The contribution of small shrubby patches to the functional diversity

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53 Abstract

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Wood-pastures are grazed systems resulting from a long-term use of natural woodlands by humans. These social-ecological systems, covering vast areas of Europe and other temperate regions, have both high biodiversity and economic values, so many are classified as High Nature Value Farmlands. However, in some regions a loss of spatial heterogeneity threatens this natural value. We investigated the potential contribution of tiny shrubby patches to increase spatial heterogeneity and functional diversity in wood-pasture landscapes. Specifically, we compared functional composition (Community Weighted Means) and functional diversity (Functional Dispersion and Functional Evenness) of assemblages of plants, beetles and lichens in those patches (252 to 3000 m²) and in the wood-pasture matrix. We found that shrubby patches and matrix harbour species assemblages with very distinct functional compositions in all studied taxonomic groups. Evergreen, woody, broad-leafed and fleshy-fruited are better represented in the patches. In beetles, the main differences were a greater prevalence of small-sized and fungivore species in the patches. Shrubby patches also mostly harboured lichens with fruticose- and foliose-broad growth forms, a greater humidity preference, and lower eutrophication tolerance. Moreover, the two indexes used to quantify functional diversity (Functional Dispersion and Functional Evenness) show that, overall, diversity is greater in patches than in the matrix; in patches Functional Dispersion is statistically higher for plants, and Evenness is statistically higher for beetles and lichen. These differences are all consistent with the very distinct ecological conditions in the matrix and patches. The greater overall functional diversity of shrubby patches, and the major differences in functional composition between patches and matrix, observed for all taxa, indicate that these patches greatly enhance the functional diversity of species assemblages in wood-pasture landscapes. Consequently, preserving and promoting tiny shrubby patches is a potentially valuable low-cost management tool to increase biodiversity and improve ecosystem functioning in wood-pasture landscapes.

Keywords: functional diversity; habitat management; montado/dehesa; multi-taxa; native

1. Introduction

Wood-pastures are savanna like systems, common across Europe, that have been shaped by a long-term history of animal grazing and the interaction between various land-use regimes and natural factors (Hartel and Plieninger, 2014). They are in general used for livestock grazing, produce various timber (such as cork, firewood, etc.) and non-timber forest products, and have a high socio-cultural value (Plieninger et al., 2015; Moreno et al., 2017). Despite their anthropogenic character, wood-pastures often retain many features of their original semi-natural vegetation and support a rich biodiversity (Bugalho et al., 2011; Bergmeier and Roellig, 2014). As a consequence, many wood-pastures in Europe are considered High Nature Value Farmlands (HNVF), agricultural landscapes holding a high biodiversity value, often as a result of a high spatial heterogeneity (Andersen et al., 2003; Pinto-Correia and Ribeiro, 2012). For example, it has been shown that in a context of wood-pasture the presence of landscape elements such as lines of riparian vegetation or small orchards can increase landscape level species diversity in arthropods (Taboada et al., 2006; Silva et al., 2011), birds (Leal et al., 2011) and mammals (Diaz et al., 1997; Rosalino et al., 2009).

Despite their socio-cultural and biodiversity value, and economic relevance, wood-pastures are reportedly declining due to land-use changes driven mostly by intensification or land abandonment (Bugalho et al., 2009; Godinho et al., 2014). In some regions, traditional land-uses have been greatly simplified, or even abandoned, due to changes in the market value of products and rural socio-economic conditions, resulting in human migration to urban areas (Plieninger et al., 2015). In more productive regions, changes in livestock type and increasing animal densities have been observed, generally in response to changing market incentives, resulting in higher grazing pressure (Pinto-Correia and Godinho, 2013). Livestock grazing is an important aspect of wood-

pasture dynamics as it usually contributes to maintain the characteristic vegetation structure and spatial heterogeneity (Moreno and Pulido, 2009). However, most intensively managed wood pastures end up being dominated by just two vegetation layers, an herb layer and a tree layer of variable density, because the regeneration of shrubs is repressed mechanically or by intensive grazing (Sales-Baptista et al., 2015; Listopad et al., 2018). The near or total absence of a shrub layer results in a simplified habitat structure and reduced spatial heterogeneity, with potential negative consequences for taxonomic and functional diversity of wood-pastures (Peco et al. 2012; Almeida et al., 2015).

