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Diversity patterns of herbaceous community in environmental gradients of *dehesa* ecosystems

Katherine Onoszko [a,*], Francisco José Ruiz Gómez [a], Lorenzo Lazzaro [b], Ángel Lora González [a], Pablo González-Moreno [a]

[a] *Department of Forest Engineering, Universidad de Córdoba, Campus de Rabanales, Edificio Leonardo Da Vinci, Laboratorio de Repoblaciones, Crta. N-IV km. 396, Córdoba, Andalucia 14071, Spain*

[b] *Department of Biology, Università degli Studi di Firenze, Via G. La Pira 4, Firenze, Toscana 1-50121, Italy*

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ABSTRACT

Dehesa is a unique ecosystem associated with high biodiversity, that integrates trees, livestock, and pasture, making agro-pastoral production compatible with sustainability. However, in the last few decades, a manifold of factors have caused a decline in tree vitality, density, and coverage, leading to long-term changes in species composition and ecosystem structure. This study aims to determine changes in the diversity of the herbaceous plant community in relation to environmental characteristics, the phytosanitary state of the holm oak *(Quercus ilex* L. subsp. *ballota* (Desf.) Samp.), and possible interactions with biotic agents, including *Phytophthora cinnamomi*. For this purpose, the floristic composition and alpha diversity of the understory were assessed in two *dehesa* stands in Southern Spain. Additionally, the spatial heterogeneity (beta diversity) patterns of herbaceous plants were evaluated in relation to a climatic gradient and subplot orientation at the regional, plot, tree, and subplot scales. Our findings show that microsite features and climate substantially impact the herbaceous plant community in *dehesa* stands. Annual precipitation is a crucial factor affecting the diversity and biomass of herbaceous plants on a broader, regional scale, consistent with its role as a limiting factor in the Mediterranean climate. However, site-level differences, such as soil clay content and plot slope angle, positively correlate with plant biodiversity, growth, and richness, varying with the Biodiversity Index considered. Moreover, microsites resulting from the combined effects of plot and tree are the main drivers of dissimilarities between samples, as expressed by beta diversity. Contrary to our initial hypothesis, our results reveal no significant association between tree health and herbaceous biodiversity decline.

1. Introduction

Forest ecosystems are vital for terrestrial biodiversity and significantly influence the socio-ecological and cultural aspects of human societies, including the livelihoods of traditional communities connected to these forests (Baboo et al., 2017; Fartyal et al., 2022; Herrmann, 2006). Nowadays, forests worldwide face serious threats from human activities such as agricultural expansion and

* Corresponding author.
E-mail addresses: g02ononk@uco.es (K. Onoszko), g72rugof@uco.es (F.J. Ruiz Gómez), lorenzo.lazzaro@unifi.it (L. Lazzaro), cr1logoa@uco.es (Á. Lora González), pablo.gonzalez@uco.es (P. González-Moreno).

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infrastructure development, which harm biodiversity and the environment (Bargali et al., 2019, 2022; Bisht et al., 2022, 2024; Davidar et al., 2010). Agroforestry systems might counterbalance these impacts, by providing relevant ecosystem services and keeping high biodiversity levels. A relevant example is the forest landscape of the southwestern Iberian Peninsula, dominated by savannah-like grassland systems called *dehesas*. This is a unique Mediterranean ecosystem due to the combination of ecological and socioeconomic services it provides (Moreno et al., 2018). These man-made ecosystems represent a hotspot of diversity, offering services, such as livestock management, forestry, and agriculture (Costa Pérez et al., 2006). This ecosystem is structured by an open tree layer with a canopy cover usually lower than 80 %, accompanied by a variable understory layer with mostly open pastures (Pulido and Picardo, 2010). The pastures host a highly diverse herbaceous layer consisting mainly of annual plants with a therophyte life form (López-Carrasco et al., 2015; Montero et al., 1998). This herb layer is an important resource for grazing and holds high genetic diversity, providing resilience to environmental changes (Lloveras et al., 2006; Rodríguez-Rojo et al., 2022).

The tree layer of *dehesas* in the Iberian Peninsula is dominated by the sclerophyllous species holm oak (*Quercus ilex* L.) and cork oak (*Quercus suber* L.). Both species exhibit xerophytic and perennial habits, with rounded, wide crowns that can reach up to 25 m in height and 30 m in canopy diameter (Ruiz de la Torre, 2006). This tree layer is fundamental to the high herbaceous biodiversity levels of dehesas (Bélair et al., 2010), as it provides a favourable microclimate under the canopy, reducing stress from the extremely dry and hot summer conditions (Madrigal et al., 2008). The effects of tree presence on herbaceous plants may vary depending on the size of the crown, foliar area, or specific location beneath the canopy. For instance, Erdős et al. (2018), reported that in central Hungary, juniper-poplar forest edges on its northside had the highest species richness in herbaceous plants, while south-facing edges were primarily important for tree recruitment. Furthermore, in this multi-layered complex, trees and understory plants can influence each other not only through resource-mediated interactions like light interception but also through chemical signaling via numerous plant secondary metabolites, which help them endure drought stress (Hashoum et al., 2017). This combination of interactions between oak trees and the herbaceous community beneath their crowns forms a complex interplay that is still poorly understood.

Plant diversity in the *dehesa* may also be affected by the health and condition of the tree layer. Increased crown transparency and reduced tree cover can significantly alter biodiversity levels. In this context, *dehesas* are threatened nowadays by a multifactorial syndrome of oak decline, known as '*La seca*'. Among the factors contributing to this disease, one of the most relevant is the root rot caused by the alien invasive forest pathogen *Phytophthora cinnamomi* (Ruiz-Gómez et al., 2019). This soilborne oomycete feeds on the absorbent root system and has been identified as a causative factor of tree death through chronic progressive decline or sudden collapse and death of the trees (Brasier et al., 1993). This decline in tree density increases canopy gaps, which in turn alters light, evapotranspiration and temperature conditions under the canopy (Breshears et al., 1998; Royer et al., 2011). Moreover, this tree decline phenomenon affects the soil physical and chemical signalling between the herbaceous layer, the trees, and the rest of the soil ecosystem, influencing the diversity of the herbaceous community in *dehesas*. Although, the effects of tree canopy on the herb layer in the *dehesa* has been thoroughly studied (López-Sánchez et al., 2016; Marañon, 1986) there is a lack of research on how this effect is mediated by the oak decline syndrome. Furthermore, there is also a notable lack of comprehensive studies taking into consideration the environmental variations at different levels (beneath the canopy, at plot level and at regional level).

