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Agricultural intensification erodes taxonomic and functional diversity in Mediterranean olive groves by filtering out rare species

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Abstract

1. Agri-Environmental Schemes (AES) have been proposed to mitigate the impact of agriculture on both taxonomic and functional biodiversity. However, a better knowledge of the mechanisms involved in the loss of agrobiodiversity is needed to implement efficient AES. An unbalanced effort on research towards arable lands compared to permanent crops, and on fauna relative to plants, is patent, which limits the generalization of AES effectiveness.

2. We evaluated the effects of agricultural management and landscape simplification on taxonomic and functional diversity of the ground herb cover of 40 olive groves. We use a recently developed approach based on Hill numbers (rare, common and dominant species based) to analyse taxonomic and functional dissimilarity between farms with contrasting agricultural practices, and its potential attenuation by landscape complexity. We further explore the filtering effect of agricultural intensification on functional traits, and the relationship between functional and species richness across landscapes.

3. We found that taxonomic and functional dissimilarity of herb assemblages between intensively and low-intensively managed fields was mainly due to rare species. Dissimilarity decreased as landscape complexity increased, evidencing that complex landscapes attenuate the impact of agriculture intensification on herb assemblage composition. Agricultural intensification favoured more functionally homogeneous assemblages and disfavoured the herbs pollinated by insects, while it did not seem to affect wind-pollinated species.

4. Overall, functional richness increased exponentially with species richness across landscapes, but the latter was insufficient to drive any clear enhancement in functional richness in simple landscapes. In contrast, high species richness accelerated the enhancement in functional richness in intermediate and complex landscapes. These results highlight the functional filtering that intensive agriculture has generated for decades in homogeneous olive-dominated landscapes.

5. *Synthesis and applications.* Herb cover is essential to support the fauna of permanent croplands and their sustainable production. Hence, Agri-Environmental Schemes (AES) in these croplands should promote management practices favouring the diversity and functionality of herb assemblages. Such AES should be particularly prioritized in homogeneous landscapes, where ground herb cover composition and function has long been homogenized to a great extent.

1 | INTRODUCTION

Changes in land use and intensive agriculture are the main drivers of species loss world-wide (Tilman et al., 2001). As a remediation policy for farmland biodiversity loss, Europe launched in 1992 the so-called Agri-Environmental Schemes (AES) within the Common Agricultural Policy (CAP). The AES are economic incentives for farmers adopting agrobiodiversity-friendly practices and they will have continuity in the new CAP post 2020, together with voluntary eco-schemes (Marsden & Jay, 2018).

Herbs and annual plants are essential within agroecosystems since they support the rest of agrobiodiversity, for example, fauna and soil micro-organisms (Marshall et al., 2003). Prominently, in the past decades, the use of herbicides and recurrent tillage has diminished the diversity of plants and contributed to taxonomic and functional filtering of their communities. The decrease in herb diversity has generated cascading effects on arthropods (Lichtenberg et al., 2017; Marshall et al., 2003; Martínez-Núñez et al., 2019) and farmland birds (Marshall et al., 2003). Thus, ecosystem services such as crop pollination by insects (Martínez-Núñez et al., 2020) or pest control by birds have been compromised (Nave et al., 2017). Surprisingly, declines in farmland flora have received little attention in comparison to faunal declines, despite the crucial role that herbs play in crop sustainability.

Two major anthropogenic drivers are known to determine herb diversity: local (infield) management and landscape context. First, ground cover management can strongly affect the diversity of annual herbs in crops (Bengtsson et al., 2005; Winter et al., 2018). Ground cover can be managed intensively, through active and recurrent removal of herbs, either mechanically (e.g. tillage) or chemically (by herbicide application). Alternatively, it can be low-intensively managed, and in a more sustainable way, maintaining the herbaceous cover during most of the year and avoiding herbicide application. Second, the landscape context in which the crops are embedded can influence their ability to host biodiversity (Tscharntke et al., 2005). In very simple and homogeneous agricultural landscapes, natural habitat patches are extremely rare and are expected to contribute negligibly to crop biodiversity, while as landscape complexity increases, the diversity within crops is expected to increase by spillover from natural habitats until saturation at high levels of complexity (Concepción et al., 2008; Tscharntke et al., 2005). In the case of herbs, increases in natural habitat cover surrounding the crop could mitigate agricultural intensification effects at the farm scale, providing a pool of herb species less similar to the ones in the field core (Bourgeois et al., 2020). The interplay between the level of local agricultural intensification and the degree of landscape complexity is thought to determine the effectiveness of AES on farmland biodiversity recovery (Kleijn et al., 2011; Tscharntke et al., 2005, 2012), and their synergistic effects have been confirmed in infield herb assemblages (Roschewitz et al., 2005).

