



## Response of soil carbon and plant diversity to grazing and precipitation in High Nature Value farmlands

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### ABSTRACT

Mediterranean oak-dominated agro-silvo-pastoral systems of southwestern Europe (called *montado* in Portugal and *dehesa* in Spain) are semi-natural, savannah-style High Nature Value farmlands (HNVfs) shaped by centuries of anthropogenic (e.g., cultivation, grazing) and natural (e.g., drought) disturbances. Therefore, changes in grazing and precipitation may alter their vegetation composition and ecosystem properties and impact upon their long-term viability. We quantified the responses of soil organic carbon (SOC) and plant taxonomic and functional trait diversities to cattle grazing and inter-annual changes in precipitation across three open-woodland sites within the *montado* landscape in Alentejo, southern Portugal. The sites are characterised by the presence or absence of cattle grazing and different amounts of mean annual precipitation (ranging from semiarid to dry subhumid). Three different precipitation periods were used: a shorter autumn-to-spring period and longer 12- and 18-month periods before sampling. Specific leaf area, plant height and seed mass were used to estimate single-trait community weighted means and a multi-trait measure of community functional diversity (Rao's Q). SOC and plant species richness responded negatively to the presence of cattle grazing but positively to increase in precipitation (and its interaction with cattle grazing), while trait-based measures were largely unresponsive to cattle grazing and precipitation (though RLQ analysis revealed strong controls of the environmental variables on plant life cycle, growth form, leaf phenology and dispersal strategies). SOC was most responsive to longer-term (18-month) changes in precipitation, whereas plant species richness was most responsive to shorter-term (autumn-to-spring) changes in precipitation. These results suggest that different components of plant diversity respond differently to external drivers in *montado* HNVfs, while the response time of soil properties may be longer than that of plant taxonomic diversity.

### 1. Introduction

Open oak-dominated Mediterranean woodlands (referred to as *montado* in Portugal and *dehesa* in Spain) are multifunctional semi-natural agro-silvo-pastoral systems occurring over c. 3.5 million ha in the southwest region of the Iberian Peninsula (Pinto-Correia et al., 2011; Ferraz-de-Oliveira et al., 2016). Classified as High Nature Value farmlands (HNVfs), they form a dominant ecosystem in the Alentejo region in southern Portugal (Fig. 1A) and consist of cork oak (*Quercus suber*), holm

oak (*Quercus ilex* subsp. *rotundifolia*) and mixed-oak savannah landscapes associated with cork and food production and a variety of grazing practices. Managed for centuries, they have resulted in novel biocultural landscapes in which climate, land management (e.g., grazing) and the resident flora interact to provide multiple ecosystem services, including supporting biodiversity and regulating soil carbon storage (Batista et al., 2017; Pinto-Correia et al., 2018). The provision of these services is modulated by the relationships between biodiversity and various ecosystem functions (Cardinale et al., 2012; Tilman et al., 2014)

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underpinned by complex interactions between plant functional traits (PFTs) and ecosystem processes at the community level (Lavorel and Grigulis, 2012; Violle et al., 2012; Garnier et al., 2015).

Soil and vegetation properties of terrestrial ecosystems, including the *montado*, are known to respond in a myriad of ways to grazing (van de Koppel et al., 1997) and precipitation (Li et al., 2022). For instance, plant functional and taxonomic diversities may vary independently of each other in response to grazing (Köbel et al., 2021) and the interaction between grazing and precipitation (De Bello et al., 2006), with outcomes highly dependent on local environmental constraints (Chillo et al., 2017) and type of ecosystem (Plexida et al., 2018; Carvalho et al., 2020), as well as on climatic and historical contexts (Díaz et al., 2007). Indeed, the effects of grazing and precipitation on biodiversity and ecosystem properties can vary from positive to negative depending on local conditions (Li et al., 2018; Maestre et al., 2022). Importantly though, the introduction of grazing is generally known to favour certain life strategies and result in changes to plant functional composition in a variety of ecosystems globally (Díaz et al., 2007), including the *montado* (Castro et al., 2010), where grazing has been a common land management practice for centuries (see below).

Recent studies in the *montado* have indeed suggested that grazing exclusion can enhance structural (height) and taxonomic diversities (Listopad et al., 2018) and favour shrub and tree regeneration (Köbel et al., 2021), as well as lead to changes in plant traits at the community level (Bugalho et al., 2011). In addition, grazing has been shown to have a positive effect on plant functional trait diversity in transitional semi-arid Mediterranean systems, despite their lower taxonomic diversity attributed to reduced precipitation compared to more humid locations in the Iberian Peninsula (De Bello et al., 2006). In turn, these changes in

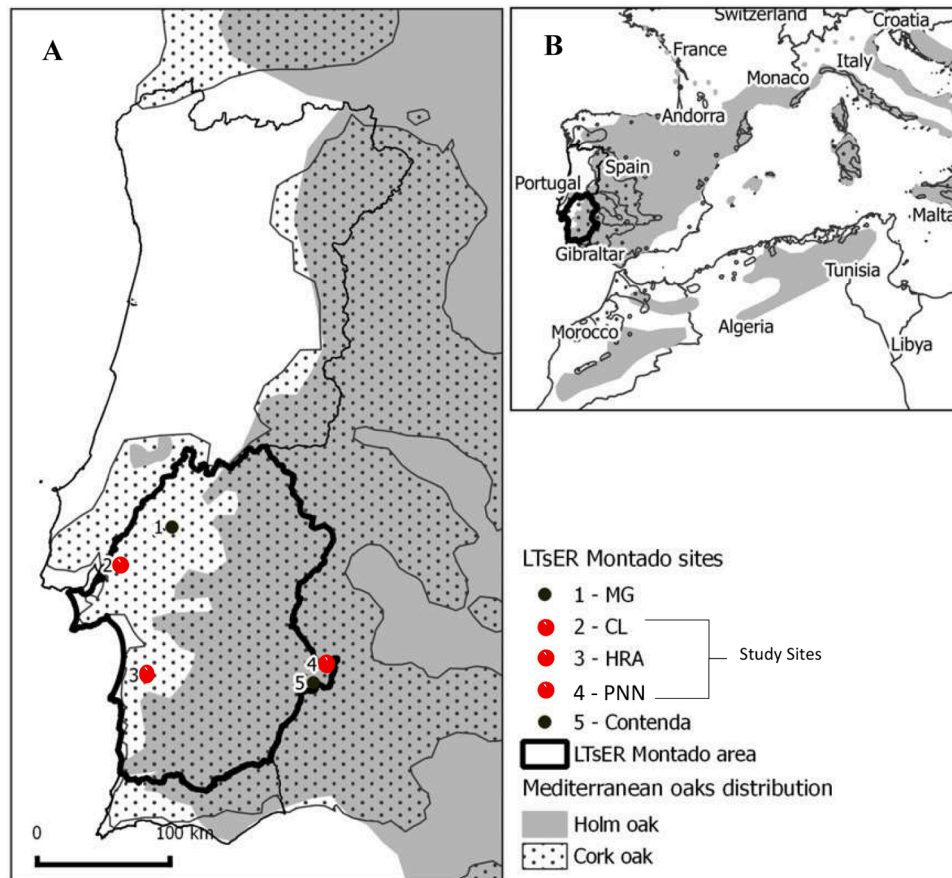
the functional trait composition of plant communities can lead to changes in soil processes (e.g., litter decomposition rates) and thus affect nutrient cycling and soil organic carbon (SOC) stocks (Castro et al., 2010), though the response of SOC to external drivers can also be highly variable and context-dependent (Zdruli et al., 2004).