Finally, at larger scales, plant biodiversity in the *dehesas* and other (semi-) natural ecosystems may be affected by many factors, including climate and edaphic features. Topographic factors such as altitude, slope, and orientation are also expected to cause significant changes in climatic conditions, and consequently species composition. For instance, changes observed in species richness and composition along the altitudinal gradient are widely recognized patterns (Di Musciano et al., 2021; Dip et al., 2020). Studies on vascular plants by García Del Barrio et al., (2014) in Spanish *dehesas* showed a decrease in plant species richness and diversity with increasing terrain elevation. On the other hand, precipitation and water availability are key factors shaping Mediterranean ecosystems. Therefore, we anticipate that communities with less extreme conditions (e.g., lower aridity) will exhibit higher alpha diversity. Similarly, soil properties, such as geological composition, electrical conductivity, organic matter content, pH, cation exchange capacity and other edaphic variables can be considered as potential environmental drivers of vegetation and its diversity. Plant community assemblage differences across sites (i.e., beta diversity) and is affected also by environmental factors operating at large and local scale. For instance, García Del Barrio et al., (2014) found that similarity levels among *dehesa* sites were explained by both climatic and biogeographic gradients.

This study aimed to understand the relationship between the biodiversity and biomass patterns of herbaceous vegetation in holm-oak *dehesa* ecosystems and environmental characteristics (climate, soil, and topographic properties), tree characteristics, and phytosanitary state across two *dehesa* regions with contrasting climatic conditions. Specifically, the study examined herbaceous alpha- and beta-diversity and biomass in *dehesas* at different scales (regional, plot, and tree) and identified key patterns related to spatial scale and environmental factors. It also quantified the effect of tree phytosanitary state (i.e., defoliation) on herbaceous plant biodiversity and investigated potential interactions with biotic agents, including *Phytophthora cinnamomi*. Ecological theory suggests that community similarity increases with environmental similarity along gradients, such as topographic or climatic gradients (Nekola and White, 1999). Thus, we expect that herbaceous plant communities in *dehesas* with similar environmental conditions will have similar species composition. However, this similarity may also be influenced by effective distance, which limits dispersal and species exchange (Vega et al., 2020). Characterizing these patterns will provide valuable information for conserving genetic diversity in *dehesa* pastures and will serve as a useful tool for their sustainable management.

2. Materials and methods

2.1. Study area

To understand the contrasting patterns of plant biodiversity in *dehesa* ecosystems, we used the Sierra Morena Mountain range in northern Andalusia (Spain) as a case study, covering 425,000 ha (Santos, 2004). Our work focused on two climate-contrasting regions within the Andalusia autonomous community in southern Spain (Fig. 1). The regions investigated were Los Pedroches Valley (north of Córdoba Province, hereafter CO plots) and the Aracena Mountains (north of Huelva province, hereafter HU plots), which represent a broad climatic range and encompass extensive *dehesa* ecosystems. The CO region is characterized by a continental Mediterranean climate and extensive pastures. This area, with its slightly undulating terrain, is situated in the peneplain of the Sierra Morena Mountain range and is dominated by granite batholiths, which result in acidic soil pH values. The climate is classified as dry, sub-humid, and humid (Melendo et al., 1996) with a summer drought period and annual precipitation ranging from 493.6 to 584.1 mm. The HU region features soils predominantly composed of acidic and metamorphic materials. The climate is typically Mediterranean, but due to exposure to Atlantic winds, it is relatively mild and humid. The oceanic influence brings abundant rainfall, with average annual values ranging from 680.1 to 1,039.6 mm. Rainfall is concentrated in the cooler months, while a prolonged summer drought occurs from June to September, marked by high temperatures and water deficit. During late spring to early autumn, plant-available water is quickly depleted due to high evapotranspiration.

2.2. Experimental design

Twenty plots in the study area were selected from the plots of the "Red Andaluza de Seguimiento de Daños sobre Ecosistemas Forestales", hereinafter the SEDA Network (Fig. 2). The SEDA Network is a monitoring program, established in Andalusia (Spain) as part of the European network of monitoring plots (ICP Forest Level I regional network; Servicio de Ordenación y Defensa de los Recursos Forestales, 2006). SEDA network consists of systematic grid of an 8 × 8 km covering the whole region, with plots situated at the intersections where forest occur. Each plot spans a radius of 50 m where 24 trees are randomly selected (Fig. 2) and monitored annually on health status (i.e., defoliation, crown discoloration, damage levels, and the presence of biotic and abiotic agents) and every 5 years on tree growth. The data are publicly available at https://portalrediam.cica.es/descargas (last consulted on 26th February 2024).