The benefits of AES for biodiversity are commonly studied in annual crops and grasslands (Kleijn et al., 2006). Woody crops have received comparatively less attention (Tuck et al., 2014) despite tree (agroforest) crops hosting high levels of diversity in some biodiversity hotspots such as coffee and cacao plantations in Central America (Bhagwat et al., 2008) or olive groves in the Mediterranean region (Rey et al., 2019). In particular, several studies have assessed how agricultural intensification affect herb diversity of perennial crops [e.g. apple orchards (Miñarro, 2012); olive groves (Rey et al., 2019)]. However, few studies investigated the interplaying effects of agricultural intensification and landscape simplification or considered diversity from a functional perspective (Trivellone et al., 2014).

The latter is relevant since functional diversity, rather than taxonomic diversity, can be an accurate predictor of the human impact on ecological functions and services (Wood et al., 2015). Thus, studies of anthropogenic impacts on functional diversity should be incorporated into protocols to assist practitioners and decision-makers (Cadotte et al., 2011). Functional diversity can be fostered by the occurrence of non-productive areas inside farms, which, in turn, can boost the resilience of agricultural ecosystems against disturbances (Rader et al., 2014). In parallel, it is known that natural patches of native vegetation (e.g. field margins) act as 'herb diversity reservoirs', where herbs partly evade its filtering by non-friendly agricultural practices (Alignier et al., 2020; Bourgeois et al., 2020). Thus, considering the occurrence of these areas is important when studying the factors influencing plant agrobiodiversity. Finally, the response of plant species to agricultural intensification (winners—usually dominant or common species—vs. losers—more specialist

and rare species - Carmona et al., 2020; Suding et al., 2005) should also be considered since the loss of rare species could eventually compromise the maintenance of the functional structure of species assemblages.

In this paper, we aim to evaluate: (a) how agricultural intensification in permanent agroecosystems affects rare, common and dominant arable herbs; (b) to what extent agricultural intensification filters functional traits and whether such filtering is consistent across landscape complexity levels; and (c) the interactive effect of herb cover management and landscape complexity on the relationship between functional and taxonomic diversity.

For this, we compiled a large dataset of infield herb assemblages in 40 olive groves in 20 localities (two paired olive groves with different herb cover management) broadly distributed along the Guadalquivir Valley in South of Spain. We used a recently developed approach, grounded on the Hill numbers to estimate the dissimilarity between species assemblages based on non-shared species and non-shared traits (Chao et al., 2019). We expect: (a) that the dissimilarity between assemblages in low-intensively and intensively managed farms will attenuate as landscape complexity increases due to a higher spillover from nearby natural habitats, especially for taxonomically and functionally rarer species; (b) a functional homogenization triggered by the environmental filtering of traits under intensive management and simple landscape conditions, because the environmental filtering caused by intensive practices cannot be counteracted by the almost inexistent natural herb sources in the landscape; and (c) differences among landscapes in the relationship between functional and taxonomic diversity since the anthropogenic-driven filtering will homogenize the type of species that appear in simple landscapes. Therefore, an increase in species richness will not lead to functional diversification in these sites. In contrast, it will increase in complex landscapes because more species will add more functional traits in heterogeneous landscapes.

2 | MATERIALS AND METHODS

2.1 | Study area and experimental design

The Guadalquivir basin (Andalusia, southern Spain) is the region with the largest area devoted to olive cultivation in the world (http://www.fao.org/faostat/en/#home), with c. 1.5 million ha of olive groves and a millenary olive farming tradition. In this region (Figure 1 and Table S1), we selected 40 paired olive groves from 20 localities, covering a cultivated area circa 35 km² and encompassing a distance of 310 km between the most distant ones, hence widely distributed across the Guadalquivir Valley. Localities were selected to cover a wide gradient in landscape complexity, from landscapes dominated by olive groves to landscapes including a large fraction of natural (forests, scrublands, streams and pastures with native plants) or semi-natural habitats (gullies, vegetated edges and field margins) or other woody and annual crops. At each locality, the pair of olive groves differed in the herb cover management (20 low-intensity and

20 intensive groves), while sharing the same landscape context, farm size and climatic and edaphic conditions (see details in Table S1). The climatic conditions (Table S1) of the study sites were typically Mediterranean, with a prolonged summer drought and rainfall concentrated in spring and autumn. Low-intensity management involved the maintenance of the ground herb cover most of the year through agroecological practices, such as grazing (mainly with sheep), mowing or stand maintaining between olive trees. Ground herb covers are fundamentally composed by native species spontaneously emerging from the seed bank or dispersed from habitat remnants. They were not sown by farmers. In contrast, intensive management persistently reduced herb cover by herbicides or recurrent tillage. We verified by farmer surveys that management practices within each grove have been relatively invariant for a long time (at least one decade, more frequently several). The mean distance between paired groves within localities was 1,461 ± 796 m (mean ± SD, range: 500–3480 m).

