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RESEARCH ARTICLE

Small rocky outcrops: Natural features to promote biodiversity in oak wood-pastures

Sergio Chozas[1] | **Susana Tapia**[1] | **Jorge Palmeirim**[1] | **Carla Alegria**[2] | **Otília Correia**[1]

[1]cE3c – Centro de Ecologia, Evolução e Alterações Ambientais, Universidade de Lisboa, Lisbon, Portugal

[2]SFCOLAB - Associação Smart Farm COLAB Laboratório Colaborativo para a Inovação Digital na Agricultura, Espaço SFCOLAB, Torres Vedras, Portugal

Correspondence

Sergio Chozas, cE3c – Centro de Ecologia, Evolução e Alterações Ambientais, Faculdade de Ciências, Universidade de Lisboa, Campo Grande, 1749-016 Lisbon, Portugal.
Email: schozas@hotmail.com

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Abstract

Aims: The Iberian oak wood-pastures are unique agroforestry systems supporting high levels of biodiversity and ecosystem services. Small rocky outcrops are geological features commonly found in these systems and constitute biodiversity reservoirs, protecting sensitive species from grazing and farming activities. We aimed to assess the relevance of including rocky outcrop conservation within wood-pastures to increase biodiversity. To achieve this goal, we studied the plant communities occurring within the outcrops and in the wood-pasture matrix to evaluate the impact of rocky outcrops on the overall plant taxonomic and functional diversities of these systems.

Location: Montemor-o-Novo (Alentejo, Portugal).

Methods: We sampled 102 plant communities occurring in outcrops and the adjacent wood-pasture matrix, and analysed alpha, beta, gamma and functional diversities. We identified the main intrinsic factors affecting outcrop plant composition and their functional groups using Linear and Generalized Linear Mixed models, and characterized the effect of outcrop size through Generalized Additive Models.

Results: We found plant richness to be similar in wood-pasture matrix and outcrops. However, β-diversity analysis revealed a high species turnover between both communities. Functional indices indicated higher plant functional diversity in outcrops and trait analyses identified three functional groups dissimilarly distributed in both communities: (a) perturbation- and stress-sensitive plants, with outcrops constituting an important refuge for this group; and (b) grazing-tolerant and (c) weedy herbs dominating the wood-pastures. Finally, we also found increased plant richness in outcrops with a longer length for their minor axis, i.e. wider outcrops, and greater rock cover area.

Conclusions: Our results indicate that the presence of small rocky outcrops in evergreen oak wood-pastures greatly increases their gamma and functional diversities. Consequently, outcrop protection strongly impacts overall wood-pasture biodiversity and underlines the suitability of including outcrop conservation as a cost-effective solution capable of increasing biodiversity in these agroforestry systems.

KEYWORDS
agroforestry, conservation, environmental heterogeneity, functional diversity, *Montado*/*Dehesa*, nature-based solutions, plant diversity, SLOSS debate, small habitat patches, sustainable development

1 | INTRODUCTION

Global biodiversity has been declining over past decades (Davis et al., 2018; Pereira et al., 2013). Among the global change factors responsible for biodiversity loss, land-use change, habitat fragmentation and climate change are the most detrimental (Tilman et al., 2017). Biodiversity loss linked to climate change strongly impacts ecosystem functioning (EF) and the delivery of multiple ecosystem services (Allan et al., 2015). Thus, a paradigm shift is needed to develop strategies that conciliate economic development, biodiversity conservation and ecosystem functioning (Oliver & Morecroft, 2014).

In this context, nature-based solutions (NbS), defined as actions to protect, sustainably manage and restore natural or modified ecosystems (Cohen-Shacham et al., 2016), constitute cost-effective means to safeguard biodiversity and EF while mitigating climate change (Keesstra et al., 2018). For example, increasing green space and planting trees in urban areas can mitigate the impact of the urban heat island effect (Grilo et al., 2020). Agroforestry systems have been identified as promising systems to implement NbS because they support high biodiversity levels (Torralba et al., 2016), contribute substantially to climate change strategies (Verchot et al., 2007) and foster EF (Jose, 2009) while generating socio-economic benefits (Pavlidis & Tsihrintzis, 2018).

The Iberian evergreen oak wood-pastures, known as *Montados* in Portugal and *Dehesas* in Spain, occupy an area of 3.5–4 million ha and emerge as key semi-natural systems to implement NbS promoting climate change mitigation and supporting biodiversity in the Iberian Peninsula (Olea & San Miguel-Ayanz, 2006). This system is structurally similar to savannah-type ecosystems, with cork oak (*Quercus suber*) and holm oak (*Quercus rotundifolia*) co-existing with pastures and crops (Pinto-Correia et al., 2011). It results from the transformation of ancient evergreen oak woodland areas by human activity over hundreds of years (Bugalho et al., 2011). This low-intensive farming regime maintains ecosystems that deliver a wide range of ecosystem services. These goods and services range from direct provisioning (e.g. cork production, livestock) to indirect regulation and support (e.g. carbon sequestration, soil conservation) and cultural services (recreation or conservation of rare species) (Branco et al., 2010). In addition to its socio-economic relevance, when managed adequately, this system maintains its internal structural diversity (Bugalho et al., 2011). Because of their role in biodiversity conservation in Iberian landscapes, these wood-pastures are considered High Nature Value farming systems (Paracchini et al., 2008). Despite its significance, this habitat endures various negative pressures being classified as Near Threatened by the European Red List of Habitats (Janssen et al., 2016), while its conservation status was assessed as Unfavourable/Bad by the Habitats Directive (EEA, 2013).