The aim of this study was to assess whether functional and taxonomic plant diversities and SOC (as proxies of ecosystem services) respond to the presence of cattle grazing and to inter-annual changes in precipitation in the *montado*, an HNVf in southern Portugal. The objectives were to 1) collect vegetation and soil data from three sites within the LTsER *montado* platform in southern Portugal subject to different amounts of mean annual precipitation (and under considerable annual variability), 2) source precipitation data comprising three different periods immediately before sampling (autumn-to-spring, 12-month and 18-month periods) from nearby weather stations, and 3) determine how plant diversity and SOC are associated with cattle grazing and precipitation in the *montado* by fitting linear and multivariate models to the data after estimating plant species richness and abundance-dependent measures of single- and multi-trait functional diversity.

## 2. Materials and methods

### 2.1. Study sites

The LTsER *montado* platform in Portugal (<http://www.ltsermontado.pt/>) covers a wide range of environmental and socio-economic conditions representing different land management practices, degrees of pressure and levels of precipitation within oak-dominated open woodlands. It is currently comprised of five main research and monitoring



**Fig. 1.** Locations of the three sites chosen for this study (red dots in panel A) within the wider LTsER *montado* platform in Portugal (panel B). CL = *Companhia das Lezírias*, HRA = *Herdade da Ribeira Abaixo*, PNN = *Herdade da Coitadinha*. Black dots 1 and 5 in panel A are two additional *montado* sites within the LTsER platform not included in this study. MG = *Herdade da Machuqueira do Grou*, Contenda = *Herdade da Contenda*.

stations, including the three sites chosen for this study (Fig. 1 and Table 1) based on their historical and current land management characteristics. All information presented below was extracted from the LTsER *montado* platform in DEIMS (<https://deims.org/ecfcc7e2-82e5-4ec1-adee-a3f9f815fc0d>) or obtained directly from site managers.

Companhia das Lezírias (CL) (38.83760, -8.81871) (<https://deims.org/ef87d551-9bae-467f-9c5d-b538b8206b0b>) covers 17,952 ha of relatively flat topography and low altitudes that range between 1 and 53 m above sea level. The site is under a transitional subhumid-semiarid climate (Table 1) and has been managed as an agro-silvo-pastoral system for over 100 years. *Quercus suber* (cork oak) is the dominant tree species (68 mature trees per hectare on average). Current cattle grazing stocks average 0.47 animal units per hectare, though some land within the site is left ungrazed. Cork is produced on a nine-year cycle with a mean production rate of 986 kg ha<sup>-1</sup>. Today, 78% of the forested land (6751 ha) is dedicated to *Q. suber* woodlands, while 1900 ha are occupied by *Pinus* spp. and *Eucalyptus* spp. stands, arable land and pastures (Rui Alves, 2019, personal communication). Composed mainly of regosols and podzols, there is tree decline on the latter soils and heterogeneous tree regeneration across the site due to grazing and clearing of the shrub layer, which is currently being combined with fencing to promote natural regeneration.

Herdade da Ribeira Abaixo (HRA) (38.10690, -8.57045) (<https://deims.org/c887da3c-776c-4b42-a5be-7dd69c26f27b>) covers 221 ha and ranges in altitude from 150 to 240 m above sea level with a subhumid and mesothermic climate (Table 1). The main soil type is a skeletal lithosol and the dominant tree is *Q. suber*, with 43 mature trees per hectare on average. In general, north facing slopes present oak woodlands with a dense shrub-dominated understory, while south facing slopes maintain more open woodlands with mixed patches of shrubs and grasslands. The site was managed for cork production until the 1940s (harvested on a nine-year cycle and producing 450 kg ha<sup>-1</sup> on average) but is now owned and managed by the Faculty of Sciences at the University of Lisbon for research and conservation. The site has historically experienced cattle grazing but has been under low intensity sheep grazing (0.1 animal units per hectare) since 1998, with large tracts left ungrazed. Heterogeneous clearing of the shrub layer occurs on a four- to five-year cycle.

Herdade da Coitadinha (PNN) (38.17550, -7.03960) (<https://deims.org/e30b32bd-da6f-4adc-a40c-a92769340907>) covers 1000 ha of hilly

topography bounded by the Ardila river and Murtega stream. The altitude ranges between 150 and 300 m above sea level and the climate is meso-Mediterranean and semi-arid (Table 1). Most soils are eutric lithosols derived from schist and the dominant tree is *Q. ilex* subsp. *rotundifolia*. The site was managed as a self-sufficient farm from the 1800s to 1976 and extensively grazed by goat, sheep, cattle and Iberian black pigs. Cereal cultivation (wheat and barley) and livestock densities were intensified between 1976 and 1990 but declined afterwards. Presently, it is managed as a biodiversity offset to the Alqueva dam and facilitates winter fattening of black pigs, hunting and tourism, but also includes cattle grazing at a stocking density of 0.5 animal units per hectare. The *Q. ilex* woodlands are managed to promote natural regeneration, abundant acorn production and maintain tree health.

## 2.2. Vegetation data

Fifteen plots were sampled across the three sites (five in each site) over a one-week period in April 2019 within modified 1000-m<sup>2</sup> Whitaker plots (Stohlgren et al., 1995). This involved establishing 20 m x 50 m rectangular plots and dividing them into three equal subplots, within which 20 m diagonal transects were established for vegetation surveying using the line-point intercept method (Herrick et al., 2005). A plumb bob was lowered at 50 cm intervals along the 20-m transect line (starting at 0) and species were recorded on a 'first hit' basis (i.e., all species hit were recorded once every 50 cm), resulting in 41 sampling points along the transect. Bare soil, litter or moss cover were recorded if no species were hit at a given sampling point. Plot-level vegetation cover was estimated by discounting the percentage of bare soil, plant litter and moss cover recorded along each transect. A total of 149 plant species were recorded between the three sites [54 at CL (36.2%); 87 at HRA (58.4%), and 83 at PNN (55.7%)]. Of these, full trait data (see Section 2.5 below) were available for 102 (68.5%) plant species [37 for CL (68.5% of total number of species recorded at CL); 57 for HRA (65.5%) and 55 for PNN (66.3%)].