The selection of the 20 plots was carried out as follows. First, plots with more than 80 % of trees present in the plot belonged to

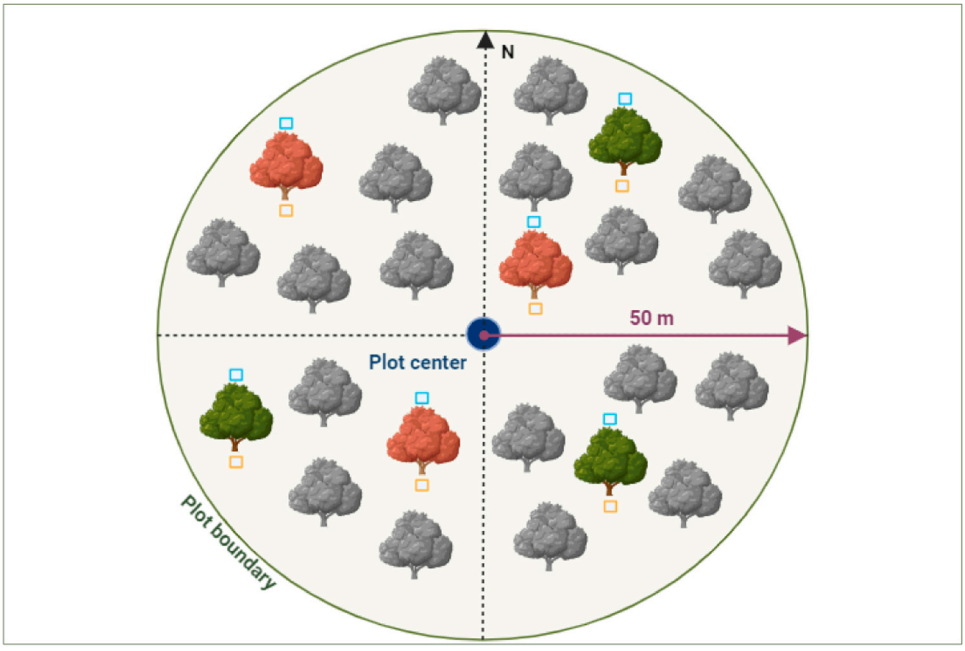

Fig. 1. | Sampling design in each plot. This figure illustrates an example of a *Phytophthora cinnamomi* infected plot (red trees). In the case of an infected plot, three symptomatic trees and three asymptomatic trees were selected. In plots without evidence of holm oak decline, trees were also randomly chosen from the set of 24 monitored trees. Red trees indicate those infected by *P. cinnamomi,* while green ones depict healthy trees. Grey trees are the remaining holm oak trees, not selected for this study but monitored by the SEDA Network. Squares shown in the immediate vicinity of the selected trees represent rectangular 0.25 m^2 quadrats used as sampling units for herbaceous plant assessment. The blue quadrats represent northern side, and the orange quadrats represent the southern side of the tree crown. Specifically, the quadrats were placed at the edge of the crown projection, the boundary between the tree canopy and open land.

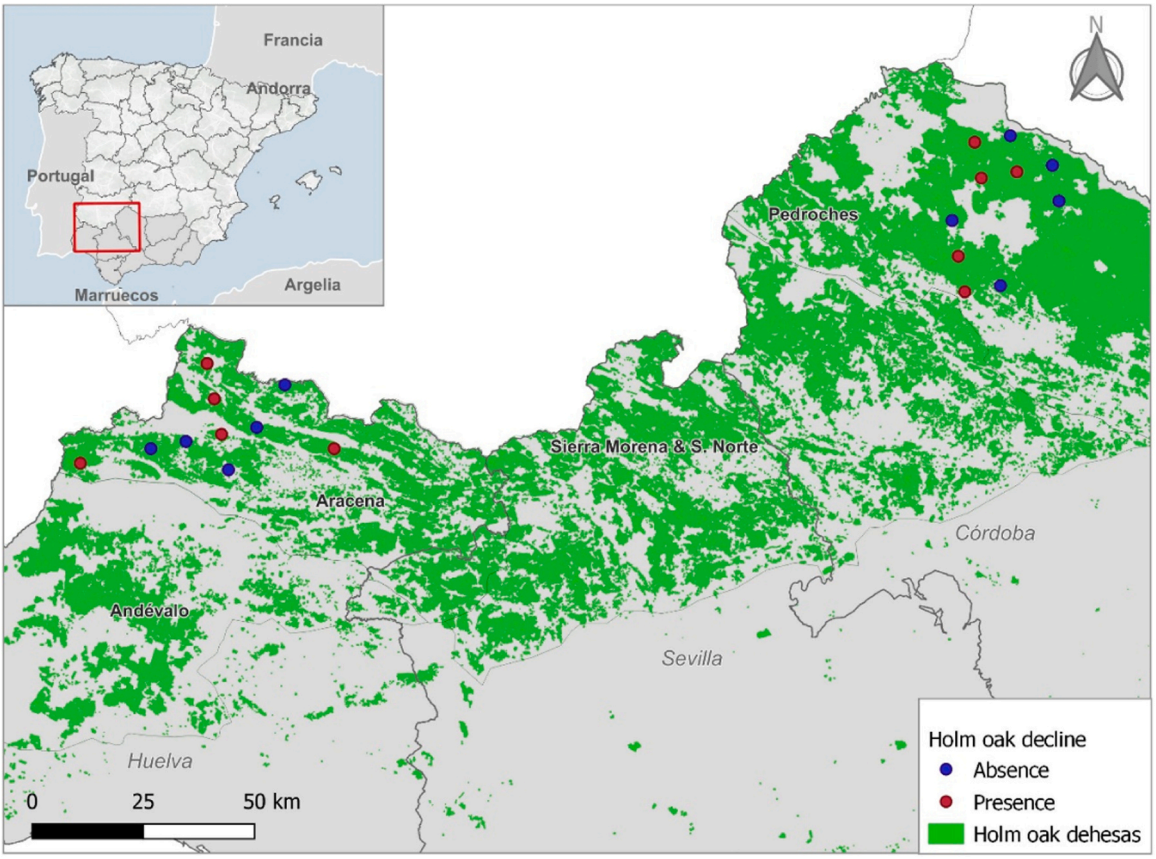

Fig. 2. | The locations of the study plots are in Los Pedroches Valley (CO) and the Aracena Mountains (HU). The dots represent the positions of the selected plots. Red dots indicate plots withholm oak decline symptoms, while blue dots represent plots without holm oak decline symptoms.