Underlining the importance of small patches for conservation in the context of the single large or several small (SLOSS) debate (Deane et al., 2020; Fahrig, 2020; Wintle et al., 2019), especially in countryside ecosystems (Mendenhall et al., 2014; Pereira & Daily, 2006), several authors have demonstrated that habitat heterogeneity resulting from small landscape discontinuities can substantially improve overall biodiversity wealth in wood-pastures (Concepción et al., 2020; Leal et al., 2016; Moreno et al., 2015). Previous research showed that small natural features (according to Hunter et al., 2017) such as olive orchards and riparian galleries enhance environmental heterogeneity and, consequently, the species diversity of mammals and birds in oak wood-pastures (Leal et al., 2011; Rosalino et al., 2009). Recently, Oksuz et al. (2020) identified small shrubby patches as promising NbS to increase *Montado* biodiversity, finding them to be frequently, but not always, associated with small rocky outcrops. Rocky outcrops are geological formations that are common in *Montados* and contribute to increasing their structural heterogeneity (Martín & Lopez, 2002). These features constitute reservoirs of biodiversity, protecting sensitive species from grazing and farming activities (Fitzsimons & Michael, 2017), developing small forest habitat fragments embedded in a grassland matrix (Plieninger et al., 2004). The buffering capacity of outcrops towards environmental changes, e.g. by conducting and retaining run-off water (Speziale & Ezcurra, 2015), make them potential "stepping-stones" within metacommunity systems that may allow the persistence and migration of species in response to global change impacts (Ottaviani et al., 2019). Outcrops also provide additional features for the ecosystem services of wood-pastures such as refuges and food for birds, mammals and pollinators, including small and big game species (Bauer et al., 2017); outcrops enhance carbon sequestration and storage and contribute to local water balance control (Centeno et al., 2010) and they constitute recreation and tourism areas (Twidale, 2000).

Given these facts, outcrops enhance the structural heterogeneity of wood-pastures and can, therefore, support a higher variety of communities (Benton et al., 2003). However, there is a knowledge gap in the literature addressing the conservation value of rocky outcrops. In this work, we continue the line of research initiated by Oksuz (2020) regarding the impact of small natural features on biodiversity in Portuguese *Montados*. Oksuz's study included several taxa, but had limited reach owing to the small number of surveyed patches compliant with all the taxa. Free of that constraint, in the present study, we analyse the impact of rocky outcrops on plant taxonomic and functional diversity, and the influence of the outcrop's characteristics (e.g. vegetation and rock cover, outcrop size) on that diversity. We hypothesize that these small geological elements are occupied by distinct plant communities enhancing both plant diversity and the plant functional diversity of the total landscape in Iberian oak wood-pastures, and that this distinctiveness is dependent on the outcrop's characteristics. The results provide information about the effectiveness of including rocky outcrops as a cost-effective NbS capable of increasing biodiversity and promoting the ecosystem services of wood-pastures.

2 | METHODS

2.1 | Study system

The study area, comprising ca. 33.5 km^2, is located in Montemor-o-Novo, Alentejo, Portugal (Figure 1), in the southern margin of the Tagus River (38°46′N, 8°14′W; 38°41′N, 8°20′W), with elevation varying from 130 to 180 m a.s.l. The climate is mild Mediterranean with an oceanic influence, characterized by a warm, dry summer and strong seasonal and interannual variability in precipitation and temperature (mean annual precipitation of 660 mm and mean annual air temperature of 15.4°C (SNIRH, 2019). Nine farmsteads were sampled. These farmsteads contain large oak wood-pasture areas used for cork extraction, livestock raising (cattle, sheep and pig) and hunting. Dominant soil types are dry acidic soils, and small rocky outcrops cover less than 0.5% of the total wood-pasture area (Oksuz et al., 2020). The vegetation of these patches usually includes holm and cork oaks, olive trees and a mixed-species shrub and lianoid understory composed of typical Mediterranean evergreen oak woodland species. Fieldwork was conducted in May and June 2013.

2.2 | Community surveys and explanatory variables

We sampled plant communities from 32 identified outcrops within the nine-farmstead area. On each outcrop, we placed one 10 m × 10 m plot assuming that: (a) the generalized shape of the outcrops is an ellipse; and (b) the central axis of the plot includes the centre of the ellipse and is perpendicular to the major axis of the ellipse (Figure 2). Simultaneously, we placed 32 plots (each 10 m × 10 m) on pastures in the vicinity of the sampled outcrops. Plots were located randomly but were always in flat areas, avoiding