Plant trait data were derived from bibliographic sources (Nunes et al., 2017) and further complemented with data from the BROT (Paula et al., 2009; Tavşanoğlu and Pausas, 2018) and LEDA (Kleyer et al., 2008) trait databases. The traits assessed were plant height, specific leaf area (SLA), seed mass, life cycle, growth form, leaf phenology and dispersal strategy. These traits were chosen since they are closely related

**Table 1**

Climate, management and vegetation characteristics of the three sites sampled within the *montado* platform in Portugal. 'Grazed' refers to cattle grazing. Climatic data extracted from *WorldClim 2.1* (2.5 minutes resolution; <https://www.worldclim.org/data/worldclim21.html>; Fick and Hijmans, 2017).

Site	Climate	Plot code	Dominant canopy	Grazing category	Main plant species
Companhia das Lezírias (CL)	Transitional subhumid-semiarid • Mean annual temp. 16.7°C • Mean annual rainfall 691 mm	CLS2	<i>Quercus suber</i>	Ungrazed	<i>Cistus salvifolius</i> , <i>Cistus crispus</i> , <i>Daphne gnidium</i>
		CLS4	<i>Quercus suber</i>	Ungrazed	<i>Lolium rigidum</i> , <i>Myrtus communis</i> , <i>Cistus salvifolius</i> , <i>Briza minor</i>
		CLS5	<i>Quercus suber</i>	Grazed	<i>Anthoxanthum aristatum</i> , <i>Briza maxima</i> , <i>Tuberaria guttata</i> , <i>Tolpis barbata</i>
		CLS7	<i>Quercus suber</i>	Grazed	<i>Briza maxima</i> , <i>Rumex acetosella</i> , <i>Daphne gnidium</i> , <i>Avena barbata</i>
Herdade da Ribeira Abaixo (HRA)	Subhumid & mesothermic • Mean annual temp. 15.9°C • Mean annual rainfall 636 mm	CLS10	<i>Quercus suber</i>	Grazed	<i>Hordeum murinum</i> , <i>Bromus diandus</i> , <i>Malva sylvestris</i> , <i>Rumex pulcher</i>
		HRAA1	<i>Quercus ilex</i>	Ungrazed	<i>Dactylis glomerata</i> , <i>Bromus madritensis</i> , <i>Vicia sativa</i> , <i>Plantago lanceolata</i>
		HRAS1	<i>Quercus suber</i>	Ungrazed	<i>Bromus madritensis</i> , <i>Rubus ulmifolius</i> , <i>Cistus salvifolius</i> , <i>Aristolochia longa</i> , <i>Geranium robertianum</i>
		HRAS3	<i>Quercus suber</i>	Ungrazed	<i>Cistus salvifolius</i> , <i>Bromus madritensis</i> , <i>Dactylis glomerata</i> , <i>Lavandula stoechas</i>
		HRAS4	<i>Quercus suber</i>	Ungrazed	<i>Arbutus unedo</i> , <i>Molinieriella laevis</i> , <i>Cistus salvifolius</i> , <i>Carex panicea</i> , <i>Lavandula stoechas</i>
Herdade da Coitadinha (PNN)	Meso-Mediterranean & semi-arid • Mean annual temp. 16.4°C • Mean annual rainfall 545 mm	HRAS9	<i>Quercus suber</i>	Ungrazed	<i>Dactylis glomerata</i> , <i>Cistus salvifolius</i> , <i>Lavandula stoechas</i> , <i>Geranium robertianum</i>
		PNNA2	<i>Quercus ilex</i>	Grazed	<i>Brachypodium distachyon</i> , <i>Hordeum murinum</i> , <i>Raphanus raphanistrum</i> , <i>Trifolium subterraneanum</i> , <i>Crepis vesicaria</i>
		PNNA5	<i>Quercus ilex</i>	Grazed	<i>Lolium rigidum</i> , <i>Tolpis barbata</i> , <i>Chamaemelum mixtum</i> , <i>Glebionis segetum</i>
		PNNA7	<i>Quercus ilex</i>	Grazed	<i>Cistus ladanifer</i> , <i>Brachypodium distachyon</i> , <i>Cistus abidus</i> , <i>Troilus arvensis</i>
		PNNS1	<i>Quercus suber</i>	Grazed	<i>Cistus salvifolius</i> , <i>Lavandula stoechas</i> , <i>Brachypodium distachyon</i> , <i>Vicia pubescens</i>
PNNS2	<i>Quercus suber</i>	Grazed	<i>Cistus salvifolius</i> , <i>Brachypodium distachyon</i> , <i>Lavandula stoechas</i> , <i>Cistus ladanifer</i>		

to resource acquisition strategy and dispersal ability and commonly influenced by land management and climate (Castro et al., 2010; Pérez-Harguindeguy et al., 2013; Nunes et al., 2017). Since grazing is thought to be one of the most important drivers of plant trait diversity (Carmona et al., 2012), each sampling plot was assigned to one of two grazing categories: cattle grazed or ungrazed (Table 1) based on records provided by site managers.

### 2.3. Soil data

Soil sampling took place during a one-week period in September 2018 within the same sampling plots used for the vegetation surveys. Four samples of 0–10 cm depths were randomly collected from each subplot using a standard steel soil corer and later homogenised in the lab to form a composite sample for each subplot. A separate sample (0–20 cm depth) was randomly collected at the plot level for bulk density measurements.

Soil samples were ground using a ceramic mortar and pestle and sieved through a 2 mm stainless-steel sieve. Soil pH was measured in 1:2.5 (w/v) soil-water suspension using a pre-calibrated pH probe. Soil bulk density ( $\text{g cm}^{-3}$ ) was estimated by dividing the dried sample mass ( $110^\circ\text{C}$  for 24 hours) by its volume (0–20 cm samples only). Soil organic matter (SOM) was determined via loss-on-ignition (LOI) after oven-drying samples at  $105^\circ\text{C}$  for 24 hours and igniting them at  $500^\circ\text{C}$  for four hours (Jensen et al., 2018). SOM (%) was converted to SOC (%) using Jensen's et al. (2018) conversion factor of 0.513. All soil measurements (apart from bulk density) were performed on duplicated samples and averaged at the plot level.

### 2.4. Precipitation data

Precipitation data were mainly sourced from weather stations of the Portuguese Institute for Sea and Atmosphere (IPMA; <https://www.ipma.pt/en/>) located as close as possible to the studied sites. Data for the CL and HRA sites were sourced from weather stations in *Coruche* and *Alcácer do Sal*, respectively and complemented with data from in situ stations. Data for the PNN site were sourced from an in-situ weather station and complemented with data from IPMA's weather station in *Amareleja*.

Monthly averages across three different precipitation periods (Table 2) were used to assess the response of SOC and vegetation to inter-annual changes in precipitation: the autumn-to-spring period (seven months) preceding sampling and 12- and 18-month periods immediately before sampling (see vegetation and soil sampling dates in Sections 2.2 and 2.3, respectively).