2.2 | Landscape complexity

Agroecological models studying how the landscape moderates the effects of agricultural intensification on biodiversity typically consider categorical classifications (e.g. simple, intermediate or complex landscapes) based on pre-conceived thresholds of some simple landscape metrics like the cover of semi-natural habitat (Concepción et al., 2012; Tscharntke et al., 2005, 2012). However, functional landscapes are in fact the product of their configurational and compositional heterogeneities (Fahrig et al., 2011) which can be characterized by specific metrics. Thus, after visual inspection at the time of locality selection, we first tentatively classified the landscape of each locality in simple (characterized by vast extensions of olive groves with very few natural habitat patches), intermediate (olive groves are intermingled with annual crops and with greater extension of natural habitats) or complex (olive groves are scarcer and the area covered by forests, shrublands, streams and pastures with native plants is larger; Figure 1). Then, we used landscape compositional and configurational metrics and classification and regression tree analysis (CART) to validate our initial categorization and determine which variables were responsible for the final classification of the landscapes (see Appendix S1 in Supporting Information, for an extended explanation).

2.3 | Herb sampling

The herb community data were collected monthly from April to June 2016. Each month, herb richness was surveyed in non-permanent 1-m² quadrats placed randomly close (<10 m) to previously fixed sampling points (four sampling point in small groves—<10 ha—and six in large groves—>10 ha; one single quadrat per sampling point each month) in each olive grove (sample size for the whole study: 612 quadrats). Herb species were identified in the field when key
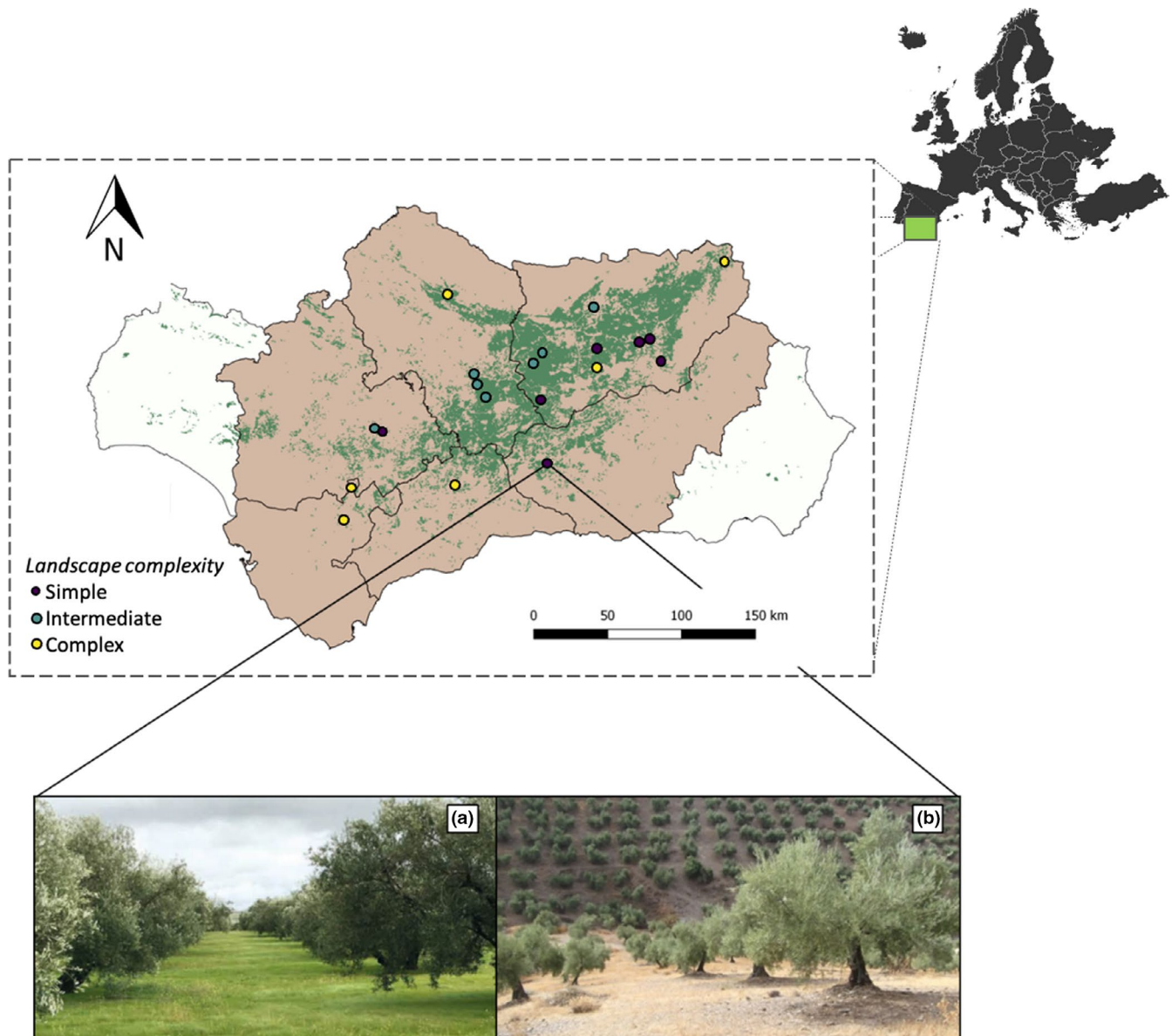
FIGURE 1 Location of the 20 study localities showing their distribution throughout south Spain. The green-shaded area depicts the distribution of olive groves in Andalusia (data from SIOSE 2013 available at http://www.juntadeandalucia.es/medioambiente/site/redia m/). Each locality includes two paired olive groves, with different ground cover management [(a) low-intensity and (b) intensive]. Dot colour codifies landscape complexity

