, both metrics were standardized using a null model approach. These four FD indices were computed for each species assemblage by means of the *multidimFD* function developed by S. Villéger.

2.7. Statistical analyses

We used linear mixed models (*lmer* function of the R package 'lmerTest'; Bates et al., 2015; Kuznetsova et al., 2017) to evaluate the effect of management type (intensive; extensive) and landscape configuration, as well as its synergistic effect on (SES) PD, (SES) MPD and the four FD indices in both taxonomic groups. Management type, landscape configuration and its interaction were included as explanatory variables, and locality as random factor to control for the potential nonindependence of our diversity estimates within localities. We repeated these analyses only considering infield diversity (i.e., individuals detected within the cultivated zone). As a preliminary step, we tested for spatial autocorrelation of the model residuals using Moran's test (R package 'spdep'; Bivand et al., 2013). We also checked visually that the residuals were normally distributed. In addition, we explored the relationships between taxonomic (i.e., species richness), phylogenetic, and functional diversities using Pearson's correlation analysis. All statistical analyses were performed using the R environment (www.r-project.org).

3. Results

3.1. Phylogenetic diversity

The amount of PD and the level of phylogenetic overdispersion (quantified as MPD) of bird assemblages did not differ significantly between management types (Fig. 2a,b; both p -values > 0.50) nor among landscape categories (Fig. 2a,b; both p -values > 0.10). The interaction between landscape complexity and management was not significant in either case (both p -values > 0.25). Results remained similar (no significant effect of both factors) when considering only infield diversity (i.e., within the cultivated zone). In ants, we did not find significant

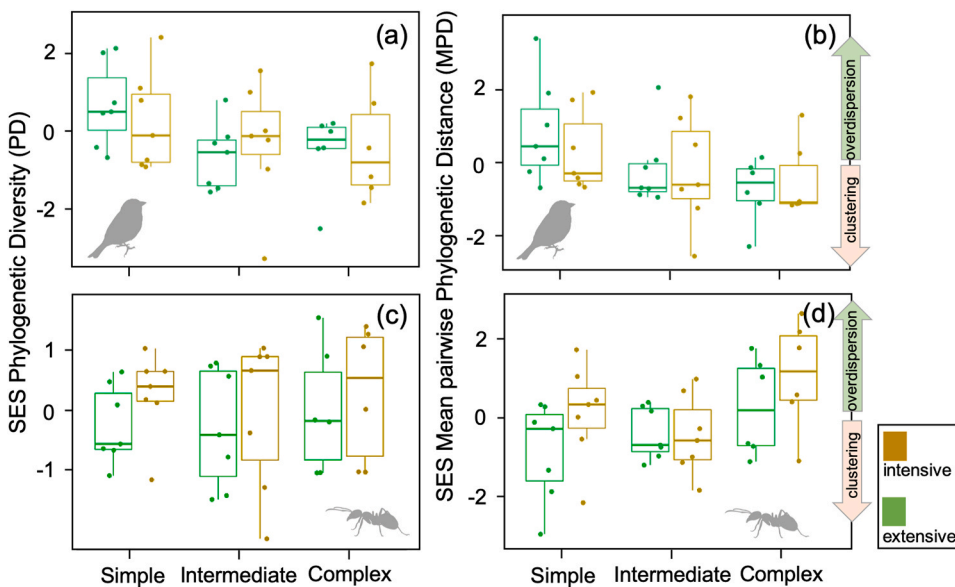


Fig. 2. Faith's phylogenetic diversity (PD) and Phylogenetic structure (quantified as mean pairwise phylogenetic distance, MPD) of (a-b) bird and (c-d) ant assemblages from olive groves under intensive (orange color) and extensive (green color) management for each category of landscape complexity (complex, intermediate, and simple landscape). Both indices are shown as standardized effect sizes (SES) in order to correct for species richness, which ranged from 36 to 63 common bird species, and from 11 to 27 ant species. The reported indices were computed using both cultivated and non-cultivated zones.

differences in terms of PD between intensive and extensive farms nor among landscape categories (Fig. 2c; both p -values > 0.10). Ant assemblages from intensive farms exhibited higher values of MPD than those inhabiting extensive farms (Fig. 2d; $F_{1,17} = 4.99$, $p = 0.04$), although this effect became non-significant when considering only infield diversity ($F_{1,17} = 2.59$, $p = 0.10$; Fig. S5). For both phylogenetic indices, the interaction landscape complexity \times management was not significant (both p -values > 0.25). See Tables S5-S8 for extended results.