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Nevertheless, even intensively managed wood-pastures are occasionally dotted with small patches that are naturally excluded from grazing and mechanical clearing (e.g. rocky outcrops). The vegetation in these patches consists mostly of native trees, shrubs and herbs that are often representative of local forest communities before human intervention (Bergmeier et al., 2010). They contrast with the wood-pasture matrix of open and regularly grazed pastures (henceforth referred to as "matrix") in terms of micro-climatic conditions, soil nutrients, shelter availability and food resources and may thus be an important contribution to the spatial heterogeneity and species diversity in wood-pastures (Oksuz et al. 2020). However, it remains to be assessed if this increased spatial heterogeneity contributes to ecosystem function by supporting species belonging to functional groups that are distinct from those present in the wood-pasture matrix. If the species added by the presence of patches are functionally redundant with those in the matrix, there will be no overall change in functional diversity despite the potential increase in species richness, even though functional redundancy may increase the resilience of the habitat (Mori et al., 2013). Understanding the functional contribution of small shrubby patches can contribute towards the development of biodiversity-friendly management solutions that address the adverse effects of landuse intensification and landscape homogenization, without restricting the social and economic benefits of wood-pastures. Because functional diversity is an important driver of ecosystem services and processes (de Bello et al., 2010; Gagic et al., 2015), maintaining or expanding such patches may promote species-rich and functionally diverse landscapes. However, to our knowledge, the contribution of shrubby patches to the functional diversity of wood-pastures has not been studied, so the information currently available across multiple biological groups and at appropriate spatial scales is too scarce to support management decisions.

In this study, we address this knowledge-gap using as a case study the Iberian wood-pasture system generally known as montados or dehesas, which covers vast areas throughout the western Mediterranean (Pinto-Correia et al., 2011). Their savannah-like structure has a tree layer usually dominated by cork oaks (Q. suber) and/or holm oaks (Q. rotundifolia). They are typically exploited for livestock grazing and cork or acorn production and, due to their rich biodiversity, are classified as High Nature Value Farmland. Like in most other wood-pasture systems, the intensively managed and grazed areas usually lack a well-developed shrub layer. We aimed to assess the contribution of shrubby patches to wood-pasture functional diversity by comparing shrubby patches and the woodpasture matrix using indices of functional composition (Community Weighted Means) and diversity (Functional Evenness and Functional Dispersion) across multiple taxa. Specifically, we address the following questions: 1) Are there trait-level differences in functional composition between shrubby patches and the matrix? And 2) do shrubby patches contribute to the functional diversity of landscapes dominated by wood-pastures? We explore these questions using three distinct taxonomic groups - plants, beetles and lichens. These groups were chosen as they potentially respond to important ecological factors such as direct grazing pressure (plants), vegetation structure (beetles), and micro-climatic conditions and nutrient availability (lichens).

2. Materials and Methods

2.1 Study Area

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Our study was done at two wood-pasture areas representative of the typical *montado* system, located in southern Portugal. The region has a Mediterranean climate, with hot and dry summers (Agencia Estatal de Meteorología, 2011). Small shrubby patches are common in the study area, often associated with rocky outcrops where it is difficult to mechanically clear shrubs. Moreover, once the shrub layer in the patches becomes dense, livestock tend to stop grazing in them. They usually host an ensemble of cork/holm oaks (*Q. suber/Q. rotundifolia*), wild olive trees (*Olea europaea var. sylvestris*) and fruiting evergreen shrub species such as evergreen buckthorn (*Rhamnus alaternus*) and elm leaf blackberry (*Rubus ulmifolius*). Shrubby patches are usually small but highly variable in terms of size, shrub density, woody plant richness and composition, and may constitute a substantial source of spatial heterogeneity in wood-pasture landscapes. The characteristics of each shrubby patch (patch area, proportion of ground covered by exposed rocks (on a scale of 0 to 5), height of the understory, height of the trees, and density of vegetation (on a scale of 1 to 10) are available in Appendix A. The density of shrubby patches is variable, but they covered less than 0.5% of the study areas.

Characterization of the plots was conducted during 2012-2013 in a total of twenty-four plots of which 13 were in shrubby patches (henceforth *patches*, N = 13) and 11 in the nearby woodpasture matrix (henceforth *matrix*, N = 11), at the two woodpasture areas: Herdade do Freixo do Meio (FM) (38° 42'N, 8° 19.1'W) and Barrocal dos Ricos (BR) (38° 46'N, 8° 15'W) (Fig 1). The matrix is mostly grazed by sheep and cattle and is used by free-ranging pigs. The studied woodpastures (FM and BR) are located about 10 km from each other, and in both areas all sampled plots are located within a radius of less than 1 km. We sampled all shrubby patches larger than 250 m² available in both FM and BR. These varied in size from 252 m² to 3000 m² (mean: 1226 m², SD: 793.9). The matrix plots were selected randomly within the same farm block of the sampled shrubby patches. They were more than 100 m apart, and at least 140 m from the nearest patches. Tree cover in the matrix was around 30 trees/ha. The initial number of sampled patches and matrix

plots was substantially larger than the one we used in the analyses, because in some sites pigs and wild boars destroyed the pitfall traps used to sample beetles.