features (e.g. flowers or vegetative parts) were available. Otherwise, voucher specimens were collected and subsequently identified in the laboratory following the study by Blanca et al. (2011). Herb cover was visually estimated monthly as the vegetated (annual herbs) portion of the space delimited by the four olive trees that included each sampling point.

2.4 | Herb traits

We considered five plant traits to highlight changes in functional dissimilarity that could be due to agricultural intensification. Such traits were selected according to the conceptual framework proposed

by Lavorel and Garnier (2002) that groups functional traits in *effect* (related to the effects of plants on ecosystem functioning) and *response* ones (related to the responses of traits to environmental factors). As *effect* traits, we selected SLA, vegetative height and Raunkier's phenotype, reflecting the ability of the species to capture soil resources, compete with other species and resist disturbances (Cornelissen et al., 2003). The *response* traits chosen were pollination syndrome (related to the resource abundance and availability for different pollinators; Pakeman & Stockan, 2013) and seed mass (often linked to seed dispersal capability, recruitment success and plant regeneration; Thompson et al., 1993). Trait data were collected from TRY database (Kattge et al., 2019; see Appendices S2 and S3) and 'Flora Vascular de Andalucía Oriental' (Blanca et al., 2011). We

used the Random Forest algorithm implemented in the R package ᴍɪꜱꜱFᴏʀᴇꜱᴛ (Stekhoven & Bühlmann, 2012) for complete missing trait values. We could eventually characterize functional traits for 223 species (Table S2).

2.5 | Data analyses

First, to test the effects of ground cover management, landscape complexity and their interaction on herb cover and taxonomic diversity (estimated by rarefaction in each olive grove, R package ɪNEXT, Hsieh et al., 2016), we fitted linear mixed effects models (LMMs).

Second, we applied an approach based on Hill numbers (Hill, 1973) to quantify dissimilarities in herb communities between intensive and low-intensity olive groves. Specifically, we used 'presence/absence' per quadrat to obtain an occurrence count (incidence-based frequency) for each species. Thereby, each species can reach a maximum value per sampling point of 3 if it was present in the quadrat in the three surveys (April, May and June). Thus, this incidence variable per quadrat is a proxy of temporal importance or temporal abundance in the community. The diversity inferences based on multiple incidence data are less sensitive to individual aggregation (e.g. nitrophilous herbs gathered near a nitrogen deposition; see Colwell et al., 2012). One main advantage of Hill numbers to quantify dissimilarity (Ellison, 2010) is that they enable quantifying trait-based functional diversity through functional differences between species (Chao et al., 2019), while keeping the replication principle. In particular, the beta parameter can be transformed into two indices—Jaccard and Sørensen (both ranging from 0 to 1)—which are widely adopted as indices of dissimilarity (Chao et al., 2014). Here, we focus on Sørensen-type measures, specifically: (a) richness-based Sørensen index (which weights all species equally; $q = 0$), (b) Shannon entropy-based Horn index (each species is weighted according to its incidence-based frequency; $q = 1$) and (c) frequency-based Morisita-Horn index (which is more sensitive to dominant species than to rare ones; $q = 2$; Chiu et al., 2014). Thus, the method distinguishes between rare ($q = 0$, infrequently detected species for incidence data), common ($q = 1$, frequently detected) and dominant species ($q = 2$, highly frequently), according to the group of species for which each index is disproportionately sensitive. This analysis was conducted using R code adapted from the study by Georgiev et al. (2020) and significant differences in dissimilarity indices between landscape complexity levels were based on non-overlapped confidence intervals (Cumming & Finch, 2005).