### 2.5. Data analyses

All numerical analyses described below were performed in R (R Core Team, 2023). Plot-level community weighted means (CWMs) of specific leaf area (SLA), plant height and seed mass were calculated based on the relative abundances of the species with trait data available (102 species) to represent their mean trait value per unit biomass:

$$CWM = \sum_{i=1}^s p_i x_i$$

where  $p_i$  is the relative abundance of the  $i$ -th species in a plot and  $x_i$  its average trait value (Dainese et al., 2015). The three plant traits chosen (SLA, plant height and seed mass) represent Westoby's (1998) leaf-height-seed (LHS) strategy scheme that has been shown to reflect much of the variation in plant function, including belowground root function (Laughlin et al., 2010). Traits were  $\log_{10}$ -transformed prior to the estimation of CWMs to remove the effects of different units of measurement and to meet the assumptions of linear modelling (see below). A multi-trait measure of functional diversity, Rao's quadratic entropy (Rao's Q; Botta-Dukát, 2005), was also computed at the plot level using these same plant traits with the *dbFD* function from the *FD* package (Laliberté et al., 2014).

Grazing (cattle grazed vs ungrazed) and precipitation (monthly mean values averaged over the preceding 18-month, 12-month and autumn-to-spring periods before sampling for each site) were fitted as fixed effects in linear mixed-effects models (LMMs) to determine their association with SOC and plant functional and taxonomic diversities (response variables). An interacting term between grazing and precipitation was also fitted to the models as a fixed effect. Contrasts were applied to the categorical fixed effect variable 'grazing' for more meaningful comparisons (Schad et al., 2020). SOC and the CWMs of SLA, seed mass and plant height, as well as plant species richness and Rao's Q, were fitted as response variables. In order to account for the idiosyncratic factors that affect responses across sampling plots, the categorical variable *Site* was used as a random effect variable, wherein the models would assume different baseline values for fixed effects for each of the three sites in the study. The analyses were conducted using the *lmer* function from the *lmerTest* package (Kuznetsova et al., 2017). The significance of the fixed effects in each model was assessed using Satterthwaite's method-of-moment approximation to the degrees of freedom (Satterthwaite, 1941).

A co-inertia multivariate RLQ analysis (Kleyer et al., 2012) was performed on the plant species abundance, plant trait and environmental data to reduce their dimensionality and identify any trends in their co-variation with the *rlq* function from the *ade4* package (Dray and Dufour, 2007). RLQ searches for the maximal co-variance in a combination of traits and environmental variables, weighed by the abundance of species in plots. Cluster analyses then produced functional groups based on trait co-variation, the optimum number of which was selected according to the Calinski-Harabasz Index (Caliński and Harabasz, 1974). PFTs associated with emergence, growth and dispersal strategies were used in the RLQ analysis, namely life cycle, growth-form, leaf phenology and dispersal strategy (Table 3). Plant species were also classified into functional groups as legumes or non-legumes (Table 3). The environmental variables used were grazing and precipitation (as per LMM analysis, see above), as well as % vegetation cover, % slope and soil pH. Tree species were not included in any numerical analyses since tree cover in these ecosystems is more closely related to other land

**Table 2**

Precipitation periods used to assess the response of soil and vegetation to inter-annual changes in precipitation and their interaction with cattle grazing.

	Soil data	Vegetation data
Autumn-to-spring	October 2017 to April 2018	October 2018 to April 2019
12-month	October 2017 to September 2018	May 2018 to April 2019
18-month	April 2017 to September 2018	November 2017 to April 2019

**Table 3**

Plant functional traits/groups used for the RLQ analysis and their respective categories.

Functional trait/group	Categories
Life cycle	Annual (0), biennial (0.5), perennial (1)
Legume	Yes (1), No (0)
Growth-form	Climber, erect, rosette, semi-basal, tussock, shrub
Leaf phenology	Evergreen (ES), green-stemmed leaves (GS), herbaceous (herb), summer semi-deciduous (SSD), winter semi-deciduous (WSD)
Dispersal strategy	Anemochory, barochory, ectozoochory, endozoochory, myrmecochory

management interventions (e.g., cork harvesting).

### 3. Results

#### 3.1. Soil and vegetation responses to cattle grazing and changes in precipitation

The shorter-term autumn-to-spring precipitation period offered better fitting models (i.e., lowest AICcs) than the 12- and 18-month periods for all plant variables, but the longer-term 18-month period offered the best fitting model for SOC (Table 4).

SOC and plant species richness generally responded negatively to cattle grazing but positively to increase in precipitation (and its interaction with cattle grazing), though SOC was not associated with cattle grazing when fitting the shortest-term (autumn-to-spring) precipitation period to the model (Table 4). SOC was most responsive to longer-term changes in precipitation (i.e., the preceding 18 months), whereas plant species richness was most responsive to shorter-term changes in precipitation (i.e., the preceding autumn-to-spring period) (Table 4). Further, most of the variation in SOC (84%) and in plant species richness (67%) was explained by the fixed effects (cattle grazing and precipitation) and their interaction (Table 4).

SLA generally responded negatively to cattle grazing (though only marginally when fitting the shorter-term autumn-to-spring and 12-month precipitation periods to the model) but was unrelated to

changes in precipitation (Table 4). Almost half of the variation in SLA (47%) was explained by the presence or absence of cattle grazing and changes in precipitation (Table 4). Changes in plant height, seed mass and Rao's Q were not associated with neither cattle grazing nor precipitation, irrespective of the precipitation period used (Table 4).

#### 3.2. Multivariate relationships between plant abundances and traits and the environment

The 102 plant species with trait data were partitioned into four functional groups according to the Calinski-Harabasz Index (92.7%), with 31 species in group A (30.4%), 15 in group B (14.7%), 31 in group C (30.4%) and 25 in group D (24.5%) (Fig. 2A). Cattle grazing, % vegetation cover, % slope, soil pH and precipitation explained 41.6% of the total variation in plant species composition. Overall, herbaceous species and those with semi-basal growth forms were associated with cattle grazing, while species with a wide diversity of leaf phenology were observed in ungrazed plots (Fig. 2b and d).