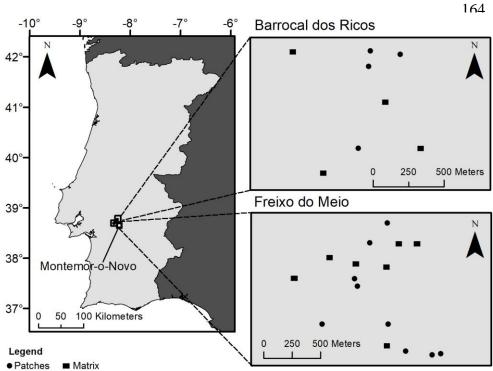


Fig. 1. Map of the

17/ study areas located in

Montemor-o-Novo county, Portugal. Circles represent shrubby patches and filled squares represent matrix plots in Barrocal dos Ricos (N=8; 4 patches and 4 matrix plots) and Freixo do Meio (N=16; 9 patches and 7 matrix plots).

2.2 Plant sampling

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We sampled shrubs, grasses and forbs at both the patches and matrix plots using 100 m² (10x10 m) quadrats between May and July 2013. The cover of each plant species in the quadrat was visually estimated by the same observer. In each shrubby patch a quadrat was placed with one of the sides along the edge of the patch, but avoiding the transition between the patch and matrix. Each matrix quadrat included areas with and without canopy cover. Plant species present in each quadrat were identified in the field or in the laboratory, and their abundance was recorded using the Braun-Blanquet cover-abundance scale scored from 1 to 5 (Kent and Coker, 1996). For statistical

analysis these scores were converted to a percentage scale ranging from 2.5% to 87.5% (1=2.5%, 2=15%, 3=37.5%, 4=62.5%, 5=87.5%) (Appendix B).

To characterize the functional composition of the matrix and shrubby patches we selected six functional traits related to distinct vegetation characteristics that potentially reflect the differences in grazing pressure between the patches and matrix: woodiness, growth form, leaf shape, leaf phenology, fruit type and dispersal strategy traits (Appendices C and D). Trait data for most species was extracted from the BROT database (Paula et al., 2009; Tavṣanoğlu and Pausas, 2018). For species not in this database, we used the TRY (Fitter and Peat, 1994; Castro-Díez et al., 1998; Kühn et al., 2004; Kattge et al., 2011) and LEDA (Kleyer et al., 2008) databases and published resources (Herrera, 1995; Manzano and Malo, 2006; Lengyel et al., 2009; Guzmán and Vargas, 2009; Groom and Lamont, 2015; Linder et al., 2017). A description of each plant trait and their related trait syndromes is presented in Table 1.

Table 1

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Comparison of community weighted mean (CWM) values using Wilcoxon rank sum test between the matrix and patches for the traits of plants, beetles and lichens. The values of p and W resulted from Wilcoxon rank sum test. The plus (+) and minus (-) signs indicate in which treatment (patch/matrix) the significantly different CWM values increase and decrease, respectively (Wilcoxon rank sum test; $p \le 0.05$).

Taxa	Traits	Categories /Unit	p	w	Direction of the differences in CWM values	
					Patch	Matrix
	***	Woody	<0.001	0	+	-
PLANTS	Woodiness	Non-woody	<0.001	143	-	+
ILANIS	Growth form		<0.001	3	+	-
	Growm form	Shrub	<0.001	0	+	-

		Herb	≤0.005	138	_	+
		Graminoid	<0.001	141	-	+
		Broad	<0.001	3	+	-
	Leaf shape	Linear	<0.001	140	-	+
	Laaf nhanalaay	Evergreen	<0.001	0	+	-
	Leaf phenology	Deciduous	0.01	116	-	+
	Fruit type	Fleshy fruit	<0.001	0	+	-
	Fruit type	Dry fruit	0.45	79		
	Dispersal	Autochory	0.69	79		
	strategy	Allochory	0.7	141		
	Body size	mm	0.02	111	-	+
		Predator	0.55	77		
	Fooding wild	Herbivore	0.36	88		
	Feeding guild	Saprovore	0.94	77		
BEETLES		Fungivore	0.03	28	+	-
		Brachypterous	0.22	64		
	Dispersal strategy	Dimorphic	0.24	55		
	232333	Macropterous	0.07	96		
		Crustose	0.07	37		
		Foliose narrow- lobed	≤0.005	128	-	+
	Growth form	Foliose broad- lobed	0.02	32	+	-
		Fruticose	0.01	17	+	-
		Squamulose	0.7	72		
LICHENS		Chloroccocoid	0.30	42		
	Photobiont type	Trentepohlia	0.40	94		
		Cyanolichen	0.46	76		
		Asexual sorediate	0.78	66		
	Reproduction strategy	Asexual isidiate	0.82	79		
		Sexual	0.88	57		
	Humidity	Hygrophytic	0.05	25	+	-
	preference	Mesophytic	0.95	35		