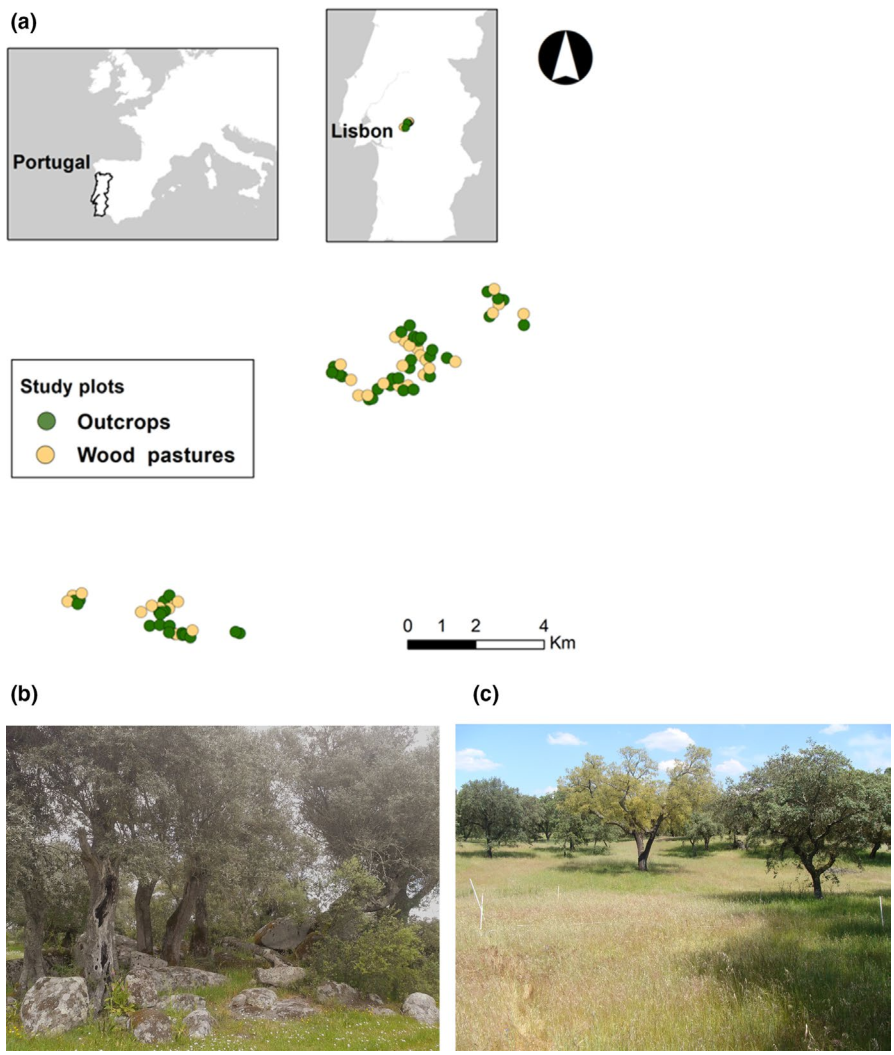

FIGURE 1 (a) In total, 102 plots, each 10 m × 10 m, were studied in Alentejo, Portugal: 51 located in rocky outcrops (32 for analyses comparing outcrops and wood-pasture communities, and 19 for analysing the effect of size and spatial distribution of outcrops) and 51 (32 + 19) in wood-pastures. Examples of (b) outcrop and (c) wood-pasture plots sampled

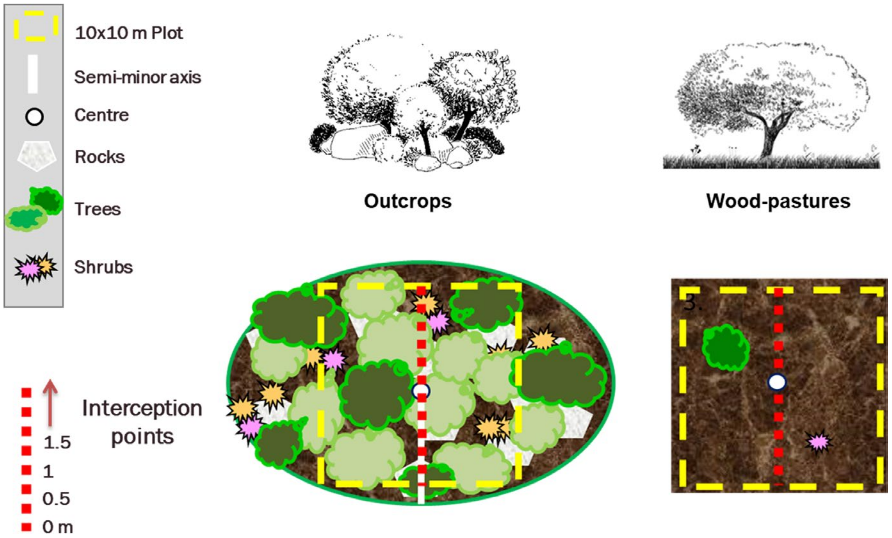

FIGURE 2 Sampling design. Cover of plants, rocks, mosses, lichens, bare soil and litter was registered in the studied 10 m × 10 m plots, first in the whole plot area (*n* = 64: 32 outcrops + 32 wood-pastures) and then, using the point-intercept method, in the outcrop (*n* = 51) and wood-pasture (*n* = 51) axes (refer to Methods for details)

slopes and notable topographic variations. Hereafter, "outcrop" or "matrix" are used to identify the respective plots.

The plant species composition and cover in the plots were estimated using an extended scale adapted from the Braun–Blanquet cover–abundance scale (5 = 75%–100%, 4 = 50%–75%, 3 = 25%–50%, 2 = 5%–25%, 1 = few individuals, 0.5 = very few individuals and 0.1 = one individual) (Damgaard, 2014). In each plot, we registered rock, moss, lichen, bare soil and litter cover using the same scale (Appendix S1). The heights of trees, shrubs, herbs and rocks were also measured.

Plant nomenclature followed the Checklist da Flora de Portugal (ALFA -Associação Lusitana de Fitossociologia., 2010), and species identities were determined using *Flora Iberica* (Castroviejo, 1986–2015) and *Nova Flora de Portugal* (Franco, 1971–1984; Franco & Afonso, 1994–2003).