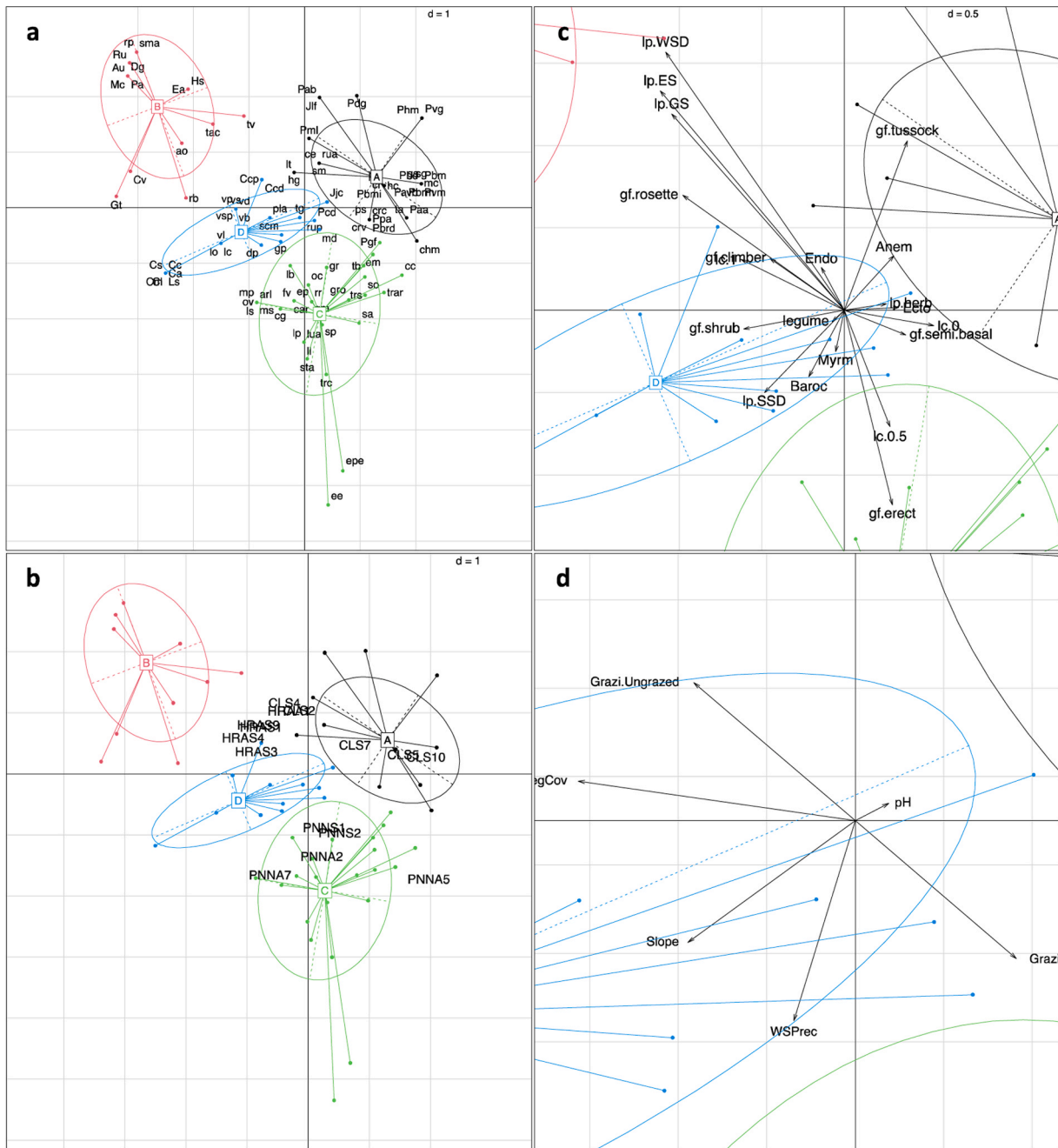
Group A was primarily associated with annual life cycle strategies, semi-basal and tussock growth morphologies, anemochory dispersal strategies and herbaceous species (Fig. 2b). This group was more prominent in drier conditions, flatter topographies, and relatively alkaline soils with sparse ground cover (Fig. 2d).

Group B was associated with a diverse array of leaf phenology characteristics, including evergreen, green stemmed and winter semi-

**Table 4**

Summary results of univariate linear mixed effects models assessing the associations between grazing (cattle grazed vs. ungrazed) and different precipitation periods (autumn-to-spring, 12- and 18-month) with soil (soil organic carbon – SOC) and vegetation (CWMs of specific leaf area – SLA, plant height and seed mass, as well as species richness and Rao's Q) data. Significant associations ( $p < 0.05$ ) between fixed effects (rows) and response variables (columns) are shown in bold and tabulated alongside respective model estimates (Est.) and  $\pm 1$  standard error (bracketed numbers). Model estimates were assessed using Satterthwaite's method-of-moment approximation to 15 degrees of freedom. All plant traits were  $\log_{10}$ -transformed prior to analyses. Number of sites = 3 and number of observations = 15 per response variable (five per site). *Grazing \* precipitation* denotes the interaction term between the two variables.  $\sigma^2$  is the residual (random effects) variance and  $r^2$  is marginal  $r^2$  (i.e., the proportion of total variance explained by the fixed effects alone) of the best fitting model. AICc is Aikake Information Criterion corrected for small sample sizes (values in bold denote the lowest AICc and thus the best fitting precipitation period). Model summary results were obtained with the *tab\_model* function from the *sjPlot* package (Lüdecke, 2023) in R (R Core Team, 2023).