	Xerophytic	0.01	110	-	+
Eutrophication	Oligotrophic	≤ 0.005	4	+	-
tolerance	Mesotrophic	0.79	88		
	Nitrophytic	≤0.005	120	-	+

2.3 Beetle sampling

Beetles were sampled in each individual plot using sets of three pitfall traps buried in the soil, with the top level with the surface of the ground. They were made from polystyrene cups with a 95 mm diameter and were filled with water, soap and salt to a depth of 3 cm. In total, three traps were used in each shrubby patch and matrix plot. The location of the first trap was chosen randomly, and the other two traps were placed at around 10 m distance from each other forming a triangle. Traps were active for 5 weeks from 20th May to 25th June in 2013, but the captured arthropods were removed weekly. Captures in the same patch or matrix site were pooled before analyses. All Coleoptera species were identified to species level and the number of captures of each taxon was recorded (Appendix B).

We used body length, feeding guild and dispersal strategy (hind wing morphology) traits to characterize the beetle species assemblages (Table 1; Appendix C and D). Body length was measured in the laboratory from the tip of the head to the tip of the abdomen for 5 individuals of each species and averaged for the species. Feeding guilds were collected from available databases (Homburg et al., 2014) and published resources (Harde and Severa, 1984; Baraud, 1992; Viñolas and Cartagena, 2005). The hind wing morphology of each species was recorded from sampled individuals to define the dispersal ability trait (Aukema, 1986; Desender, 1989; Homburg et al., 2014).

2.4 Lichen sampling

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Lichen sampling was performed by the same observer using the European standard protocol (Asta et al., 2002) between December 2013 and January 2014. All cork oaks (*Q. suber*) and holm

oaks (*Q. rotundifolia*) with a diameter at breast height (dbh) greater than 15 cm (usually fewer than five) were selected for sampling in shrubby patches. In the matrix, we sampled a fixed number of five trees per plot, located within the quadrats used for sampling plants or adjacent to them. A 10 x 50 cm frame divided into five 10x10cm grid-cells was vertically placed over each tree trunk at about 1 m above the ground. All lichen species occurring inside each grid cell were identified to species level and recorded. This process was repeated in each tree trunk at the four cardinal directions (N, S, E, W) and the number of quadrats where each species was identified was used to estimate species abundance (Appendix B).

For each species recorded, we then collected information on five traits representing resource use characteristics and dispersal ability from the ITALIC database (Nimis and Martellos, 2017). These traits included growth form, photobiont type, reproduction strategy, humidity preference and eutrophication tolerance. All lichen traits, and their associated groups used for the analysis are listed in Table 1 and Appendix C and D.

2.5 Data analysis

We tested differences in functional composition between the wood-pasture matrix and shrubby patches using the community weighted mean (CWM) index. This index represents the average trait value in a community, and it was estimated for each trait using species-trait and species-abundance matrices. In the case of continuous traits, the CWM is the weighted mean of that trait in the community, in which each species is weighted by its relative abundance. In categorical and binary traits CWM is the proportion of each category in the community (i.e. representing their relative abundance) (Lavorel et al., 2007).

Multi-trait functional dispersion (FDis) and functional evenness (FEve) indices were used to characterize and compare the functional diversity of the three taxonomic groups in patches and matrix. Functional dispersion (FDis) measures the degree of dissimilarity in a community by

calculating the weighted mean distance of each species to the weighted centroid of all species in multidimensional trait space of the community, with weights corresponding to species relative abundances. Functional evenness (FEve) index measure the evenness of species abundances distribution in the community trait space. These indices were selected because they can be calculated for any type of trait data (e.g. numerical, binomial, categorical) and are independent from species richness (Mason et al., 2005; Villéger et al., 2008). Before each index was calculated, we assessed the correlation between traits using Spearman correlations because highly correlated traits may bias measurements of functional diversity. There were no significant correlations (p > 0.05), so we calculated the multi-trait functional diversity indices using all traits compiled for each taxon, giving each trait an equal weight.