2.3 | Comparative analyses

First, we assessed the plant richness in both communities. Variation in species composition among outcrops and wood-pasture matrices, i.e. β-diversity, was calculated using presence and absence data accounting for the spatial turnover (species replacement between both communities) and nestedness (species loss from community to community) components (Baselga & Leprieur, 2015). Pair-wise Wilcoxon tests comparing richness and plant life form, namely herbaceous, shrub, climber and tree, were performed to assess differences in community structure between the outcrops and matrix. We also compared the cover between the two communities for all tree species, both adult and shrubby stages. As a measure of regeneration, we considered individuals to be trees when they were 2 m or more in height.

Indicator species are used as ecological indicators of communities, and ultimately represent the qualitative characteristics of the ecosystem (De Cáceres et al., 2010). We identified the indicator species in both communities by calculating all species' indicator values (IndVal; Legendre & Legendre, 1998). This index quantifies the fidelity and specificity of each species to a given type of community. We used the R package *labdsv* (v2.0-1; Roberts, 2019) to calculate IndVal.

The description of the vegetation composition was achieved by a Non-metric Multidimensional Scaling (NMS, McCune & Grace, 2002) ordination of the study plots based on plant species cover (van der Maarel, 2007), using the function "metaMDS" of the R package *vegan* (v2.5-7; Oksanen et al., 2013). Braun–Blanquet cover–abundance 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%). We used Bray–Curtis clustering to measure the dissimilarity between plots and assessed the goodness-of-fit of the ordination through the percentage of variance represented by each consecutive axis (see McCune & Grace, 2002 for details). NMS axes resulting from these analyses represent the dissimilarity in plant composition.

We explored the relationships of outcrop and wood-pasture matrix characteristics, namely cover and height of trees, shrubs, herbs (maximum) and rocks (maximum and average) and bare soil cover, with their plant communities by correlating these characteristics with the NMS ordination using the "envfit" function of *vegan*. The strength of those relationships was evaluated through the squared correlation coefficient (r^2).

To assess the functional diversity of both outcrops and the oak wood-pasture matrix, we classified plant species according to 10 selected traits (Appendix S2, Table S1). We considered seven traits associated with plant responses to grazing (tolerant or not), disturbance (weed behaviour or not), drought (drought-tolerant, indifferent or drought-avoiders), edaphic conditions (acidophilous, indifferent or basophilous; rupicolous or not; and nitrophilous or not) and light (sciophilous or heliophilous). We also included dispersal strategy (short or long dispersal, following Vittoz & Engler, 2007) and life and growth forms as generalist traits informing about climate, disturbance, competitive ability and defence responses of plants (Wright et al., 2006). Together, the 10 traits allow characterization of the adaptive responses of sampled species to outcrops and matrix (Cadotte et al., 2011) by (a) calculating functional diversity indices, namely functional richness, evenness, divergence, dissimilarity and Rao's quadratic entropy (Villéger et al., 2008), and (b) identifying functional groups. Plant functional groups were defined using a dendrogram of species based on the 10 trait values and built according to Ward's hierarchical agglomerative clustering method (Murtagh & Legendre, 2014). Functional diversity analyses were performed using the *FD* package (v1.0-12; Laliberté et al., 2014).

Finally, pair-wise Wilcoxon tests comparing functional indices and groups of both communities were performed to assess differences in the functional diversity between outcrops and the matrix.

2.4 | Outcrop characteristics' effect

To assess the effect of rocky outcrop characteristics on plant composition and functional diversity, we included 19 additional outcrops; we measured the area and the perimeter of the 51 outcrops using orthophotos extracted from Google Earth and analysed with ArcGIS software (v10.7.1; ESRI, 2019). We registered the plant species composition and cover in the outcrops along the transect defined by the semi-minor axis of the ellipse, identified as outcrop axis, using the point-intercept method (Nunes et al., 2015). At each (intercepted) point, spaced every 50 cm along the transect, a 5-mm diameter rod was stuck in the ground making a 90° angle. All plant species, rocks, litter and bare soil touching the rod were recorded. We calculated cover estimates as the proportion of points intercepted per transect. The same measurements were taken in the matrix plots, using as the sampling transect the segment linking the centre of two opposite sides of the plot (matrix transect).

We tested the effects of outcrop size (area, perimeter and length of the outcrop axis); cover of rocks, plants, trees, shrubs, herbs, bare soil and litter; and height of trees, shrubs and herbs on the outcrop taxonomical diversity (richness, Simpson and Shannon indices) and functional diversity (functional group cover). This was done by performing Linear (LM) and Generalized Linear Mixed models (GLMMs) (van Oijen, 2010). Multicollinearity among potential explanatory variables was handled by dropping collinear covariates when correlated at $|\text{Spearman } r| > 0.8$ (Zuur et al., 2010). We modelled outcrop size, cover and height variables as fixed effects and farmsteads as a random effect to control for their potential variability using the restricted maximum likelihood method. To compare the fits of LM and GLMM models, we performed ANOVAs with the regression objects as two separate arguments. These analyses were performed using *nlme* (v 3.1-149; Pinheiro et al., 2021) and *lme4* (v1.1-26; Bates et al., 2015) packages. When necessary, data were transformed for normality and beta regression was performed using R package *glmmADMB* (v0.8.3.3.; Skaug et al., 2013), and package *glmmTMB* (v1.0.2.1; Brooks et al., 2017) when the dependent variables were beta-distributed. In addition, when the dependent variable assumed the extremes 0 and 1, the transformation $(y \times (n - 1) + 0.5)/n$ where n is the sample size, was performed to allow the application of beta-regression analyses (Smithson & Verkuilen, 2006). Marginal and conditional coefficients of determination for the models were calculated using the package *MuMIn* (v1.43.17; Barton, 2020) and the fit for each model was validated using *DHARMa* (v0.4.4; Hartig, 2020). We then characterized the relationship between the cover of the functional groups and the length of both the outcrop axis and the matrix transect using Generalized Additive Models (GAMs; van Oijen, 2020) from the *mgcv* software package (v1.8-33; Wood, 2006). "DHARMa" was also used to validate GAM models.