Quercus ilex L. subsp. *ballota* (Desf.) Samp. Second, for each study region (CO and HU), we randomly chose 10 plots: 5 with holm oak decline and 5 without. Holm oak decline was determined using tree mortality and crown transparency data from the past 10 years, along with positive diagnoses of *Phytophthora cinnamomi* from the SEDA Network (Sánchez-Cuesta et al., 2021). All plots selected showed a similar management system corresponding to a typical *dehesa* with both tree and herbaceous layers and the livestock presence. Soil management is sporadic, with cereal sowing and light tillage to prevent shrub encroachment every 4–6 years.

For each plot selected, 6 trees from the 24 monitored by the SEDA network were chosen from the plot center (120 trees in total). For plots without holm oak decline, trees were also randomly chosen. For affected plots, the selection was adjusted to cover the range of defoliation levels in the plot. Trees were classified as high- or low-defoliated based on the overall state of the plot, and three trees were randomly selected from each subgroup. The field campaign was conducted in the spring, from March to May 2021, to coincide with the peak flowering period of the main herbaceous species in these latitudes (Peco et al., 2005).

Table 1
| Tree-related variables and the corresponding abbreviation used in the model fitting. Variable selection was carried out based on the Pearson's correlation analysis, by determining the correlation coefficients between the independent variables. nd = non-dimensional variable; Q.i. = *Quercus ilex* L. subsp. *ballota* (Desf.) Samp.). In bold, subset of variables that were chosen for the linear mixed model analyses.

Description	Abbreviation	Units
Tree height	HEIGHT_m	m
Diameter at breast height (DBH)	DIAM_m	cm
Tree crown diameter	CANOPY_m	m
Percentage of tree crown defoliation	DEF_POR	%
Defoliation class (5 levels; 0–4)	DEF_CLASS	nd
***Phytophthora cinnamomi* (Pc) presence (1) / absence (0)**	Pc1 / Pc0	nd
Subplot orientation beneath *Q. ilex*.	ORIENT	N / S

2.3. Tree phytosanitary and dasometric data

Defoliation percentage was found to be the most informative variable related to phytosanitary state. The defoliation of the 120 trees was visually estimated as a percentage from 0 to 100, using a local "reference tree" based on the ICP Forest intercalibration manual (Ferretti et al., 2016; Sánchez Peña et al., 2010). In addition to defoliation, dasometric characteristics (tree height, diameter at breast height, and crown diameter) were measured for each selected tree (Table 1).

2.4. Soil sampling and processing

Soil samples of the tree rhizosphere were collected to detect *P. cinnamomi* presence and for physicochemical analysis. For each selected tree, two samples were taken — one from the north side and one from the south side — yielding a total of 240 samples. Each sample consisted of two subsamples: one taken at 1 m distance from the trunk on the specified side (north or south), and other from below the outer edge of the crown. For each subsample, the organic topsoil layer within a 0.8 × 0.8 m square was first removed. Soil was then excavated to a depth of 20 centimeters or until the *Q. ilex* roots appeared. This procedure aimed to collect soil from around the fine roots of the tree, exposing the rhizosphere soil. Subsamples of the same orientation were mixed, then stored in plastic bags and kept at 4–6°C during transport. In the laboratory, samples were preserved at –20°C until analysis (Agnelli et al., 2004; Lorenzo et al., 2010). Soil physicochemical properties were analyzed by a certified third-party laboratory (APROA Laboratories SCP, Córdoba, Spain – ISO 9001:2000) following standard methods (see Table 2 for details).

2.5. Phytophthora cinnamomi diagnostic

The presence of *P. cinnamomi* was assessed in all the rhizosphere soil samples. We used PCR-based molecular diagnostics to detect the pathogen DNA in the rhizosphere of the 120 trees. Detailed methods for *Phytophthora cinnamomi* molecular diagnostics are provided in the Supplementary Material (**Appendix B**).

2.6. Herbaceous data sampling and identification

Two samples of herbaceous plants were collected from the ground beneath the tree canopy (n=240) using a rectangular quadrat of 0.25 m^2 as sampling unit. One quadrat was placed to the north and the other to the south of the tree crown. Specifically, the quadrats were placed at the edge of the crown projection (the boundary between the tree canopy and open land). One plot showed recent tillage, so only the quadrats without tillage were sampled. We recorded the cover of the herbaceous, bare soil, and shrub layers in each quadrat, as well as the height of the herbaceous vegetation. All living parts of the herbaceous plants were then harvested from their bases. The samples were processed determining the floristic composition per quadrat by species or morphospecies. Over 2500 plants were separated into (morpho-)species, photographed, and identified according to Valdés et al. (1987) and Castroviejo (2020). If identification at the species or genus level was not possible, the sample was categorized into the corresponding family. Each species was then assigned to one of the functional group (i.e., forb, legume, and grass). (Morpho-)species were also divided into five frequency groups (quintiles), according to (Rodwell, 2006) and based on five 20 % bands (I – scarce, II - occasional, III - frequent, IV - constant, V – constant). Only 1 % of the plants found in Córdoba were not assigned to any of the functional group due to the impossibility to

Table 2
| Physicochemical soil and topographic characteristics of plots. Variable selection was carried out based on the Pearson's correlation analysis, by determining the correlation coefficients between the independent variables. nd = non-dimensional variable. Variables chosen for the linear mixed model analyses are shown in bold.

Variable	Abbreviation	Units
sandy texture	texSANDY	nd
sandy-loam texture	texSANDY-LOAM	nd
clay texture	texCLAY	nd
clay-loam texture	texCLAY-LOAM	nd
loam texture	texLOAM	nd
pH of the whole soil profile	pH	nd
soil electrical conductivity	microS	µS/cm
assimilable phosphorous	P	ppm
assimilable potassium	K^+	ppm
assimilable calcium	Ca^{2+}	ppm
assimilable magnesium	Mg^{2+}	ppm
organic matter content	OM	%
total nitrogen	N	%
total carbonate	CO_3	%
clay content	clay	%
sand content	sand	%
silt content	silt	%
plot slope	slp	degrees
mean curvature of the terrain	cur_m	1/m

determine the belonging to either a family or a genus (undeterminable subsample). After identification, all separated plant species per quadrat were oven-dried at 75°C for 72 hours and weighed to estimate biomass.