Community weighted mean (CWM), functional dispersion (FDis) and functional evenness (FEve) differences between the patches and the matrix were compared with Wilcoxon rank sum tests (p≤0.05) (Hollander and Wolfe, 1973). All indices were calculated using the "dbFD" function in package "FD" (Laliberté et al., 2014), Wilcoxon rank sum test was applied using "wilcox.test" function in "stats" package, and figures were produced using "ggplot2" (Wickham, 2009) in R v.3.4.3 computing environment (R Core Team, 2016).

We also tested whether the spatial distance between sampling sites had any effects on functional diversity and structure using a Mantel test (Mantel, 1967; Sokal, 1979), implemented with "ade4" package (Bougeard and Dray, 2018) also in R v.3.4.3, but no statistically significant (p>0.05) spatial effects were detected. Moreover, the comparisons of functional diversity and composition of plants, beetles and lichens between the patches and matrix for each study area is available in Appendix E.

3. Results

3.1 Shrubby patches and the matrix host assemblages of plants, lichens and beetles with very distinct functional compositions

We identified a total of 73 species of plants, 57 of lichens and 43 of beetles (Appendix A). We detected highly significant differences in plant trait CWM values between patches and matrix for several of the trait syndromes tested (Fig 2 and Table 1). Plants with evergreen and woody growth forms, broad-leafed and with fleshy fruit were much better represented in the patches than in the matrix. In contrast, linear-leaved plants and annual graminoids were better represented in the matrix than in the patches (Table 1). There were no differences between matrix and patches in the relative abundance of plants with dry fruits, allochorous and autochorous dispersal (Table 1).

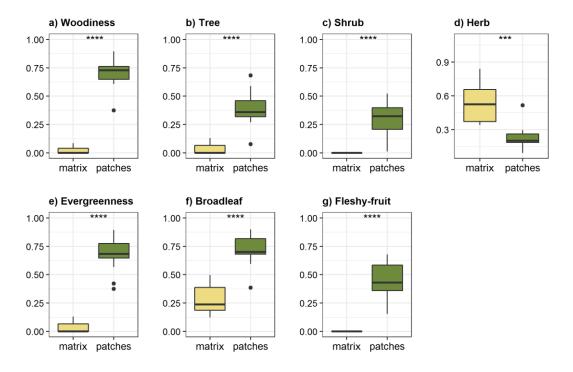


Fig. 2. Comparison of community weighted means (CWM) of plant traits in wood-pasture matrix and shrubby vegetation patches. Boxes show the median, lower and upper quartiles, whiskers represent extreme values and dots outliers. All differences are highly significant (**** p < 0.001, **** $p \le 0.005$). See Table 1 for details on test statistics.

In beetles, CWM values of body size and fungivore feeding guild significantly differ between habitats, with small body-sized and fungivore species more prevalent in patches than in the matrix (Fig 3). We did not observe differences for saprovore, herbivore and predator feeding guilds (Table 1). Dispersal strategies did not differ between the patches and the matrix, but there is a nearly significant greater abundance of macropterous beetles in the matrix (Table 1).

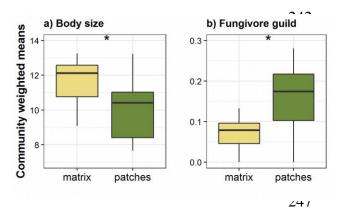
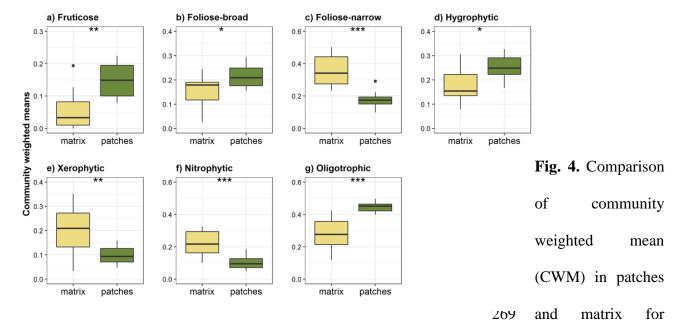


Fig. 3. Comparison of community weighted mean (CWM) for (a) body size and (b) fungivore beetle guilds. Smaller beetles and fungivore species were more prevalent in patches than in the matrix. Boxes identify the median, lower and upper quartiles, and whiskers show extreme values. Asterisks (*) indicate significant differences ($p \le 0.05$). See Table 1 for details on test statistics.