There was no significant correlation between species richness and (standardized) PD in either group (birds: $n = 40$, $\rho = -0.08$, $p = 0.62$; ants: $n = 40$, $\rho = -0.22$, $p = 0.17$).

3.2. Functional diversity

There were no significant differences between extensive and intensive farms nor among landscape categories for any of the analyzed FD metrics in birds (all p -values > 0.10 ; see Fig. 3a,b). However, when analyzing only infield diversity, we found a significant effect of management type on functional richness (Fig. 3c; $F_{1,17} = 4.51$, $p = 0.048$), and a significant management landscape \times complexity interaction for functional evenness ($F_{2,17} = 3.98$, $p = 0.038$), which indicates that the effectiveness of extensive practices differed among landscape categories (Fig. 3d). In ants, all examined FD indices showed non-significant differences between extensive and intensive farms (all p -values > 0.10). Farms located in simple landscapes harbored ant assemblages with lower functional richness (Fig. 3e; $F_{2,17} = 3.49$, $p = 0.05$) and lower functional originality (Fig. 3f; $F_{2,17} = 4.06$, $p = 0.04$) in comparison with those from farms embedded within a more heterogeneous matrix. Both effects remained significant or marginally significant when excluding those species detected in non-cultivated areas (FRic: Fig. 3g, $F_{2,17} = 4.25$, $p = 0.03$; FORi: Fig. 3h, $F_{2,17} = 2.79$, $p = 0.089$). See Tables S5-S8 for extended results.

We found strong significant positive correlations between species richness and (standardized) functional richness in both groups (birds: $n = 40$, $\rho = 0.88$, $p < 0.001$; ants: $n = 40$, $\rho = 0.81$, $p < 0.001$).

4. Discussion

Although several studies have investigated the effects of agro-environmental practices on abundance and richness of species in olive groves, our study is the first one examining the effects of different management regimes from both a phylogenetic and functional

perspective across various taxa. We focused on ants and birds as biodiversity indicators since they represent two contrasting model organism groups with different key functional aspects (resource use, mobility) that could result in different responses to local habitat characteristics and landscape configuration. In birds, we found that olive farms under extensive management harbored communities with moderately higher functional diversity, but not higher phylogenetic diversity. However, this effect only arose when excluding the non-productive zones. In ants, communities from intensive farms were phylogenetically less clumped than those under extensive management, but again this effect was canceled out when excluding the non-productive zones. Functional diversity of ant communities increased with landscape complexity. Thus, overall, our results indicate that phylogenetic and functional diversity respond differently to intensive management.

4.1. Phylogenetic diversity

In accordance with an 'environmental filtering' effect prevailing under more stressful conditions, we predicted that phylogenetic diversity (PD) and the level of phylogenetic structuring (MPD) should decrease with increasing intensive management and decreasing landscape complexity, as only a small number of lineages with certain traits combinations may be able to exploit these highly-modified habitats (see e.g., Cadotte et al., 2009). Here, we did not find support for this hypothesis. In birds, the lack of an effect of management type on both phylogenetic indices suggests that ground cover removal does not entail so meaningful differences in environmental conditions as to be detected at this level. That is, the absence of herbaceous cover does not act as a filter precluding the presence of certain bird clades as shown in previous studies carried out on steeper environmental gradients (e.g., across elevations; Graham et al., 2009). In this vein, we neither found significant differences among landscape categories in terms of phylogenetic diversity. Although complex landscapes harbor a greater number of species, the evolutionary distinctiveness of these communities might be not as high as expected since many species associated to forests and woodlands (e.g., warblers *Sylvia* spp., tits Paridae, thrushes, *Turdus*) belong to the same clade and thus, their level of genetic isolation is limited in comparison with those species that prefer croplands and dry pastures, and many of which constitute the sole representative of their genus in the Iberian Peninsula (e.g., greater short-toed lark *Calandrella brachydactyla*; rufous-tailed scrub robin *Cercotrichas galactotes*). Accordingly, we found no significant correlation between species richness and PD,