2.7. Alpha herbaceous biodiversity indices

To assess herbaceous diversity in our plots, species richness was determined as the number of different (morpho-)species present in each subsample. We also calculated two widely used alpha diversity indices considering the relative abundance of each species in terms of dry biomass. Simpson's Diversity Index (D_{sim}) was calculated as follows (He and Hu, 2005):

$$D_{sim} = \sum_{i-1}^{S} \left(\frac{n_i(n_i - 1)}{N(N-1)} \right) \quad (1)$$

Where:
S – the number of species
n_i – the abundance of the n_{th} species
N – the total abundance of each species
Shannon Diversity Index (H) was calculated following the expression (2):

$$H = -\sum_{i=1}^{S} (P_i(\ln P_i)) \quad (2)$$

Where:
S – the number of species
P_i– the proportion of individuals found in the i_{th} species
Both diversity indices were calculated using "**vegan**" R package (Oksanen et al., 2022) in R version 4.3.2 (R Core Team, 2023).

2.8. Environmental information

Twenty climatic and topographic variables per plot were extracted from the Forest Biomass project of Andalusia at a 100 m resolution (Guzmán Álavarez et al., 2012) (Tables 2 and 3). Annual climatic variables were derived from interpolations of monthly precipitation and temperature data from the period 1971–2000, sourced from all official weather stations in Andalusia at 500 and 100 m resolution, respectively, and can be accessed through REDIAM (https://portalrediam.cica.es/descargas, last accessed on February 26, 2024).

Table 3
| Variables for the climatic characterization of the site, based on data collected by REDIAM and Forest Biomass project of Andalusia. nd = non-dimensional variable. Hamsl, ins and slp_ex are topographic variables directly related to climatic conditions and reflect the microclimate of the site. Variables were selected based on the Pearson's correlation matrix depicting the linear dependence between two variables. Variables chosen for the linear mixed model analyses are shown in bold.

Variable	Abbreviation	Units
height above mean sea level	hamsl	m
Insolation (power density of the solar radiation)	ins	nd
slope orientation	slp_ex	degrees
annual precipitation	preca	mm
Winter precipitation	pwin	mm
Spring precipitation	pspr	mm
Autumn precipitation	paut	mm
Summer precipitation	psumm	mm
average annual temperature	ta	°C
average minimal temperatures of the coldest month	tmincol	°C
average temperature of the coldest month	tmedcol	°C
average maximal temperatures of the hottest month	tmaxhot	°C
mean temperature of the hottest month	tmedhot	°C
thermal oscillation	osc1	°C
total thermal oscillation	osc2	°C
annual evapotranspiration	evapo	mm
precipitation surplus	ssup	mm
precipitation deficit	sdef	mm
duration of droughts	ddroug	month
annual water index	awi	nd

2.9. Statistical analyses

2.9.1. Alpha diversity

We analyzed the relationship between herbaceous biomass, alpha biodiversity metrics, — such as species richness (number of species per unit area), Shannon Diversity Index (Shannon and Weaver, 1949), Simpson's Diversity Index (Simpson, 1949) — with a set of predictors: (a) tree dasometry and phytosanitary state, (b) environmental factors (climate, soil and topographic), and (c) region (CO and HU). Linear mixed models were applied across the 240 quadrats. First, to identify a subset of non-collinear variables, we used the "**corrplot**" R package (Wei and Simko, 2021) to perform correlation analysis, estimating Pearson's correlation coefficient ($r < 0.65$) (Figures A1, A2 and A3). The final list of variables was selected based on the Pearson's correlation matrix (Tables 1, 2, and 3**)**. Next, the R packages "**lme4**" (Bates and Maechler, 2023) and "MuMIn" (Bartoń, 2023), were used for fitting and analyzing the mixed models. The plot ID was included as a random factor to account for pseudo-replication (quadrats within each plot), and 999 permutations were used for fitting purposes. First, we modeled each dependent variable (biomass, richness, Shannon Diversity Index, and Simpson's Diversity Index) separately, using the `**lmer**` function from the "**lme4**" R package to identify the best predictors within each group. Normality and homoscedasticity of the model's residuals were checked using the Anderson-Darling test and the residuals plots, respectively. As the assumptions for linear regression were met, no data transformation was necessary. We then applied multimodel inference with the `**dredge**` function from the "**MuMIn**" R package (Bartoń, 2023). For each dependent variable, the final model was selected based on three criteria:

(a) Predictors from the best model according to AIC using the `**dredge**` function from "**MuMIn**" package, with $\Delta AIC \leq 0$.
(b) Model averaging with the `**model.avg**` function from "**MuMIn**", based on Akaike's information criterion with $\Delta AIC < 4$.
(c) Selection of variables with Akaike weights summing to ≥ 0.8, based on the `**sw**` function from "**MuMIn**".

Subsequently, we used the "**lmerTest**" package (Kuznetsova et al., 2022) to perform one-way (univariate) ANOVA to test the significant differences ($p < 0.05$) among the dependent variables (biomass, richness, Shannon, and Simpson's Diversity Index) and tree and environmental information. A significance level of $p = 0.05$ was used to reject null hypotheses, with means showing p-values between 0.05 and 0.1 considered marginally different. The second model selection using the `**lmer**` function was performed with a reduced number of response variables based on the three selection criteria, following the same procedure as the first modeling. The final full model was computed for each response variable, incorporating significant variables from distinct environmental groups into a single complete model.