Finally, we studied the effect of spatial distance among sites on existing plant communities. To do this, we performed Mantel tests considering the geographic distances and species cover matrix to determine if plant communities were spatially structured, using the "ecodist" package (Goslee & Urban, 2007).

All statistical analyses were performed using the computing environment R version 4.0.3 (R Core Team, R Foundation for Statistical Computing, Vienna, AT) (R Core Team, 2021).

3 | RESULTS

3.1 | Comparative analyses

From the 64 characterized plots, we sampled a total of 205 species: 63 exclusively in outcrops, 53 in wood-pastures and 89 occurring in both plot types (Appendix S3, Table S1). For each species, the values of the 10 selected traits were compiled (Appendix S2, Table S2). Overall β-diversity between wood-pasture matrices and outcrops was 0.398, clearly dominating the turnover component (0.375) over nestedness (0.023).

Pair-wise Wilcoxon tests indicated that plant richness was not significantly different between outcrop and wood-pasture plots (Table 1). The same tests comparing the species number regarding life form found significant differences among the number of herbaceous species, shrubs, climbers and trees occurring in outcrops and wood-pastures. Regarding the abundance of tree species for both communities, pair-wise Wilcoxon tests indicated significant differences between outcrops and matrix for holm oak cover for tree (and shrubby) stages. Moreover, olive trees (*Olea europaea*), in adult or shrubby stages, occur only in outcrops. Similarly, kermes oak (*Quercus coccifera*) occurs only in tree form within the outcrops. No differences between outcrops and matrix were found regarding cork oak cover stages. Only a shrubby cork oak individual was registered in a wood-pasture plot, probably indicating cork oak regeneration limitations.

IndVal analyses identified 9 and 14 species with indicator values higher than 0.7 for outcrops and wood-pastures, respectively (Appendix S4). Outcrop species with the highest IndVal values were *Geranium robertianum* and *Umbilicus rupestris* (0.968 and 0.867, respectively), two rupicolous species (SPBotanica, 2013). However, typical ancient oak woodland species such as holm oak (0.769) and shrubs (0.791 for both *Ruscus aculeatus* and *Rhamnus alaternus*) also had high IndVal values. Regarding the matrix species with high IndVal values, all were herbaceous species, characteristic of grazing pastures such as *Agrostis pourretii* and *Echium plantagineum* (0.975 and 0.916, respectively).

TABLE 1 Pair-wise Wilcoxon test summary on the differences between outcrops and wood-pastures for variables and indices regarding species and functional diversities.

	Outcrops	Wood-pastures	Pair-wise Wilcoxon tests		
	Mean (*SD*)	Mean (*SD*)	Statistic	*n*	*p*-Value
Species diversity					
Richness	26.25 (7.49)	28.59 (9.00)	322	32	ns
Herbaceous richness	19.94 (8.68)	27.81 (6.85)	424	32	0.003
Shrubs richness	3.62 (1.66)	0.37 (0.87)	0	32	7.33×10^{-7}
Climbers richness	1.15 (1.08)	0 (0)	0	32	8.09×10^{-6}
Trees richness	1.5 (0.88)	0.4 (0.61)	19	32	2.32×10^{-5}
Holm oak cover – tree (%)	12.98 (21.26)	1.01 (2.76)	5.5	32	4.62×10^{-4}
Holm oak cover – shrub (%)	2.75 (10.96)	0.47 (2.65)	16	32	0.02
Olive tree cover – tree (%)	19.14 (28.57)	0 (0)	0	32	6.81×10^{-4}
Olive tree cover – shrub (%)	0.7 (2.71)	0 (0)	0	32	ns
Kermes oak cover - tree (%)	4.84 (16.81)	0 (0)	0	32	ns
Cork oak cover – tree (%)	5.94 (18.49)	2.97 (11.47)	15	32	ns
Cork oak cover – shrub (%)	0 (0)	0.003 (0.018)	1	32	ns
Functional diversity					
Functional richness	0.08 (0.02)	0.05 (0.02)	97	32	0.001
Functional evenness	0.55 (0.08)	0.48 (0.08)	105	32	0.002
Functional divergence	0.90 (0.10)	0.81 (0.13)	120	32	0.006
Rao's quadratic entropy	0.064 (0.03)	0.046 (0.02)	140	32	0.019
Functional dissimilarity	0.20 (0.08)	0.19 (0.07)	208	32	ns
Sensitive species	78.54 (35.46)	7.31 (18.36)	5	32	1.34×10^{-6}
Grazing-tolerant herbs	5.42 (7.09)	85.71 (40.89)	528	32	4.66×10^{-10}
Weedy herbs	8.98 (11.47)	46.57 (54.10)	455	32	1.62×10^{-4}

Abbreviation: ns, not significant.