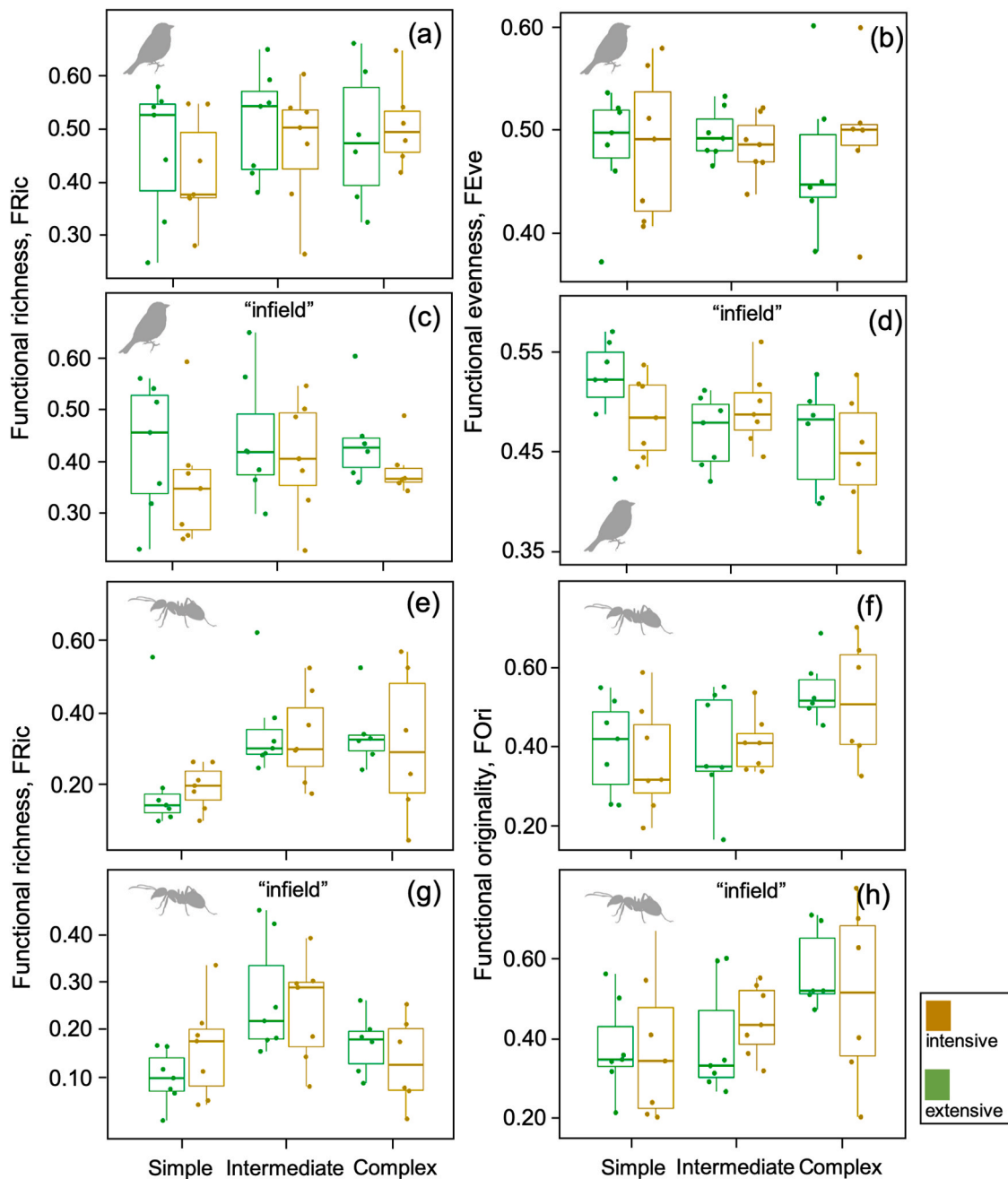


Fig. 3. Differences in functional diversity indices for (a-d) bird and (e-h) ant assemblages in relation to farming management (intensive olive groves: orange color; extensive olive groves: green color) and level of landscape complexity (complex, intermediate or simple). The reported indices were computed using both cultivated and non-cultivated zones (a-b; e-f) and only including those species detected in cultivated zones (“infield”) (c-d; g-h).

which suggests that species-rich communities are phylogenetically more redundant than communities with lower taxonomic diversity.