2.9.2. Beta diversity

We analyzed beta diversity patterns using `**beta.pair**` function form "**betapart**" R package (Baselga et al., 2023) on the herbaceous (morpho-)species occurrence list of the entire study area. We computed the two principal components of beta diversity - spatial turnover (beta.sim) and nestedness (beta.sne) - as well as total beta diversity (beta.sor), which is the sum of the two beta diversity components. We studied beta diversity at different spatial scales within our sampling design, ranging from region to subplot (region, plot, tree, and subplot). We verified the contribution of these geographical levels to total beta diversity, nestedness, and turnover using a permutational multivariate analysis of variance (PERMANOVA) with the `**adonis2**` function from the "**vegan**" R package (Oksanen et al., 2022). The selected variables were tested for both regions separately and combined.

We used the `**varpart**` function from the "**vegan**" package to conduct a variation partitioning analysis. This function assess the effects of the different spatial scales in our sampling design (region, plot, tree, and subplot) on total beta diversity, nestedness, and turnover. The `**varpart**` function partitions the variation in community data or community dissimilarities with respect to explanatory variables, using adjusted R^2.

Non-metric MultiDimensional Scaling (NMDS) analysis using Bray-Curtis dissimilarity was conducted with the `**metaMDS**` function from the "**vegan**" package to visualize differences in species assemblages among the subplots. Global patterns in species composition and abundance were examined based on their separation in the NMDS plot. In addition, environmental factors were fitted to the major structure of the data. For NMDS purposes, (morpho-)species were divided into quintiles (see the '*Herbaceous data sampling and identification'* section). Fifty-three (morpho-)species in the "constant group" with frequencies exceeding 17 per subplot were considered the most frequent and included in the NMDS ordination, along with CO and HU plots and subplot orientation. Environmental information was overlaid onto the NMDS ordination plot using the `**envfit**` function from the "**vegan**" package, which identified variables significantly associated with the herbaceous plant community through multiple linear regression of selected factors to the NMDS axes. The selection of variables for NMDS included statistically significant and marginally significant variables ($p < 0.06$) from the alpha diversity regression analyses (Table A1), occurrence of *P. cinnamomi*, and region. Vectors and centroids were added to the NMDS plot with the `**ggplot**` function from the "**ggplot2**" package. All data analyses were conducted using R 4.3.2 (R Core Team, 2023).

3. Results

3.1. Floristic composition

A total of 263 different plant (morpho-)species were identified. Herbaceous communities in both regions were predominantly composed of annual species with spring flowering. Forbs dominated both regions (CO: 63 %; HU: 48 %), followed by grasses (CO: 19 %; HU: 31 %), and legumes (CO: 16 %; HU: 22 %). Within forbs, the most frequent families were *Asteraceae, Plantaginaceae,*

Caryophyllaceae, and *Geraniaceae*. Grasses were mainly from the *Poaceae* family, and legumes (*Fabaceae* family) included *Trifolium*, *Ornithopus*, *Medicago*, and *Coronilla* genera. In Córdoba plots, the most abundant species were *Trifolium* spp., *Plantago* spp., and *Ornithopus compressus* L. (Fig. 3). In Huelva, *Trifolium* species such as *T. lappaceum* L., *T. angustifolium* L., *T. campestre* Schreb., and *T. cherleri* L., were the most abundant. Across the entire study area, *Ornithopus compressus* L. was the most prevalent species. Other highly widespread herbaceous plants belonged to the *Trifolium* and *Plantago* genera (Fig. 3). When considering both regions together, the most represented families were *Asteraceae, Poaceae, Fabaceae*, and *Plantaginaceae*.

3.2. Herbaceous biomass

Plots in Córdoba were characterized by a lower dry herbaceous biomass (77.2 ± 10.8 g/m^2) compared to Huelva (81.6 ± 6.4 g/m^2), but there were no significant differences between regions or plot orientation (Table 4). Multivariate analysis revealed, that biomass variability was mainly explained by climatic variables. Annual temperature ($z = 3.263$, $p < 0.001$) and annual precipitation ($z = 3.048$, $p < 0.01$) were positively correlated with biomass, while the average minimal temperature of the coldest month ($z = -2.909$, $p < 0.01$) demonstrated negative correlation. Furthermore, height above mean sea level ($z = 2.214$, $p < 0.05$), and soil clay content ($z = 2.971$, $p < 0.01$), had significant positive influence on herbaceous biomass (Table 4 and Table A1).

3.3. Alpha diversity

Species richness in the study area averaged 12 ± 0.7 (morpho-)species per quadrat. In Córdoba, the average richness was 10 ± 0.5 species per quadrat, while in Huelva, it was 12 ± 0.6 species. The highest number of different species was recorded in Huelva, with 31 species per quadrat, while the lowest richness, —only one species per quadrat— was found in one quadrat in both Córdoba and Huelva. The maximum species richness in Córdoba was 24 species per quadrat.

The regression analysis did not show statistically significant differences between the two regions regarding richness (Table 4 and Table A1). Key soil variables associated with richness included soil clay content ($z = 5.616$, $p < 0.0001$), electrical conductivity ($z = 4.313$, $p < 0.001$), total carbonate ($z = 2.879$, $p < 0.001$), organic matter ($z = 2.775$, $p < 0.01$), and assimilable calcium ($z = 3.787$, $p < 0.05$). Plot slope showed a marginal influence ($z = 1.769$, $p < 0.1$). Species richness was marginally higher on the southern orientation of the tree ($z = 1.846$, $p < 0.1$). Tree characteristics were not relevant for species richness (Table 4 and Table A1).

The Shannon Index values were significantly higher in Huelva than in Córdoba ($z = 2.31$, $p < 0.05$), ranging from 0 (only one species per quadrat) to 2.64 in Córdoba and 2.88 in Huelva. The multivariate analysis indicated a marginally significant positive linear relationship between the Shannon Index and quadrat orientation, with higher values observed on the south side of the tree (Table 4 and Table A1). Additionally, there was a significant positive correlation with plot slope ($z = 1.957$, $p < 0.03$). The Simpson's Diversity Index ranged from 0 to 0.90 in Córdoba and from 0 to 0.93 in Huelva, with significantly higher values in Huelva ($z = 0.0297$, $p < 0.05$). Significant positive correlations with the Simpson's Index were found for plot slope ($z = 2.261$, $p < 0.05$) and annual precipitation ($z = 2.093$, $p < 0.05$, Table 4 and Table A1).