	SOC		SLA		Plant height		Seed mass		Species richness		Rao's Q	
	Est.	p	Est.	p	Est.	p	Est.	p	Est.	p	Est.	p
<b>Autumn-to-spring</b>												
Intercept	-18.61 (2.92)	<b>&lt; 0.001</b>	-3.12 (2.86)	0.29	-0.24 (1.60)	0.88	0.66 (4.83)	0.89	-528.78 (108.58)	<b>&lt; 0.001</b>	-56.75 (41.56)	0.19
Grazing	1.62 (5.83)	0.79	-11.17 (5.72)	0.07	-0.20 (3.19)	0.95	-0.54 (9.66)	0.96	-1018.74 (217.16)	<b>&lt; 0.001</b>	-106.23 (83.11)	0.22
Precipitation	0.30 (0.04)	<b>&lt; 0.001</b>	0.10 (0.06)	0.14	0.01 (0.04)	0.81	-0.005 (0.11)	0.97	12.14 (2.42)	<b>&lt; 0.001</b>	1.30 (0.93)	0.18
Grazing * precipitation	-0.02 (0.08)	0.78	0.25 (0.13)	0.07	0.01 (0.07)	0.93	0.01 (0.22)	0.96	22.82 (4.84)	<b>&lt; 0.001</b>	2.39 (1.85)	0.22
<b>12-month</b>												
Intercept	-17.74 (2.77)	<b>&lt; 0.001</b>	-0.18 (1.01)	0.86	0.01 (0.56)	0.99	0.54 (1.70)	0.76	-177.22 (38.29)	<b>&lt; 0.001</b>	-19.13 (14.65)	0.21
Grazing	-22.79 (5.55)	<b>&lt; 0.001</b>	-4.12 (2.02)	0.06	0.004 (1.13)	1.00	-0.28 (3.41)	0.94	-353.08 (76.57)	<b>&lt; 0.001</b>	-36.32 (29.30)	0.23
Precipitation	0.47 (0.06)	<b>&lt; 0.001</b>	0.05 (0.03)	0.15	0.005 (0.02)	0.80	-0.003 (0.06)	0.96	6.64 (1.32)	<b>&lt; 0.001</b>	0.71 (0.50)	0.18
Grazing * precipitation	0.56 (0.13)	<b>&lt; 0.001</b>	0.14 (0.07)	0.07	0.003 (0.04)	0.94	0.01 (0.12)	0.96	12.31 (2.64)	<b>&lt; 0.001</b>	1.29 (1.01)	0.22
<b>18-month</b>												
Intercept	-107.91 (17.24)	<b>&lt; 0.001</b>	0.08 (0.96)	0.93	-0.02 (0.53)	0.97	0.60 (1.62)	0.71	-170.75 (36.38)	<b>&lt; 0.001</b>	-18.62 (13.93)	0.20
Grazing	-207.17 (34.47)	<b>&lt; 0.001</b>	-4.21 (1.92)	<b>0.04</b>	0.09 (1.07)	0.94	-0.41 (3.24)	0.90	-320.68 (72.77)	<b>&lt; 0.001</b>	-32.54 (27.85)	0.26
Precipitation	3.66 (0.57)	<b>&lt; 0.001</b>	0.03 (0.02)	0.20	0.004 (0.01)	0.74	-0.004 (0.04)	0.92	4.21 (0.82)	<b>&lt; 0.001</b>	0.46 (0.31)	0.17
Grazing * precipitation	6.94 (1.14)	<b>&lt; 0.001</b>	0.09 (0.04)	0.05	-0.0001 (0.02)	1.00	0.01 (0.07)	0.92	7.33 (1.64)	<b>&lt; 0.001</b>	0.76 (0.63)	0.25
<b>Model summary</b>												
$\sigma^2$	0.27		0.01		0.003		0.02		12.11		1.77	
$r^2$	0.84		0.47		0.33		0.05		0.67		0.19	
AICc (autumn-to-spring)	55.65		<b>12.32</b>		<b>-0.51</b>		<b>23.86</b>		<b>92.32</b>		<b>71.19</b>	
AICc (12-month)	54.80		14.37		1.53		25.90		94.36		73.23	
AICc (18-month)	<b>50.29</b>		15.10		2.27		26.63		95.10		73.97	



**Fig. 2.** Constrained ordination scores in RLQ space of the 102 species with trait data. Scores were partitioned into four functional groups (A = black, B = red, C = green and D = blue). Species scores (R row scores) are shown in panel a (species codes used for clarity; see Table S1 for species names listed by Group) and plot scores (Q row scores) are shown in panel b. Vectors illustrating the magnitude and direction of the weights of plant functional traits (Q canonical weights) and environmental variables (R canonical weights) on species scores are shown in panels c and d, respectively. The precipitation data shown here (panel d) only covered the preceding autumn-to-spring period before vegetation sampling since this offered the best fitting linear models for all plant-based variables (see Section 3.1). In panel c, *lp* = leaf phenology grouped into *WSD* = winter semi-deciduous, *ES* = Evergreen, *GS* = green-stemmed leaves, *herb* = herbaceous, *SSD* = summer semi-deciduous; *lc* = life cycle grouped into annual (0), biennial (0.5) and perennial (1) plants; *gf* = growth form; and dispersal strategies are *Anem* = Anemochory, *Endo* = endozoochory, *Ecto* = ectozoochory, *Myrm* = myrmecochory, *Baroc* = barochory. In panel d, *Grazi.Ungrazed* = ungrazed plots, *gCov* = % vegetation cover, *WSPrec* = autumn-to-spring precipitation, *Grazi* = cattle grazed, *pH* refers to soil pH and *Slope* refers to % slope.

deciduous (Fig. 2b). Species in this group tended to be perennials and show rosette morphologies and endozoochory dispersal strategies (Fig. 2b). This group was associated with ungrazed conditions and higher vegetation cover (Fig. 2d).

Group C mainly comprised biennial species with erect growth forms and barochory or myrmecochory dispersal strategies (Fig. 2b). These species preferred wetter conditions and steeper topography and were associated with cattle grazing (Fig. 2d).

Group D was associated with leguminous species and a diversity of growth forms, including shrubs, climbers and perennials. Their leaf phenology was primarily summer semi-deciduous. This was the most diverse group in terms of dispersal strategies, encompassing species with anemochory, endozoochory, barochory and myrmecochory traits (Fig. 2b). Even though group D clustered towards the centre of gravity in RLQ space, it tended to favour wetter conditions on ungrazed acidic soils with high vegetation cover (Fig. 2d).

The ungrazed plots in HRA were densely clustered between species groups B and D, while the cattle grazed plots in PNN were more closely associated with group C (Fig. 2c). There was a partition between the plots within the CL site, whereby the three cattle grazed plots (CLS5, CLS7 and CLS10; Table 1) tended toward group A, while the two ungrazed plots (CLS4 and CLS2; Table 1) clustered with the ungrazed plots in HRA and with group D (Fig. 2c). Surprisingly, plots at the PNN site in eastern Portugal tended to be wetter than the west-coastal sub-humid plots at the CL site in the preceding autumn-to-spring period before vegetation sampling (Fig. 2c and d).

#### 4. Discussion

Our results show that the presence (or absence) of cattle grazing and inter-annual changes in precipitation are responsible for a relatively large proportion of the variation in SOC and plant taxonomic diversity in the *montado*, with both responding negatively to cattle grazing but positively to increase in precipitation. However, functional diversity (Rao's Q) was unrelated to cattle grazing and precipitation, indicating different components of plant diversity respond differently to external drivers in the *montado* and supporting similar results from other ecosystems (Carvalho et al., 2020). Importantly, SOC and plant species richness were both positively correlated with precipitation, but the magnitude of the response differed between them, with SOC being most responsive to longer-term (18-month) changes in precipitation and plant species richness to shorter-term (autumn-to-spring) changes.

Although environmental variables seem to exert strong selective pressures on plant life strategies and growth-form in the *montado* (as evidenced by the RLQ results), the weighted means of leaf, height and seed traits were mostly unresponsive to cattle grazing and precipitation (though SLA was generally negatively associated with cattle grazing), suggesting that plant traits associated with emergence, growth and dispersal strategies are more responsive to environmental change in the *montado* than those associated with resource allocation.

##### 4.1. Response of soil organic carbon (SOC) to cattle grazing and precipitation

Although SOC's response to environmental factors can vary under different climatic conditions (Zdruli et al., 2004), the positive relationship between SOC and precipitation found here has been previously observed under semiarid Mediterranean conditions (Sinoga et al., 2012). One likely mechanism to explain this relationship is the reduced water input from precipitation resulting in lower soil moisture, which can lead to lower plant cover (i.e., lower productivity) and, consequently, fewer sources of organic matter input (in the form of plant litter) to the soil. In addition, soil aggregates may become more unstable under reduced plant cover and larger areas of bare soil, leading to reduced water holding and infiltration capacity to result in further soil degradation and erosion (Sarah, 2005).