Third, we used fourth-corner analyses (Dray & Legendre, 2008) to explore the relationship between species occurrence, functional traits and indicators of agricultural/land use intensification. Thus, a permutation model (with 49,999 permutations) was conducted to test whether the species present across the 40 olive groves (Table L: 223 species) were distributed independently of environmental variables (Table R: ground herb cover management and landscape complexity) or their traits (Table Q: five traits). We used model type 1 ($\alpha < 0.01$), which permutes the abundance values for each species

independently (Dray & Dufour, 2007). This analysis, implemented by the R package ᴀᴅᴇ4 (Dray & Dufour, 2007), allows to relate categorical with categorical, continuous with continuous and continuous with categorical variables (i.e. management/landscape complexity). In the latter case (homogeneity test), estimates lower than expected would imply homogenization of our continuous traits (i.e. SLA, seed mass or vegetative height; Legendre et al., 1997).

Finally, we fitted generalized linear mixed effects models (GLMMs) to test the relationships between functional and taxonomic diversity and how this relationship varies according to ground cover management and landscape complexity. We used functional richness (the convex hull volume of the individual species in multidimensional trait space) as a functional diversity index (Villéger et al., 2008), calculated with the package ꜰᴅ (Laliberté & Legendre, 2010). A high value of functional richness indicates species assemblages with a wide variety of traits. Functional richness was rescaled to [0.01, 10] to facilitate the graphic representation of functional diversity.

LMMs and GLMMs were run with Gamma distribution and log-link function. All models included locality as random factor to account for the nested data structure (i.e. a pair of olive groves per locality). All models were fitted using the R package ɢʟᴍᴍTMB (Brooks et al., 2017), and $R^2_{GLMM(m)}$ were obtained with *MuMIn* (Barton, 2015). All analyses were conducted with R software (v. 3.6.3; R Core Team, 2013).

3 | RESULTS

We detected 319 herb species in the 40 olive orchards under study, accounting for 7.3% of the Andalusian vascular flora (Cueto et al., 2018). Estimated herb richness (after rarefaction) per olive grove ranged from 21 to 116 (mean: 63) and herb cover from 5% to 80.4% (mean: 29.1%). Estimated herb richness ($F_1 = 7.0$, $p < 0.01$) and herb cover ($F_1 = 29.8$, $p < 0.0001$) were higher in farms with low-intensity management (mean richness $\pm$ 1 *SE*: 72.2 $\pm$ 5.47; cover: 40.5 $\pm$ 4.0) compared to intensive (richness: 55.2 $\pm$ 6.42; cover: 17.7 $\pm$ 3.97) herb management (Figure S1). Moreover, estimated herb richness was affected by the surrounding landscape ($F_2 = 4.38$, $p = 0.02$), and was higher in orchards in complex (75.1 $\pm$ 6.94) than in intermediate (69.0 $\pm$ 9.45) or simple landscapes (48.8 $\pm$ 9.45). The differences in estimated richness between orchards in simple landscapes and farms in complex ones were significant ($t_{17} = -2.78$, $p = 0.01$), while the differences in richness between farms in intermediate and complex landscapes ($t_{17} = -0.64$, $p = 0.80$) and in simple and intermediate landscapes ($t_{17} = -2.23$, $p = 0.09$) were not significant (Figure S1). There was no significant interaction between the type of management and landscape complexity ($F_2 = 0.13$, $p = 0.88$).

3.1 | Management-driven dissimilarities

In general, taxonomic and functional dissimilarities between low-intensity and intensive plots were driven by rare species in all levels

of landscape complexity. In fact, their mean values of q_0 dissimilarities (rare species) were always higher than both q_1 (common species) and q_2 (dominant species) dissimilarities, and confidence intervals did not overlap (Figure 2). Moreover, we found a consistent pattern of dissimilarities following $q_0 > q_1 \approx q_2$ (Figure 2), although 95% confidence intervals indicate that, within each landscape level, dissimilarities of common and dominant species did not differ significantly between management types. As expected, the average taxonomic dissimilarity between management types of rare (q_0), common (q_1) and dominant (q_2) species decreased with increasing landscape complexity (Figure 2a). Moreover, we detected significant differences between simple and complex landscapes for rare and dominant species, as shown by the non-overlapping 95% CI (Figure 2a). Regarding functional dissimilarity, we found significantly higher dissimilarity in simple compared to intermediate and complex landscapes in rare species (see non-overlapping 95 CIs, Figure 2b). In contrast, common and dominant species did not show significant functional dissimilarities between management types across landscapes. For details in Jaccard-type dissimilarity, see Figure S2.

3.2 | Functional filtering due to environmental gradients

Using frequency of occurrence data, we detected more homogeneity (negative statistic value) than expected in SLA, vegetative height and seed mass of plants from groves with intensive management than in plants from low-intensively managed groves (Table 1). Moreover, SLA and vegetative height were more homogeneous in plants of orchards surrounded by simple landscapes than in plants of farms in complex or intermediate ones. Conversely, animal pollinator syndrome was positively associated with low-intensity management and complex landscape and negatively related to the persistent removal of herb cover (intensive management) and landscape simplification. Similarly, hemicryptophyte and therophyte life-forms were favoured in low-intensively managed farms and complex landscapes

and filtered out in intensively managed farms and simple landscapes. Chamaephytes, geophytes, as well as the remaining pollinator syndromes showed neutral patterns of variation across management types and landscapes (Table 1).