The two-dimensional NMS ordination based on the plant species cover data, with final stress of 21.84% (Figure 3), described the main differences in vegetation composition. The first axis accounts for the most variance (28.15% of 39.21%), and clearly separates the communities occurring in outcrops and the wood-pasture matrix. Correlation analyses show that the main characteristics separating outcrops and wood-pasture matrix were herb cover, tree maximum height and rock cover ($r^2 = 0.89$, 0.83, and 0.73, $p < 0.001$, respectively), followed by tree cover and the height of shrubs and rocks ($r^2 = 0.60$, 0.56 and 0.55, $p < 0.001$, respectively) and, to a lesser extent, the height of herbs and bare soil cover soil ($r^2 = 0.45$ and 0.26, $p < 0.001$, respectively) (Appendix S5).

Regarding functional diversity, the average of functional richness, functional evenness, functional divergence and Rao's quadratic entropy were significantly higher in outcrops than in the matrix, whereas functional dissimilarity presented no significant differences between the two communities (Table 1). Trait analyses clearly identified combinations of traits linked to one of the communities, namely annual and grazing-tolerant herbaceous species for the wood-pasture matrix, and rupicolous and sciophilous woody species for outcrops. It also defined three large functional groups: (a) species with low tolerance towards environmental stress and perturbation (sensitive species), including woody, rupicolous and sciophilous species; and two perturbation- and stress-tolerant species groups, namely (b) grazing-tolerant herbs and (c) weedy herbs. The three functional groups had significant dissimilar cover in outcrops and wood-pastures (Table 1; Figure 3).

3.2 | Outcrop characteristics' effect

Outcrop area ranged from 75 to 5000 m² (969.9 m² on average), perimeter from 40 to 300 m (135 m on average) and outcrop axis (outcrop edge to centre distance) from 2.5 to 10 m, with most axes between 4.5 and 5 m (4.8 m on average). A total of 94 plant species were registered in the 51 outcrops using the point-intercept method (Appendix S3, Table S2).

LM and GLMMs identified a positive relationship of plant richness with the length of outcrop axes and with their overall plant cover (Table 2). Likewise, we found an increasing trend of taxonomical diversity associated with rock cover. However, rock cover was also related to lower plant cover. In addition, outcrops with higher tree cover showed higher levels of uniformity (i.e. higher Simpson's diversity index values). Regarding functional diversity, sensitive species beneficiated from the presence of higher rocks, whereas weedy

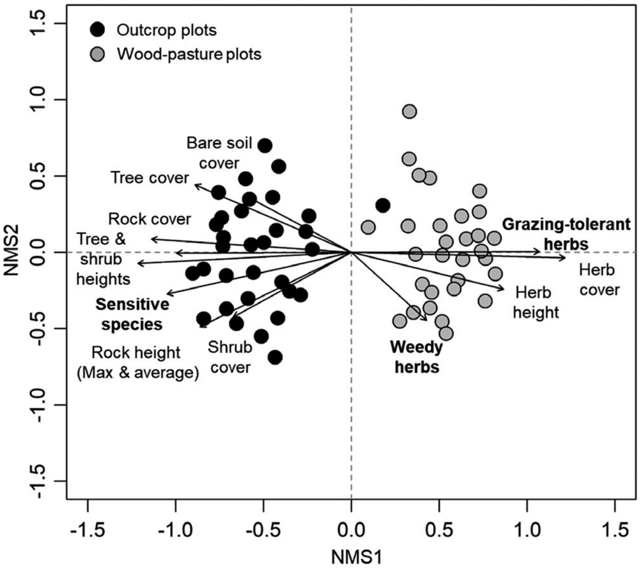

FIGURE 3 Axes 1 and 2 of the two-dimensional NMS of study plots based on plant species cover (final stress 21.84%). Vectors represent significant correlations between species composition and (i) the environmental characteristics separating outcrop and matrix communities, and (ii) the plant functional groups identified (in bold)

and grazing-tolerant herbs respond negatively to them. Finally, differences among farmsteads were only verified for the overall plant cover and weedy herb cover (Table 3).

GAMs characterized the relationships of the functional groups cover with the length of the outcrop axis (Figure 4a), identifying a sharp gradient from the margins of the outcrop to the centre for grazing-tolerant and weedy herbs, whereas sensitive species showed a slight increase to roughly the middle of the outcrop axis. Moreover, only sensitive species, the dominant functional group in the outcrops, were present in the centre of the outcrop. As expected, GAMs did not identify significant variations in sensitive species and grazing-tolerant herb distributions along the matrix axis but, surprisingly, weedy herbs decreased slightly at the end of the transect (Figure 4b). Furthermore, sensitive species cover was very low (8% on average), whereas grazing-tolerant herb cover (105% on average) and weedy herbs (67% on average) dominated the system.

Mantel test analyses indicated a low but significant spatial autocorrelation among the plant communities at a taxonomical level. These similarities were higher among wood-pasture plots ($r = 0.27$, $p < 0.001$) than among outcrops ($r = 0.15$, $p < 0.001$).

4 | DISCUSSION

According to our results, small rocky outcrops in wood-pastures remarkably impact *Montados* by greatly increasing their overall plant richness and plant functional biodiversity. Overall plant richness, i.e. γ-diversity, in *Montados* is deeply affected by the presence of outcrops: ca. 30.7% of the sampled species were recorded exclusively in outcrops, whereas 25.85% occurred only in the surrounding matrix. Both communities had significant differences regarding the cover of dominant life forms. As expected, herbaceous species dominate the wood-pasture matrix, whereas trees, shrubs and climbers play an essential role in the outcrop plant community. In addition, olive trees and kermes oaks occur only in the outcrops, and the holm oak cover is also significantly higher in the outcrops. However, we found no significant differences in the cover of adult cork oaks.