Grazing can further increase this degradation cycle by contributing to lower vegetation cover and greater compaction of the soil surface to result in reduced soil permeability. This seems to be the case at our study sites, where we found a negative relationship between cattle grazing and SOC. Yet, previous studies have reported positive, neutral or negative effects of grazing on SOC, indicating effects are highly context-specific and may depend on the interaction between grazing and several other factors, including precipitation and soil (fine textured vs. sandy soils) and vegetation type (McSherry and Ritchie, 2013; Maestre et al., 2022). Positive effects of grazing on SOC have been reported from sites with a mean annual precipitation of 600 mm or less, with a negative effect reported above that threshold, potentially as a result of lower initial SOC pools and greater root-to-soil C ratios in semiarid environments compared to more mesic environments, as well as higher (and more active) microbial biomass C and greater pools of labile organic matter leading to higher C turnover rates under grazing in relatively wet sites

(Derner and Schuman, 2007; Piñeiro et al., 2010). Contrarily, studies conducted in central Asia found negative effects of grazing on SOC at sites with less than 600 mm of mean annual precipitation (Pei et al., 2008), while a global study on drylands found decreased soil carbon stocks and increased soil erosion under warmer climates and higher grazing intensities, though positive effects were reported from colder drylands (Maestre et al., 2022). Negative effects of grazing have been attributed to a decrease in vegetation cover and an increase in soil erosion associated with continuous grazing leading to poaching (Pei et al., 2008; Golluscio et al., 2009). In addition, a global meta-analysis has also found stronger negative effects of grazing on SOC at increased levels of precipitation (McSherry and Ritchie, 2013), contradicting the positive effects found in other locations (Derner and Schuman, 2007; Piñeiro et al., 2010).

Mean annual precipitation in our study sites commonly ranges between 500 and 700 mm. The negative effect of cattle grazing on SOC was seemingly amplified by 12- to 18-month precipitation, as evidenced by a significant positive interaction between cattle grazing and precipitation in both cases. These suggest that in cattle-grazed sites, where the area of bare soils may be relatively large due to reduced vegetation cover, increased precipitation during the preceding 12 to 18 months may exacerbate soil erosion by water and negatively affect SOC content.

##### 4.2. Response of plant diversity and function to cattle grazing and precipitation

The positive response of plant species richness to increases in inter-annual precipitation found here is in agreement with results reported for plant communities dominated by annual species in ecosystems similar (i.e., under a Mediterranean climate with dry summers and peak precipitation in winter, and with conditions varying between subhumid and semiarid) to our study areas (Peco et al., 1998; De Bello et al., 2006; Carmona et al., 2012). This response is consistent with high species turnover rates and with inter-annual changes in species richness and abundance in Mediterranean annual pastures under inter-annual fluctuations in precipitation, where plant diversity loss during drought periods may be offset by a recovery in diversity in wetter years (López-Rubio et al., 2022). However, plant functional diversity (measured as Rao's Q in this study) was unresponsive to changes in inter-annual precipitation, suggesting a decoupling of plant taxonomic and functional diversities, whose relationship may vary between drier and more mesic conditions (De Bello et al., 2006; Carmona et al., 2012). Similar results have been found in studies conducted in Mediterranean grasslands, where greater temporal stability of plant functional diversity compared to taxonomic diversity in response to inter-annual climatic fluctuations was attributed to relatively high functional similarity (i.e., functional redundancy) between plant species in dry habitats (Carmona et al., 2012).

Cattle grazing showed the opposite effect of precipitation by reducing plant species richness, which is in line with past observations in similar systems, particularly in drier areas (Carmona et al., 2012). However, the negative association between the presence of cattle grazing and plant diversity found here may not hold true in more humid locations (De Bello et al., 2006; Maestre et al., 2022). Plant functional diversity was unresponsive to cattle grazing in our study, but previous studies have shown that, under more limited water availability, grazing reduced the functional diversity of Mediterranean grasslands (Carmona et al., 2012).

We found a positive interacting effect of cattle grazing and precipitation on plant taxonomic diversity, indicating that increases in precipitation may exacerbate the negative effects of cattle grazing on plant species richness. We suggest this may be due to reduced plant cover in cattle-grazed areas, making them more susceptible to soil erosion by water in the short-term, particularly under intense precipitation events in short periods of time. Such events are predicted to increase in dryland areas in southern Portugal due to climate change (Cardoso Pereira et al.,

2020) and are likely to negatively affect the diversity of plant communities.

The individual leaf, height and seed traits analysed at the community level were largely unresponsive to cattle grazing and changes in precipitation. These results contradict broad responses of plant traits to grazing in a variety of ecosystems globally (Díaz et al., 2007) and in the *montado* specifically (Castro et al., 2010), since grazing may, for instance, favour shorter plants over tall ones or promote species with smaller seeds. Grazing effects may be modulated by particular combinations of precipitation and history of herbivory (Díaz et al., 2007; Jäschke et al., 2020) and can thus vary under different climatic contexts (Rota et al., 2017; Rahmanian et al., 2019). In addition, inconsistent vegetation responses to manipulative precipitation experiments (Jongen et al., 2013; López-Rubio et al., 2022), inter-annual climatic fluctuations (Su et al., 2023) and natural precipitation gradients (Nunes et al., 2017; Boonman et al., 2021) also suggest that transient (short-term) dynamics may not reflect long-term shifts in plant functional diversity and community trait composition (Sandel et al., 2010), which may be influenced by climate legacy effects on plant communities (Vicente-Serrano et al., 2013; Hoover et al., 2021). For this study, we used species-level average trait values from existing databases to capture changes in community-level trait composition. Therefore, these changes reflect changes in species abundances rather than intraspecific trait variability. It is possible that direct field measurements of individual traits in the three sites studied (especially plant height) would have enabled us to detect more subtle functional responses to cattle grazing and precipitation that may not have been captured by using species-level information.

Despite the lack of response of individual plant traits to cattle grazing and precipitation, our results show that environmental variables exert strong selective pressures on plant life strategies and growth-form in the *montado* (as evidenced by the RLQ results), suggesting that plant traits associated with lifespan (annual vs. perennial), growth-form (rosette or semi-basal) and dispersal strategies may be more responsive to environmental change in the *montado* than those associated with resource allocation (e.g., specific leaf area, plant height and seed mass). In fact, we found that a higher proportion of herbaceous plants with annual life cycles and semi-basal growth-forms were associated with cattle grazing and lower levels of precipitation. This is consistent with grazing favouring prostrate over erect plants on, for instance, grasslands, managed pastures and other rangeland areas (Díaz et al., 2007; Castro et al., 2010) and with drier conditions favouring annuals with anemochorous dispersal strategies, as found in other Mediterranean drylands (Nunes et al., 2017).