3.3 | Relationship between functional and taxonomic diversity

Functional diversity tended to increase exponentially as the number of plant species per olive grove (i.e. taxonomic diversity) increased (best model, Table 2; Figure 3). Ground cover management, landscape complexity and their interaction did not affect the relationship between functional and taxonomic diversity (Table 2). However, in simple landscapes, species assemblages were poorer, and taxonomic diversity did not reach the threshold from which functional diversity boosted (*c*. 85 species; Figure 3). Thus, as predicted, an increase in taxonomic diversity within the interval of species richness detected in simple landscapes did not result in an increase in functional diversity (see non-exponential section of the curve before the species threshold, Figure 3).

4 | DISCUSSION

To our knowledge, this is the first study assessing the impact of agricultural intensification on taxonomic and trait-based functional diversity of herbaceous ground covers in Mediterranean permanent crops. We found that taxonomic and functional dissimilarity between species assemblages from intensively and low-intensively managed olive groves decreased from simple to more complex landscapes. As predicted, the landscape context mitigated the impact of local agricultural management, broadening (probably by spillover from natural habitat remnants), the herb species richness of those olive fields more intensively managed, and providing them with a species pool more diverse functionally (see Figure 2a,b). Similar
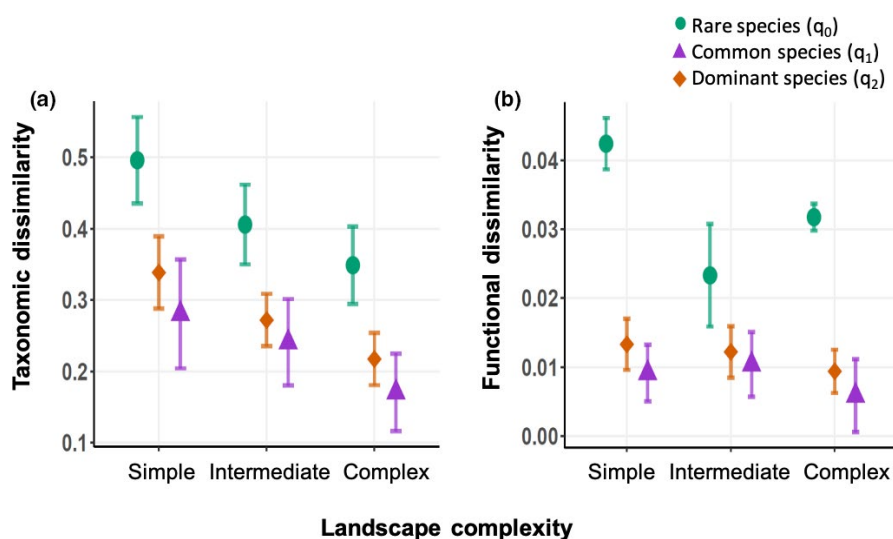

FIGURE 2 Taxonomic (non-shared species) and functional (non-shared virtual functional groups) Sørensen-type dissimilarity in herbaceous plant communities between pairs of low-intensively and intensively managed olive groves across levels of landscape complexity. Error bars show 95% confidence intervals based on a bootstrap method (see Section 2 for further details)

TABLE 1 Relationships between functional herb traits and intensification variables (landscape and ground cover management) based on permutation tests conducted by fourth-corner analysis. We used different tests as indicated with superscripts: [1]Pearson χ^2 and G-statistic, when only categorical variables are involved; [2]Pearson correlation and pseudo-F, when one categorical and one qualitative variable are involved. Adjusted p-values (using Holm-correction method) are shown (ns: non-significant, $*p < 0.05$, $**p < 0.01$)

	Pollination syndrome[1]			Raunkier's life-forms[1]				Continuous traits[2]		
	Abiotic	By animals	Selfing	Chamaephyte	Geophyte	Hemicryptophyte	Therophyte	Vegetative height	Seed mass	SLA
Ground cover management										
Intensive	ns	−7.43**	ns	ns	ns	−4.59**	−6.54**	−3.38*	−2.91*	−3.08**
Low-intensity	ns	7.43**	ns	ns	ns	4.59**	6.54**	ns	ns	ns
Landscape complexity										
Simple	−3.61**	−7.65**	ns	ns	ns	−3.61**	−6.33**	−2.89*	ns	−2.66**
Intermediate	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns
Complex	ns	8.30**	ns	ns	ns	5.73**	6.21**	ns	ns	ns