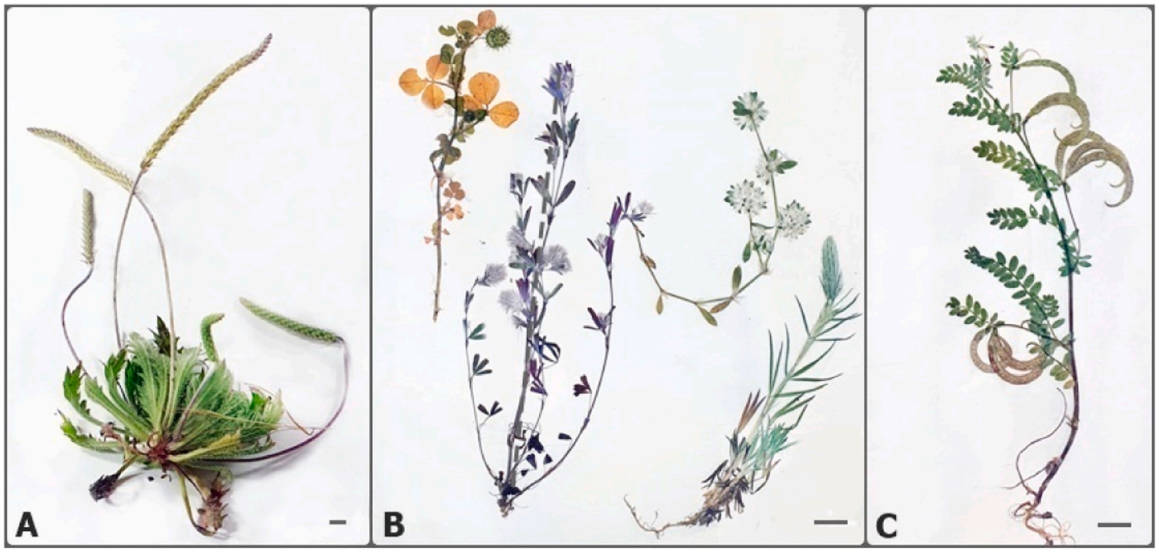

Fig. 3. | The most abundant species of herbaceous plants beneath the *Quercus ilex* L. subsp. *ballota* (Desf.) Samp. tree crown in the whole study area. **(A)** Fresh plant of *Plantago coronopus* L., collected in one of the Córdoba subplots; **(B)** Herbarium sheet of *Fabaceae* family (from left to right): *Medicago polymorpha* L. and three species of *Trifolium* genus collected in Huelva plots: *T. lappaceum*, L. *T. cherleri* L., and *T. angustifolium* L.; **(C)** Herbarium sheet of *Ornithopus compressus* L., collected in Huelva. Scale bar = 1 cm.

Table 4
| Statistical summaries obtained from fitting linear mixed-effects models (LMMs) by AIC using the 'lmer' function from the "lme4" package in R.. Results of each model by environmental group containing adjusted R^2 and AIC values for Linear Mixed-effects Models (LMMs) are shown. AIC is Akaike Information Criterion used for model selection, whereas R^2m and R^2c are marginal and conditional R-Squared (R^2), respectively. Asterisks and dots by the independent variables represent the significance codes of the Pr(>|z|) of the model averaging in the final model (signif. codes: 0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1). Abbreviations of independent variables are explained in the Tables 1–3. Metadata: dep = dependent variable; ind = independent variable; group = environmental group; SHANNON = Shannon Diversity Index; SIMPSON'S = Simpson's Diversity Index. The + sign indicates the variable selected in the final model.

dep	group	ind	AIC	R^2m	R^2c
RICHNESS	**soil**	+ clay***, + CO_3**, + microS***, + OM**, + slp., + Ca^{2+}***, pH	1356.09	0.3075534	0.5820318
	climate	hamsl, slp_ex, preca, tmincol, ta	1364.582	0.05425904	0.6037529
	tree	+ ORIENT_S.	1368.363	0.007015232	0.5391888
	region	REG	-	-	-
HERBACEOUS BIOMASS	**soil**	+ clay**, Ca^{2+}, CO_3, cur_m, micros, OM, silt, slp, pH	1978.755	0.2460722	0.6369575
	climate	+ hamsl*, + preca**, + tmincol**, + ta**, ins, slp_ex,	1992.13	0.1207498	0.634577
	tree	CANOPY_m, DEF_POR, HEIGHT_m, ORIENT, Pc	2006.468	0.01575166	0.5845139
	region	REG	-	-	-
SHANNON	**soil**	+ slp.	357.2224	0.1285226	0.570943
	climate	preca	358.2531	0.1025845	0.5724177
	tree	+ ORIENT_S.	-	-	-
	region	+ REGHU*	355.7475	0.1298121	0.5707332
SIMPSON'S	**soil**	+ slp*	−85.48296	0.140402	0.5472967
	climate	+ preca*	−84.11802	0.1081402	0.5497028
	region	+ REGHU*	86.36119	0.1277835	0.5482839

3.4. Beta diversity

When comparing plots within Córdoba and Huelva separately, total beta diversity (CO: 85 %, HU: 83 %; Table A2), was mainly determined by turnover (CO: 80 %, HU: 77 %), while nestedness contribution (CO: 5 %, HU: 6 %) was significantly lower. The same tendency could be observed, when comparing samples between the two regions (Table A2); however, in this case, turnover was slightly higher (91 %). Comparison regarding the subplot orientation within the same region showed comparable results both in Huelva and Córdoba, with the lowest total beta diversity scores on the southern orientation (CO: 85 %, HU: 81 %; Table A2).