Interestingly, ant species richness at the farm scale was not related to PD, which may explain the existence of phylogenetically less clumped communities in farms under intensive management. However, the difference in the degree of phylogenetic overdispersion (MPD) between intensive and extensive farms decreased when limiting our analyses to cultivated zones (see Fig. S5), which indicates that non-crop islands may blur the impact of extensive practices on phylogenetic diversity under certain circumstances (e.g., landscapes of intermediate complexity).

4.2. Functional diversity

Previous research has mainly compared taxonomic richness between

extensive and conventional farming (reviewed in Tuck et al., 2014), whereas only few studies have considered effects on functional diversity (FD) and most of them used a small (<5) number of functional traits (Da Silva et al., 2017; Goded et al., 2019). For instance, Hevia et al. (2019), recently reported that ant communities in non-plowed organic olive groves have higher values of FD than those in conventional plowed-sprayed farms. However, these authors quantified FD from four traits (diet and three morphological attributes; Hevia et al., 2019). This is not a trivial issue since the number of traits employed to characterize FD can strongly impact the values of the indices considered, being functional richness (FRic) and functional divergence highly sensitive to this variation (Legras et al., 2020). Furthermore, Hevia et al. (2019) considered a short period (one month) and was carried out at a small scale (max. distance among plots ~15 km), which makes their and our

study hardly comparable.

Here, we observed that FRic and functional originality (FOri) of ant communities were positively related to landscape complexity, but not to management type. This agrees with Gámez-Virués et al. (2015), who reported that landscape-level effects dominate functional community composition and can even buffer the effects of ‘infield’ management intensification on functional homogenization. Nevertheless, it also has been suggested that in small organisms with limited mobility like arthropods, management practices should be more determinant than landscape heterogeneity in terms of diversity (Concepción et al., 2008; Horváth et al., 2015; Froidevaux et al., 2017). The lack of a stronger effect at a local scale could be explained by the generalist-opportunistic nature of ant species inhabiting olive groves and the broad range of nesting habits that they exhibit, which could make them respond in different ways to disturbances caused by farming practices (Campos et al., 2011). Nevertheless, the existence of increased FD in communities surrounded by more heterogeneous landscapes where taxonomic diversity is higher (see Rey et al., 2019), could be explained by a spillover of forest species (*Lasius* and *Camponotus* spp.) from semi-natural habitats to olive crops.

In birds, FD was not related to farm management or landscape heterogeneity when considering both cultivated and uncultivated areas. However, when restricting our analyses to cultivated zones, we found that extensive farms foster bird assemblages with higher FRic than those inhabiting farms with a conventional management. It implies that under intensive management the bulk of FD agglutinates on non-cultivated areas and does not have a direct impact in the form of enhanced ecosystem services on the crop area. In addition, bird communities from extensive farms exhibit a more even distribution of species in functional space, which means that they are using resources more efficiently and thus, they are more resilient to disturbances (Mouillot et al., 2013). Yet, this effect was only evident in simple and (in a lesser extent) complex landscapes, which contradicts what is predicted by the LDH (Tschamtké et al., 2012). Comparison of Fig. 3b and d helps to understand this pattern; evenness values remain relatively invariant across management and landscape categories regardless of whether the uncultivated areas were considered or not. This is especially true on intermediate landscapes, while holds but with variants at both extremes of the landscape-complexity gradient, where the ecological contrast represented by the presence or absence of herbaceous cover is greater. This probably relates to the fact that, in simple landscapes, some functionally distinctive species associated to grasslands (see below) avoid bare ground soils associated to intensive farming. Whereas in complex landscapes where forest species predominate, these being more reluctant to go deep into olive crops if they do not include ground-herb covers (Díaz, 2006), which ultimately further impulse FD by attracting other non-forest specialists.