TABLE 2 Results of GLMM testing the relationship between functional and taxonomic diversity (estimated species richness per olive grove) across ground cover management types (intensive and low-intensity) and landscape complexity levels (simple, intermediate and complex). Locality was entered in the model as a random factor. Best model (according to ΔAICc < 2 and higher $R^2_{GLMM(m)}$) is in bold

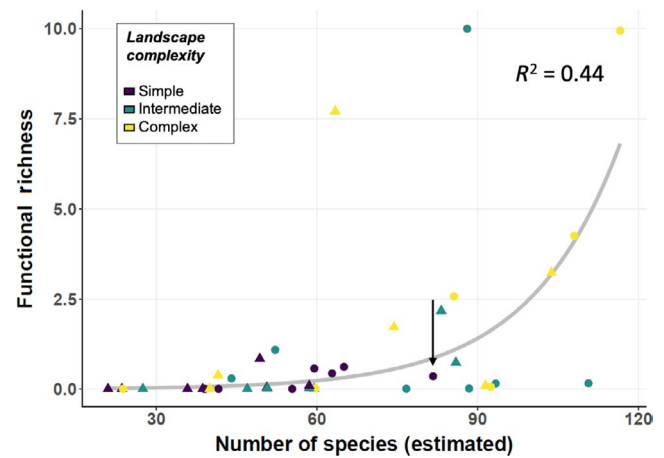| Model code	Models predictors and goodness-of-fit		Wald χ^2 test	p-value
Frichness-1	TD		22.59	0.006
	AICc	10.1		
	$R^2_{GLMM(m)}$	0.44		
Frichness-2	TD		21.25	0.003
	Management		0.11	0.620
	TD × Management	0.16		0.344
	AICc	15.2		
	$R^2_{GLMM(m)}$	0.44		
Frichness-3	TD		18.09	0.009
	Landscape		2.04	0.497
	TD × Landscape		1.46	0.143
	AICc	18.3		
	$R^2_{GLMM(m)}$	0.49		

FIGURE 3 Relationship between functional richness and taxonomic diversity (number of species estimated per olive grove). R^2 values are $R^2_{GLMM(m)}$ of the best-fit model including the effect of taxonomic diversity (see Table 2). The arrow indicates the number of species threshold (highest taxonomic diversity reached in simple landscapes) from which functional diversity rises exponentially. Triangles and circles indicate intensive and low-intensity ground herb cover management respectively

findings was found by Carmona et al. (2020) across European arable systems. Moreover, we were able to show that rare herbs (q_0) were the most affected by intensification in olive groves, while more common (q_1) and dominant (q_2) species were seemingly more tolerant to agricultural intensification, a pattern that was consistent across the landscape complexity gradient (Figure 2). Regarding functional traits, we found that, as predicted, intensive management and landscape simplification homogenized SLA, vegetative height and

seed mass of the species in olive fields. Intensive management and landscape simplification also harmed the herb species pollinated by insects, while they did not affect apparently wind-pollinated species (see Table 1). Finally, high levels of taxonomic diversity, mainly driven by increased landscape complexity (Figure 3), led to increases in functional diversity (Figure 2) but, congruent with our expectations, the latter remained virtually invariant within the range defined by herb richness detected in simple landscapes.

4.1 | Agricultural intensification erodes rare rather than common and dominant species

In agreement with previous studies in arable crops (Pinke & Gunton, 2014), we found a negative effect of agricultural intensification mainly on rare plants. Intensification could act on rare species directly (e.g. herbicide use or recurrent plough). For instance, the prolonged use of herbicides may have depleted the seed banks and purged the herb community so much (José-María & Sans, 2011) that rare species are simply not found, even in latent states. Intensification could also indirectly impact rare species by simplifying the assemblage of essential animal taxa (e.g. pollinators). Martínez-Núñez et al. (2019) found in the same study plots that agricultural intensification resulted in a decrease and spatial homogenization of cavity-nesting bee diversity. This is congruent with the impoverishment of insect-pollinated plants compared to wind-pollinated ones by agriculture intensification and landscape simplification (see Table 1). Rare species typically contribute disproportionately to functional richness, and their loss can compromise the integrity of different ecological processes (Leitão et al., 2016). Therefore, it is important to preserve the taxonomic and functional uniqueness of the herb cover of olive groves (Jiménez-Alfaro et al., 2020). Interestingly, the impact of intensive management on both taxonomic and functional diversity was clearly mitigated as landscape complexity increased, and this was particularly evident for rare species. Dissimilarities between intensively and low-intensively managed orchards were notably smaller for common and dominant species, both in taxonomic and functional terms (see Figure 2a,b). Species such as *Anagallis arvensis* (L.) and *Medicago polymorpha* (L.), present in many low-intensity and intensive plots, could have contributed to this low dissimilarity across landscapes. These results unveil a remarkable resilience of the system to intensive management, since common and dominant herb species tend to be the ones contributing the most to the structure, energy turnover and biomass production of agroecosystems (Grime, 1998).