In lichens, CWM values of fruticose and foliose-broad lobe growth forms are higher in patches, while foliose-narrow lobes species are higher in the matrix (Fig 4). The CWM for crustose or squamulose growth lichens were not significantly different between habitats, although the difference was nearly significant in the former (Table 1). We did not observe any differences in lichen photobiont type and reproduction strategy traits (Table 1). Hygrophytic and oligotrophic lichen functional groups had higher CWM in the patches, and xerophytic and nitrophytic in the matrix (Fig 4). Mesophytic and mesotrophic lichens are similarly prevalent in patches and matrix (Table 1).



lichen traits, Growth form (a), (b) (c); Humidity preference (d), (e) and Eutrophication tolerance (f), (g). Fruticose (a) and foliose-broad growth forms (b) as well as hygrophytic (d) and oligotrophic (g) lichens are better represented in patches than in the matrix. Boxes show the median, lower and upper quartiles, whiskers show extreme values and dots outliers. Asterisks indicate significant differences (* $p \le 0.05$, ** $p \le 0.01$, *** $p \le 0.005$, **** p < 0.001). See Table 1 for details on test statistics.

3.2 Functional dispersion and evenness in shrubby patches and matrix

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matrix

patches

Functional dispersion is significantly higher in patches than in the matrix for plants (W=5, p=0.003), but there are no significant differences for beetles and lichens (Fig 5). Functional evenness (FEve) values for plants were similar between the patches and the matrix but differed

a)

Significantly for both beetles (W = 33, p-value = 0.03) and lichens

(W = 29, p-value = 0.02).

Plants Beetles Lichens

matrix patches

Fig. 5. Functional dispersion (a) and functional evenness (b) of plants, beetles and lichens in patches and matrix. Functional dispersion of plants is greater in patches than in the matrix, but differences for beetles and lichens are not significant. Functional evenness (FEve) is higher for beetles and lichens in patches than in the matrix, while it is not different for plants between the treatments. Boxes show the median, lower and upper quartiles, whiskers show lower and upper extreme values of FDis and FEve values and black dots are outliers. Asterisks indicate significant differences (* $p \le 0.05$, *** $p \le 0.005$) and ns indicates non-significant results (p>0.05).

4. Discussion

Our results show substantial trait-level differences between shrubby patches and the woodpasture matrix in the species assemblages of the three studied taxonomic groups.

4.1 Functional diversity and composition of plants

As expected, shrubby patches have a higher diversity (Fig. 5a) and relative abundance of woody plants, often with evergreen broad leaves and fleshy-fruits. In contrast, the open matrix is dominated mostly by linear-leaved and dry-fruited herbs and graminoids (Fig. 2). Functional dispersion (FDis) of plants was higher in shrubby patches than in the matrix (Fig. 5a), but

functional evenness (FEve) was similar (Fig. 5b). These results imply that the high functional distinctiveness of shrubby patches does not arise from the presence of a few rare woody species that are absent from the matrix, but from the presence of a diverse and abundant woody vegetation. In a previous paper we demonstrated that shrubby patches harbour plant species distinct from those in the matrix (Oksuz et al., 2020), and here we show those different species are also functionally dissimilar, supporting the potential contribution of shrubby patches to the ecosystem functioning in wood-pastures (Diaz et al., 2007; Pakeman, 2011).

The higher plant functional dissimilarity found in the patches contrasts with the simpler structure of plant communities in the matrix, and contributes to increase vegetation heterogeneity in wood-pasture landscapes. Higher plant functional dissimilarity indicates a high niche availability in the patches, due to the provision of a broader range of unique microhabitats, food and breeding resources as the differences in CWM values of specific plant traits shows. For example, several studies have revealed a crucial role of dense shrubs with fleshy-fruits for increasing feeding and nesting opportunities in pastures (Hartel et al., 2014, Godinho et al., 2010; Martínez, 2009). Furthermore, higher availability of broad-leafed woody plants may have substantial potential to alter abiotic conditions including shade, soil nutrient richness and micro-climate, that profoundly influence species composition patterns (Moreno and Pulido, 2009). For instance, a higher shrub cover increases soil moisture and promotes a higher diversity of ground-dwelling arthropods in arid landscapes (Taboada et al., 2006). Moreover, stopping grazing allows shrub regeneration and has been shown to greatly enhance fruticose lichen growth (Concostrina-Zubiri et al., 2016).