4.3. Synthesis and applications

Unraveling the differences among multiple facets of biodiversity and how these vary across trophic levels can draw a more comprehensive picture of the way in which farm management (and its synergy with the landscape context) affects community assembly and ultimately, ecosystem stability. Here, we found that the loss of species richness associated to intensive management previously reported elsewhere (Rey et al., 2019) does not translate into a meaningful loss of PD mainly due to the existence of phylogenetic redundancy (i.e., species-rich communities are not the ones with higher PD). On the contrary, FD increased linearly with taxonomic diversity in both taxonomic groups, which may be indicative of functional complementarity (Gagic et al., 2015). In line with this, we observed that both extensive management and landscape complexity had a positive effect on FD of biological communities in cultivated (productive) zones. Specifically, and in contrast to that expected according to their dispersal capacity, we found that landscape complexity had a greater influence in shaping ant assemblages, the less

mobile taxonomic group, from a functional perspective (see also Goded et al., 2019 for a similar conclusion). A higher proportion of natural vegetation surrounding olive farms facilitates the replacement of generalist species (well adapted to perturbation) by taxa with more singular traits, which may explain this finding. Meanwhile, local management plays a more important role in trait filtering than landscape heterogeneity in birds, a group with high dispersive potential. Two factors could be the main reason for this. First, the presence/absence of herbaceous cover constitutes a discriminant factor from a functional perspective since it provides food, shelter, and nesting place for several functionally distinctive species (e.g., common quail *Coturnix coturnix*, Eurasian stone-curlew, *Burhinus oedicnemus*, red-legged partridge); and second, perennial savanna-like agroforest croplands like olive groves allow the coexistence of open-habitat and forest bird species giving rise to a broad functional space compared to that of other cropping systems. Our findings are in line with those recently reported by Barbaro et al. (2021) in vineyards. They found that organic viticulture enhanced bird functional diversity, but its positive effect partially depended on grass cover management in the inter-rows and the amount of semi-natural habitat in the surrounding landscape (Barbaro et al., 2021).

Overall, this study highlights the importance of non-cultivated areas (e.g., hedgerows; Castro-Caro et al., 2015) to preserve functional biodiversity, and warns about the need to consider it when evaluating the effectiveness of agri-environmental practices. This is because the joint consideration of non-cultivated and cultivated areas may obscure the conservation benefits of local extensification within cultivated areas (infield diversity). Our results also provide evidence that PD and FD indices do not respond in the same way to perturbations and can exhibit divergent trajectories. Specifically, we have shown that extensification (both on a local and landscape scale) can promote functional diversity in biological communities inhabiting olive groves, which can enhance ecosystem services (e.g., biological control of olive pests) and result in a better functioning of this agro-ecosystem.

Funding

V. García-Navas was supported by a CEEC Individual contract (ref. CEEIND/00086/2018) from the Fundação para a Ciência e a Tecnologia (Portugal) and 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 ‘Olivares Vivos’ (ref. LIFE14 NAT/ES/001094) and the projects AGRA-BIES and RECOVECOS (CGL2015-68963-C2 and PID2019-108332GB-I00, respectively, MINECO/MICIN, Gobierno de España and FEDER).

Authors’ contributions

VGN and PJR developed the main ideas of this study. PJR, AJM and FV designed the fieldwork. RT, JI, FMC, PJR, AJM and FV conducted field samplings. TS, FMN and AJM classified ants. TS processed GIS data for landscape categorization. VGN analyzed the data and wrote a first draft of this paper with PJR, FV and CMN feedback. All authors provided critical reviews of the MS and gave their final approval for submission.

Declaration of Competing Interest

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

Acknowledgments

We thank José Luis Molina and Gemma Calvo for their valuable help during the fieldwork. Xavier Arnan (University of Pernambuco) and Xim Cerdá (Estación Biológica de Doñana) kindly provided their ant phylogeny in which our phylogenetic analyses were based on. We are also

indebted to all the owners and farmers of the olive groves in which this study was conducted for allowing and facilitating our work. Two anonymous reviewers provided comments that improved an earlier version of the manuscript.

Data accessibility statement:

Data available from the Figshare Digital Repository; link: 10.6084/m9.figshare.16802383.

Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.agee.2021.107708.

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