The main factor shaping the differences between both communities was the presence of rocks; in fact, most of the indicator species of the outcrop were rupicolous or tolerant to rocky habitats. While preventing mechanical clearing and limiting grazing, rocks allow the growth of well-developed shrubs and trees. Moreover, these formations determine the development of a vegetation gradient, from the outcrop margin to the centre, ultimately intensifying the dissimilarities between both communities. Sensitive species, including rupicolous, sciophilous and oak woodland species, dominate the outcrop communities, whereas matrix communities are composed mostly of grazing-tolerant and weedy herbs. Among the functional indices, the significantly higher functional dissimilarity in outcrops points to a more functionally diverse community with a higher niche differentiation and lower competition between species (Morcillo et al., 2019). It is precisely this contrast between both communities that points to outcrops as a critical factor in maintaining high diversity levels in this managed habitat. Outcrops provide microhabitats and harbour species not found in the surrounding vegetation matrix. Therefore, outcrops constitute local refugia for light- and heat-intolerant plants and other organisms such as lichens and beetles (Oksuz, 2020). The structural complexity of outcrops influences the number and types of species and this variation clearly has a profound impact on the provision of ecosystem services (Plas, 2019), including refuges for small and big game species (Pia et al., 2013), food provision for birds, mammals and reptiles (Ferger et al., 2014) and cultural services (Barroso et al., 2012).

Analysing the distribution and cover of the functional groups along the outcrop axis allows us to understand how these formations affect plant wood-pasture diversity. In wood-pastures, distribution of the functional group is reasonably homogenous; however, it follows a spatial gradient from the margins to the centre in the outcrops. Two drivers appear to shape plant distribution inside the outcrops: light availability and disturbance. On the one hand, shrubs and trees limit the amount of light inside the outcrops, enabling colonization by sciophilous species and preventing the occurrence of light-tolerant species. On the other hand, outcrops constitute grazing and farming refuges (Milchunas & Noy-Meir, 2002), protecting species without grazing avoidance or disturbance-tolerance traits.

Furthermore, outcrop buffering capacity towards environmental changes (Ottaviani et al., 2019) and their widespread distribution throughout the wood-pastures of the study area, make them potential "stepping-stone" systems. This is corroborated by the low levels of autocorrelation found among outcrops, confirming

TABLE 2 GLMM results testing the influence of outcrop size, cover and height of vegetation and rocks, and the farmsteads (random effect) on the outcrop species and functional diversities

	Estimate	*SE*	*t*-Value	*p*-Value	R^2_m	*n*
log (Plant richness)						
Intercept	0.921	0.204	4.508	0.000	0.37	51
Length of the outcrop axis	0.061	0.028	2.198	0.033		
Plant cover	0.004	0.001	5.041	0.000		
Sqrt (Shannon index)						
(Intercept)	1.255	0.054	23.441	0	0.22	51
Rock cover	0.001	0.000	2.025	0.050		
Herb cover	−0.002	0.001	−2.969	0.005		
Simpson index						
(Intercept)	0.379	0.049	7.772	<0.001	0.18	51
Tree cover	0.001	0.000	2.137	0.038		
Plant cover	−0.001	0.000	−2.985	0.004		
Plant cover						
(Intercept)	204.271	9.907	20.618	<0.001	0.29	51
Rock cover	−0.984	0.240	−4.095	0.000		
Bare soil	−1.348	0.514	−2.621	0.012		
Sensitive species cover						
(Intercept)	91.636	11.733	7.810	0	0.11	51
Rock height	18.088	7.414	2.440	0.019		
Grazing-tolerant herb cover						
(Intercept)	−1.897	0.486	−3.900	0.000	0.57	51
Richness	0.196	0.051	3.850	0.000		
Maximum rock height	−0.504	0.164	−3.080	0.002		
Weedy herb cover						
(Intercept)	11.873	6.838	1.736	0.089	0.49	51
Rock height	−8.208	3.210	−2.558	0.014		
Herb cover	0.387	0.067	5.739	0.000		

Note: Values correspond to the estimate, *SE*, *t*-value, *p*-value and the marginal coefficient of determination (R^2_m) returned by the models and the sample size (*n*). Sqrt, Square root.

that dispersal ability is not a limiting factor in the assembly mechanisms of plant communities in the studied outcrops. These systems also lead to the establishment of source–sink dynamics between outcrops and wood-pastures because they foster the persistence and, when disturbance intensity lowers, the migration of species with different levels of tolerance to disturbance (Ron et al., 2018). Likewise, by increasing the connectivity in the matrix of these agroforestry systems, outcrops promote recolonization and greater abundances of local populations through immigration, for example for birds (Renjifo, 2001). This also stands for other taxa such as reptiles, lichens and beetles (Martín & Lopez, 2002; Oksuz, 2020).

Similarly to Milchunas and Noy-Meir (2002), we did not find a significant effect of the full outcrop extent and perimeter on the plant diversity of these geological formations. Milchunas and Noy-Meir found that 86% of small refuge studies reported positive effects on plant diversity compared with 50% for larger refuges. However, we found a clear spatial-dependent effect; taxonomical and functional

TABLE 3 Influence of farmsteads (random effect) on plant cover and taxonomical and functional diversities of outcrops as described by the models' log-likelihood ratio test

	log-Lik	*p*-Value	*n*	R^2_c
Log (Plant richness)	−16.819	0.513	51	
Sqrt (Shannon index)	18.14	0.315	51	
Simpson index	33.029	0.385	51	
Plant cover	−250.930	**0.003**	51	**0.61**
Sensitive species cover	−254.434	0.225	51	
Grazing-tolerant herb cover	45.366	0.902	51	
Weedy herb cover	−217.2243	**0.039**	51	**0.64**

Note: Values correspond to the log-likelihood value (log-Lik), *p*-value and sampling size (*n*). Values in bold indicate $p < 0.05$. When the impact of farmsteads was significant, the conditional coefficient of determination (R^2_c) returned by the models was calculated.