4.2 Functional diversity and composition of beetles and lichen

Interestingly, the observed trait-level differences of beetle and lichen assemblages did not result in distinct functional dispersion (FDis) patterns (Fig. 5a), indicating that the functional dissimilarity level of the patches is not different from that of the matrix. However, in both taxa, we observed higher functional evenness (FEve) in the patches (Fig. 5b). FEve reflects how regularly

the abundance of different traits is distributed across the habitat (Villéger et al., 2008). Therefore, the higher values of FEve observed for these two distinct taxa in woody vegetation patches suggests that the patches provide a diversity of food resources and micro-habitats that allows for an even distribution of the various traits. In contrast, low values of FEve in the matrix may indicate an under-utilization of some of the available functional niches (Mason et al., 2005), particularly when these are evenly distributed across the habitat (Gerisch et al., 2011). Because the open matrix has a regular distribution of plant functional groups, as indicated by the high FEve values for plants both in the patches and in the matrix (Fig. 5b), our results suggest that the lower FEve values observed for beetles and lichens probably represent an uneven trait distribution in the matrix habitat driven by higher grazing intensity (Hillebrand et al., 2008; Birkhofer et al., 2017). For example, it has been reported that habitat homogenization driven by intensive land-use may stimulate the dominance of specific traits and may reduce functional evenness (Hillebrand et al., 2008; Mouillot et al., 2013).

Regarding functional structure, we detected that smaller beetle species are clearly more prevalent in patches than in the matrix (Fig. 3a). Higher vegetation heterogeneity in the patches may facilitate micro-habitat complexity that favours small insects. In fact, it has been shown that small-sized staphylinids are associated to more treed micro-habitats in Mediterranean habitats (García-Tejero and Taboada, 2016). Moreover, it has been reported that, after a habitat disturbance, smaller beetles tend to prefer natural remnants to early succession stages of vegetation (Cunningham and Murray, 2006). Fungivore beetles, although quite rare in our sampling, were more prevalent in the patches (Fig. 3b). Although several studies have reported a high diversity of fungi in wood-pastures (Nordén et al., 2004; Diamandis and Perlerou, 2013), in highly managed oak wood-pastures, fungi development may be to some extent restricted to relatively humid spots, especially in the rainy season. That is the case of the studied patches of natural vegetation, where dense woody cover lowers temperature, increases humidity and provides plant material left to decompose in loco, thus creating suitable conditions for fungi and for the animal species feeding on them.

Lichen communities are regarded as an ecological indicator (Ellis et al., 2007; Pinho et al., 2011) and, although there were no significant differences in FDis between patches and matrix, we observed a shift in the composition of lichen communities. Lichens present in the patches have greater preference for moister environments than those present in the matrix (Fig. 4d). In fact, patches have a higher tree and shrub density, which increases shading and evapotranspiration. Both conditions generate a micro-climatic environment with lower temperature, lower radiation and higher moisture, to which lichen communities respond (Giordani et al., 2013; Li et al., 2013). The shift in the lichen communities is also indicative of higher nutrient availability in the matrix than in the patches (Fig. 4f). Lichens in the matrix have ecological preferences for, and are more tolerant to, higher nutrient loads than those present in the patches. Several factors may contribute to a higher nutrient availability in the wood-pasture matrix, such as a greater abundance of livestock excrements, a sparser vegetation cover due to grazing and shrub removal, and the dominance by annual plants, which are only present during part of the year. Together, they increase the exposure of the soil in the matrix to dust particles, naturally enriched in nutrients (Pinho et al., 2008). Moreover, the canopy of trees in the patches may be able to intercept particles and nutrients (Santos et al., 2017). Larger lichens with higher surface exposure in relation to dry weight, which require moister conditions and tolerate less dust particles, as well as crustose lichens, which are highly resistant to light stress and have low nutrient demand due to their slow growth (Armstrong and Bradwell, 2010), are thus more abundant in patch areas. The presence of only a few scattered trees in the matrix may provide less appropriate conditions for hygrophytic (Fig. 4d), fruticose (Fig. 4a) and large foliose lichens (Fig. 4b). In contrast, most foliose-narrow lichens tolerate nutrient-rich environments and xerophytic conditions and are thus more abundant in the matrix (Fig. 4c).

4.3 Functional diversity and composition of multi-taxa in relation to ecosystem functioning and management actions

Overall, the substantial differences in the functional structure of plants reveal the traits (Fig. 2) potentially driving the ecosystem functioning in patches and in the matrix (Grime, 1998; Lavorel, 2013). These differences are reflected in higher functional dissimilarity of plants indicating elevated niche differentiation compared to the matrix (Tilman, 1997). Higher niche diversity may facilitate enhanced complementarity in resource use (Hooper, 1998; Díaz and Cabido, 2001) in patches, which is indicated by the functional evenness patterns of beetles and lichens in our study. Moreover, several traits of beetles and lichens contribute to distinct functional composition of patches and the matrix potentially interacting with ecosystem functioning as well as services in various levels (Zedda and Rambold, 2015; Noriega et al., 2017).