4.2 | Effects of agricultural intensification on herb traits

Paralleling the situation of arable crops (see Armengot et al., 2016; Carmona et al., 2020), recurrent tillage and intense use of herbicides and synthetic fertilizers in olive orchards and simplification of the surrounding landscapes have resulted in a greater than expected homogenization of herb traits such as SLA, plant height and seed mass (see Table 1). This could reduce the multidimensional trait space, therefore causing a lack of resilience of herb communities and affecting their functional insurance (Yachi & Loreau, 1999). Furthermore, insect-pollinated herbs seem negatively affected by landscape simplification and intensive management (see Table 1). This could be partly the result of the lack of wild pollinators due to olive grove agricultural intensification (including pesticides application; Martínez-Núñez et al., 2019), that would negatively impact seed formation in native herbs. Herb communities could therefore be disrupted in the long term, biasing the composition of the herb ground covers towards plants not pollinated by insects. This, in turn, could affect the insect–pollinator assemblages and, ultimately, compromise the pollinator service for other crops in the region. On the other hand, the subterranean resistance organs of geophytes (e.g. bulbs) could help to circumvent the negative effects of agricultural intensification (especially herbicide impact) that were however detected in bulbless therophytes and hemicryptophytes.

4.3 | Are taxonomic and functional diversity connected?

The relationship between both components of diversity is complex and in many cases context dependent (Morelli et al., 2018). A greater number of species is not always linked to ecosystem functions enhancement across communities (Guillemot et al., 2011), especially when some strong functional filtering is operating for long (Armengot et al., 2016; Rader et al., 2014). We found a neat threshold, close to 85 plant species per olive grove, from which functional diversity is boosted (Figure 3). Thus, an increase in species richness within the interval found in simple landscapes did not lead to virtually any increase in their functional diversity. The relatively invariant functional diversity in simple landscapes is probably due to the functional homogenization of traits (as the fourth-corner results suggest; Table 1) compatible with an environmental filtering of traits caused by agricultural practices and aggravated by the absence of semi-natural habitats that could mitigate the negative effect of agricultural intensification. This is especially worrisome since most of the olive groves in Andalusia are in simple landscapes and are managed intensively. To recover functions, the arrival of plant species to olive groves must occur from non-cultivated areas (such as patches of semi-natural vegetation, vegetated edges, etc.), to add functionally rare species taxa (Figure 2b). Our results are congruent with the ones found in arable systems, where environmentally friendly management and landscape heterogeneity are key to maintain and recover functional diversity (Storkey et al., 2015).

4.4 | Synthesis and applications

As hypothesized, taxonomic and functional herb cover diversity were negatively affected by landscape simplification and intensive ground cover management. Specifically, rare species were the most

affected by agriculture intensification. Our results show a drastic functional homogenization in intensively managed orchards, evidencing functional filtering of the plant communities, especially in simple landscapes. Finally, we detected an exponential increase in functional diversity as plant species accumulate, especially after exceeding a richness threshold, which is out of reach in olive groves embedded in simple landscapes.

Herb cover is essential to support the fauna of permanent croplands and their sustainable production. Hence, AES in these croplands should promote low-intensity management practices favouring the diversity and functionality of herb assemblages. Our results suggest that species diversity and functionality of the herb assemblages in Mediterranean permanent croplands could easily be recovered through spillover of rare species from semi-natural habitat remnants, provided some landscape complexity is allowed. Therefore, to guarantee the functionality of the ground herb covers in the long term, it is essential that the AES and eco-schemes applied in croplands commit to preserve the habitat remnants of native vegetation. Our results also indicate that AES should be especially prioritized in simple landscapes, where the ground herb cover composition and function has been largely homogenized. There, landscape improvements could not suffice in the short term and active seed sowings for greening with rare native herb species could be a solution (see, for instance, Jiménez-Alfaro et al., 2020 for Mediterranean agroecosystems).

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CONFLICT OF INTEREST

The authors have declared no conflict of interest.

AUTHORS' CONTRIBUTIONS

P.J.R., F.V. and R.T. conceived and designed this study; R.T., F.V. and P.J.R. conducted the fieldwork; T.S. processed GIS data and obtained landscape metrics; R.T. and C.M.-N. analysed the data with support from J.P.G.-V.; R.T. and P.J.R. led the writing of the manuscript with feedback from J.P.G.-V. and C.M.-N. All authors contributed critically to the final version and gave final approval for publication.

DATA AVAILABILITY STATEMENT

Data available via the Dryad Digital Repository https://doi.org/10.5061/dryad.6wwpzgn00 (Tarifa et al., 2021).

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SUPPORTING INFORMATION

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