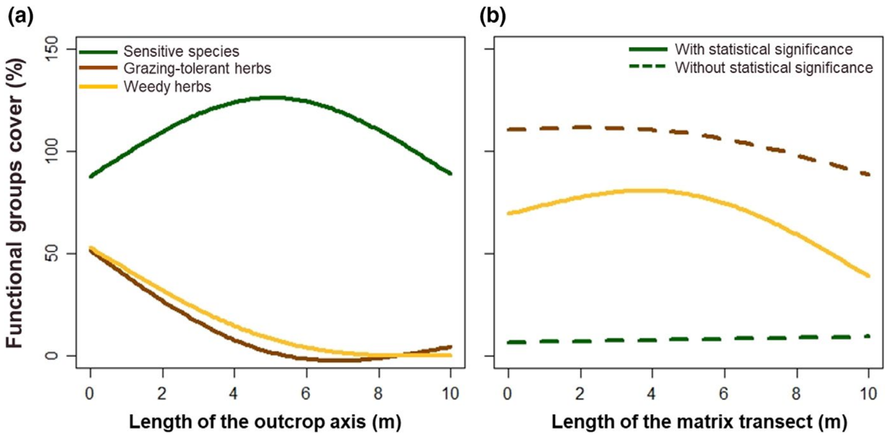

FIGURE 4 Relationships between (a) outcrop axis length (from edge to centre) and (b) matrix transect length and the cover of functional groups, namely i) sensitive species and ii) grazing-tolerant and iii) weedy herbs. Lines represent the main trend of a GAM. (a) Percentage of variance explained by the models: 59.4%***, 80.3%***and 97.6%***, respectively. Effective degrees of freedom (k): 1.96, 1.95 and 1.98, respectively. (b) Percentage of variance explained: 63.5%***. Effective degrees of freedom (k) : 1.93. *** $p < 0.001$

plant diversity varied significantly from the margin to the centre of the outcrops. These results point to an "edge effect" along the length of the outcrop axis. This buffer area constitutes an ecotone between the matrix and the outcrops with a high ecological value, not only for plants, as our results show, but also for animals which require these boundaries to fulfil their requirements (Leal et al., 2011).

Regarding the impact of the farmsteads on outcrop diversity, this was verified only for overall plant and weedy herb cover, probably resulting from the owners' different management practices, such as shrub cutting and grazing intensities. Moreover, the higher spatial autocorrelation found in the wood-pastures suggests that these communities respond similarly to the management strategies of the different farmsteads. However, our data did not allow us to test this hypothesis, and more studies are needed to explore and understand this topic.

To summarize, our results indicate that even small rocky outcrops have a strong effect on overall (γ) plant and functional diversities in evergreen oak wood-pastures, in line with authors supporting the importance of small habitat patches for biodiversity (Deane et al., 2020; Fahrig, 2020; Wintle et al., 2019). This effect is particularly relevant because the Portuguese government classified these agroforestry systems as being of high priority for biodiversity conservation. We propose that minor changes in management practices, such as the protection of small rocky outcrops or shrub patches, may notably impact the biodiversity of agroforestry landscapes. Therefore, preserving, enlarging and reshaping pre-existing outcrops or creating “artificial” outcrops where rocks are naturally available, may represent a valuable biodiversity-friendly agroforestry practice (i.e. a NbS), because they contribute to increasing heterogeneity in agroforestry systems without significant impacts on the economic activity of oak wood-pastures. Moreover, it is imperative to plan for protected area networks that promote local environmental heterogeneity, including the protection of rocky outcrops as refugia for mesic-adapted species and as potential stepping stones that allow the dispersal of these species between adjacent environments. In addition, under projected climate-change scenarios, rocky outcrops may provide micro-climatically diverse habitats, distinct from those of the surrounding vegetation matrix, serving as climatic refugia and thereby facilitating the persistence of specialist species. Finally, instead of adopting high-cost–low-return strategies, it would be important for landowners and decision-makers to include rocky outcrop preservation in the land management planning of *Montados*, because they constitute a cost-effective element for the promotion of biodiversity in this agroforestry system.

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AUTHOR CONTRIBUTIONS

All authors conceived the idea, discussed the results and commented on the manuscript. SC analysed the data, produced the figures and led the writing. ST designed and conducted fieldwork, and identified the species. CA made substantial contributions to the writing.

DATA AVAILABILITY STATEMENT

Primary data are presented as Supporting information.

ORCID

Sergio Chozas https://orcid.org/0000-0001-6741-1259
Susana Tapia https://orcid.org/0000-0002-6645-8159
Jorge Palmeirim https://orcid.org/0000-0003-4734-8162
Carla Alegria https://orcid.org/0000-0002-9461-4569
Otília Correia https://orcid.org/0000-0002-1053-0561

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SUPPORTING INFORMATION

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

Appendix S1. Plot characteristics

Appendix S2. Plant trait data

Appendix S3. Primary data

Appendix S4. Indicator values

Appendix S5. Squared correlation coefficient of environmental factors and functional groups

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