To conclude, our results highlight the positive influence of shrubby patches on the functional diversity of multi-taxa, potentially leading to improved ecosystem functioning and service provision in wood-pastures. This is very important, considering the urgent need for biodiversity-friendly management actions in wood-pastures (Arosa et al., 2017). Preserving and even establishing small shrubby patches may be a low-cost and practical conservation strategy with minimal impacts to management, because of the high regenerative capacity of the shrub layer and due to the fact that even small patches make a significant positive contribution to functional diversity. Moreover, this strategy can be easily adjusted to existing management and conservation schemes, such as High Nature Value Farmland (HNVF), aiming to preserve semi-natural elements in managed wood-pastures (Andersen et al., 2003). However, we note that the analysis in this study should be replicated in other wood-pasture areas, preferably with larger samples, to ensure that our conclusions can be extrapolated to other similar systems.

5. Conclusions and Implications for Management

Our results indicate that shrubby patches contribute greatly to the biodiversity and ecosystem functioning of wood-pasture landscapes. We demonstrated that shrubby patches contribute to the functional diversity of these habitats, maintaining a high level of biodiversity beyond species richness. Functional diversity is important to preserve healthy and functional ecosystems (Cadotte et al., 2011) an issue that is particularly relevant for threatened wood-pasture systems (Hartel et al., 2015). For this reason, the establishment and long-term maintenance of small shrubby patches should be stimulated to preserve the High Nature Value Farmland (HNVF) status of wood-pastures.

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The ensuing challenge is how to conciliate the preservation of such habitat patches in the current scenario of increasing intensification of the use of wood-pastures observed throughout Europe, driven by ongoing market, social and environmental changes (Plieninger and Bieling, 2013). Despite their major ecological importance, shrubby patches often occupy very small areas, usually over and around small rocky outcrops. Areas with such conditions are not amenable to be actively exploited and are often not used by land managers, so maintaining shrubby patches in such conditions is likely to have little negative impact on economic productivity. Activities that have been proposed to promote woody plant regeneration, such as controlling grazing pressure or changing grazing type and timing, as well as maintaining grazing-excluded areas (Plieninger, 2007; Almeida et al., 2015), can also benefit shrubby patches. Similarly, landscape restoration schemes (Ockendon et al., 2018) could aim to actively establish small vegetation patches composed of native species. Such actions could be stimulated through policy directives or implemented as prescriptions under forest certification frameworks (Auld et al., 2008; Bugalho et al., 2011). These prescriptions, such as the set-aside areas required by the Forest Stewardship Council (FSC) certification scheme, have shown remarkable success in stimulating tree regeneration and shrub diversity in woodpastures (Dias et al., 2014). Likewise, recommendations to maintain and promote small vegetation 365 patches could substantially boost the functional wealth of wood-pastures at a very low 366 implementation cost. **Contribution of the authors** 367 368 All authors contributed to the study conception and design. Material preparation, data collection and analysis were performed by D.P. Oksuz, C.A.S. Aguiar, S. Tápia, E. Llop, P. Lopes, A.R.M. 369 370 Serrano, A.I. Leal, O. Correia, P. Matos, A. Rainho, C. Branquinho, R.A. Correia, J.M. Palmeirim. 371 The first draft of the manuscript was written by D.P. Oksuz and all authors commented on previous versions of the manuscript. All authors read and approved the final manuscript. 372 373 **Declarations of interest** 374 None. 375 **Funding** 376 This work was supported by Fundação para a Ciência e a Tecnologia (FCT), through project 377 PTDC/AGR-AAM/108448/2008 and several doctoral and post-doctoral grants: **DPO** 378 (PD/BD/106044/2015), AIL (SFRH/BPD/88056/2012), RAC (SFRH/BPD/118635/2016), and AR 379 (SFRH/BPD/101983/2014). 380 Acknowledgements 381 We are thankful to the various landowners who kindly allowed us to work in their farms, especially 382 to Eng. Alfredo Cunhal Sendim, of Herdade do Freixo do Meio, who also provided logistic support 383 and gave us valuable advice. We also thank Marta Acácio for providing assistance in data collection. References 384 385 Agencia Estatal de Meteorología, Instituto de Meteorología, Atlas Climático Ibérico / Iberian 386 Climate Atlas. Madrid and Lisbon, Agencia Estatal de Meteorología (España) and Instituto

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