#### 4.3. Implications for land management in the *montado*

Our findings highlight the importance of considering the environmental context of grazing in land management decisions. The effects of grazing, particularly overgrazing, will vary according to climatic, soil and biodiversity conditions, making it important to consider local conditions when managing livestock in drylands (Maestre et al., 2022). Therefore, the optimal grazing intensity for maintaining good soil conditions and plant diversity will differ between drier and more mesic locations.

Our results also show that different plant diversity components (taxonomic and functional) can respond independently to external drivers (Carvalho et al., 2020). This indicates that different measures of plant diversity must be considered together since using a single indicator (e.g., species richness) may provide an incomplete assessment of the effects of changing conditions on vegetation diversity. Finally, for the sustainable management of the *montado*, it is important to account for legacy effects of long-term climate and land use histories on both soil and vegetation properties since their responses to inter-annual changes in precipitation can be transient and show varying recovery rates over time (e.g., between soil and vegetation), particularly when dealing with

plant communities dominated by annual species with high resilience to inter-annual fluctuations in precipitation.

It is possible some of the significant relationships (or their absence) observed here between cattle grazing, precipitation and the response variables (SOC and plant diversity) may have been confounded by the absence of other variables not measured in this study. For example, including predictors such as lithology and other soil characteristics (including mineralogy) in our numerical analyses, as well as assessing historical land use differences between the sites, could have either altered the results or explained a higher proportion of the variability in the response variables. While current cattle grazing has been present in these sites for at least a decade, historic land use may still influence the current vegetation patterns. Moreover, it was not possible to include both grazed and ungrazed plots within each of the three sites, which would have made it possible to further isolate the effects of cattle grazing given differences in mean annual precipitation between the sites. The addition of grazed and ungrazed plots across all sites, as well as other factors that differentiate them (e.g., additional soil properties), would thus be a positive development on the current study. These limitations notwithstanding, the multivariate RLQ analysis presented above incorporates some of these variables (e.g., % vegetation cover, % slope, soil pH) to help elucidate the associations between grazing and precipitation and vegetation characteristics. A positive development for future studies would be to expand the sampling protocol to include additional plant traits (e.g., belowground traits) to further clarify plant-soil interactions in the *montado* and determine how they may respond to the presence of cattle grazing and to changes in precipitation.

#### 4.4. Implications of climate change for the *montado*

Our findings may have implications for the future of the *montado*'s ecosystem given projected changes in climate. There has been a general increase in aridity and drought events in south Portugal in recent decades, and these are expected to increase further in intensity and frequency due to climate change (Costa et al., 2008; Andrade et al., 2021). Springtime accumulated precipitation in south Portugal is expected to decrease by up to 40% by the end of the century under a moderate greenhouse gas (GHG) emissions scenario (RCP4.5) and by up to 50% under a high GHG emissions scenario (RCP8.5; Lima et al., 2023b). Similarly, the number of wet days (precipitation above 1 mm) is projected to decrease by 18 to 24 days per year in the south and interior of the country by 2100 under RCP8.5, while the number of consecutive days with precipitation below 1 mm (i.e., length of dry spell) is expected to increase by almost 50 days per year (Lima et al., 2023a). Recent projections also indicate that precipitation will be more concentrated into shorter periods of time with an intensification of moderate/heavy rainfall events (Lima et al., 2023a). Similar projections have been made for changes in temperature, where a 5- to 6-fold increase in the number of heatwave events, as well as significant increases in their severity and areal extensions, are expected for the end of the century for most of the country under RCP8.5 (Cardoso et al., 2023).

Given the results of our study, these projected changes in climate will lead to alternative pathways for the *montado* and likely have implications for its future management which, coupled with recent socio-demographic and land management changes that have driven some Mediterranean HNVfs toward extensification and abandonment in less fertile and more peripheral lands or pressured them into intensification and exploitation, may alter their ability to deliver ecosystem services (Batista et al., 2017). We present two possible scenarios. First, given the positive interacting effects of cattle grazing and precipitation on SOC and plant species richness, the negative effect of cattle grazing shown here could be mitigated by reduced precipitation due to reduced soil erosion by water. However, more intense precipitation events within shorter periods of time may exacerbate the negative effect of cattle grazing due to reduced plant cover in cattle-grazed areas being more susceptible to soil erosion by water.



Additionally, severe future heatwaves are projected to develop beyond summer months in all GHG emissions scenarios (Cardoso et al., 2023). Coupled with projected reductions in precipitation during springtime as discussed above and given the positive response of plant taxonomic diversity to autumn-to-spring precipitation shown here, it is possible plant diversity in the *montado* will be negatively impacted by extended periods of high temperatures and dry spells between autumn and spring projected to happen before the end of the century. In turn, this negative climatic impact could be exacerbated by the negative effect of cattle grazing shown here. Therefore, it is likely the impact of cattle grazing on SOC and plant species richness will be influenced by projected changes in precipitation and temperature patterns, which will require careful consideration by site managers on how to manage cattle grazing throughout different times of the year.

## 5. Concluding remarks

The continued monitoring of both plant functional and taxonomic diversities over the coming years will be extremely important to further elucidate the mechanisms behind their differential responses to cattle grazing and inter-annual changes in precipitation in the *montado*, an important HNVf in southwest Europe. These responses will likely have consequences for vegetation community dynamics and plant-soil interactions and will inform land management practices and intensity (e.g., grazing stock type and density).

Finally, continued monitoring and analyses are needed in *montado* ecosystems in Portugal (and in *dehesa* ecosystems in Spain) to determine if either of the pathways resulting from climatic changes presented above will be realised, or if alternative pathways are possible given current uncertainties associated with future GHG emissions scenarios.

## CRedit authorship contribution statement

**Carvalho Fabio:** Conceptualization, Data curation, Funding acquisition, Investigation, Methodology, Project administration, Supervision, Validation, Writing – original draft, Writing – review & editing. **Brown Kerry A.:** Conceptualization, Data curation, Funding acquisition, Investigation, Methodology, Project administration, Resources, Supervision, Validation, Writing – original draft, Writing – review & editing. **Deosaran Rishi:** Data curation, Formal analysis, Investigation, Validation, Visualization, Writing – original draft, Writing – review & editing. **Hooda Peter S.:** Conceptualization, Data curation, Funding acquisition, Methodology, Resources, Supervision, Writing – review & editing. **Serafim João:** Data curation, Resources, Writing – review & editing. **Branquinho Cristina:** Funding acquisition, Investigation, Methodology, Resources, Supervision, Validation, Writing – original draft, Writing – review & editing. **Waller Martyn:** Data curation, Methodology, Writing – review & editing. **Köbel Melanie:** Data curation, Investigation, Methodology, Validation, Writing – original draft, Writing – review & editing. **Nunes Alice:** Data curation, Investigation, Methodology, Resources, Supervision, Validation, Writing – original draft, Writing – review & editing.

## Declaration of Competing Interest

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

## Data availability

Data will be made available on request.

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## Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.foreco.2024.121734.

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