All spatial levels (region, plot, tree, and orientation) significantly influenced total beta diversity and turnover. However, nestedness was not affected by spatial scale (Table A2). Within each region, the greatest dissimilarities in herbaceous plant species composition were observed between plots, followed by trees, and then orientations (Table A3).

When considering both regions together, turnover was strongly influenced by the region (13 %), plot (37 %), tree (26 %) and orientation (0.9 %) ($p < 0.001$). Total beta diversity showed similar patterns, while nestedness was not significantly affected (Table A3).

Variation partitioning analysis highlighted the plot level as the most influential, accounting for 38 % of the total variation. The region level contributed 10 %, while trees from different plots explained 28 %. Tree effects within the same plot accounted for 7 %, and orientation contributed only 1 %. These trends were consistent within each region (Fig. 4).

The two-dimensional NMDS fit was acceptable (stress = 0.18), clearly separating the 240 subsamples by region (Fig. 5). Plant communities were influenced by water regime and aridity gradients (Fig. 5 and Table A4). Plots in Huelva showed higher minimum temperatures and significantly more annual precipitation compared to Córdoba plots. Edaphic factors such as organic matter, calcium,

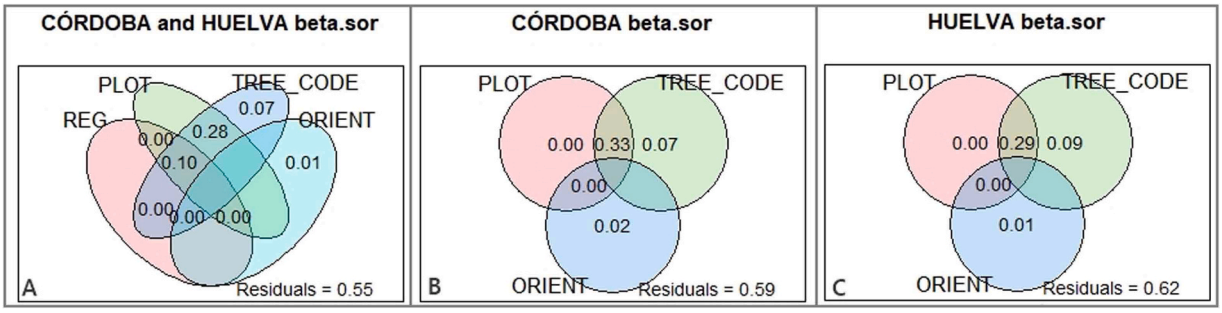

Fig. 4. | Results of variation partitioning based on redundancy analysis (RDA) relating the selected explanatory dataset (environmental factors), region (REG), plot (PLOT), tree (TREE_CODE), and subplot orientation (ORIENT), to herbaceous plant beta diversity (total dissimilarity, beta.sor) are presented for both regions, Córdoba and Huelva, considered together **(A)**, and separately: for the Córdoba region **(B)**, and Huelva region **(C)**. The values in the circles represent independent and shared effects (overlapping circles) expressed as proportions (percentages) of explained variation in beta-diversity (dissimilarity explained by turnover). The residual values are shown outside the circles, explaining other factors (explanatory variables) not considered in this Venn diagram.

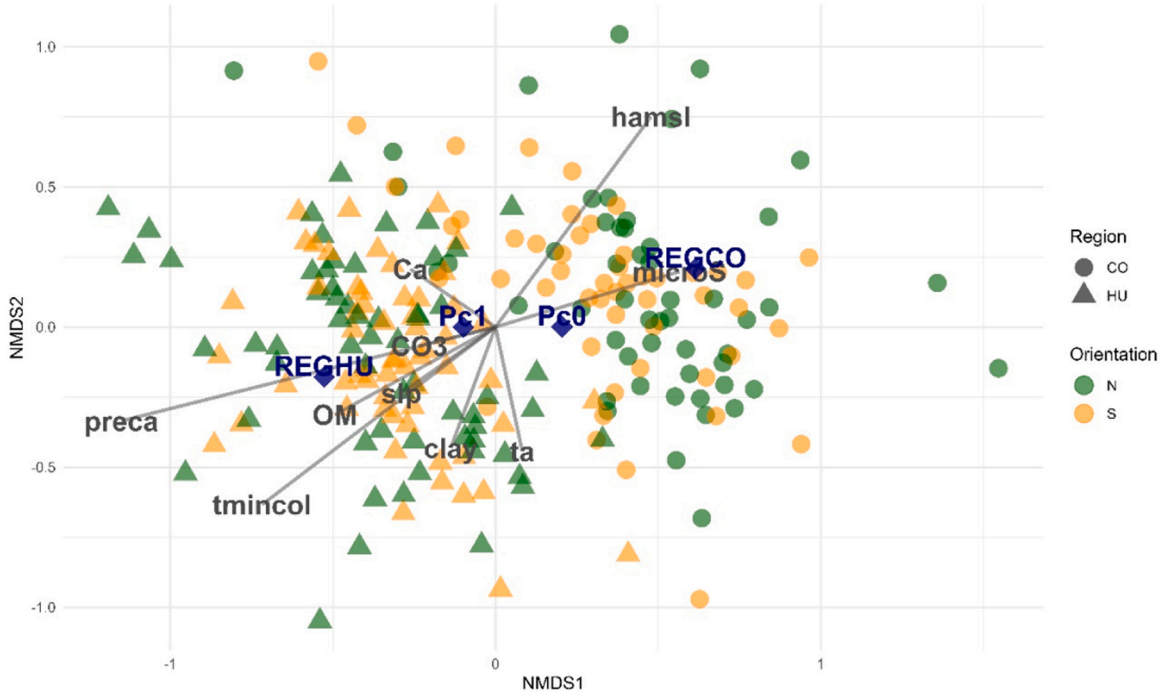

Fig. 5. | NMDS ordination of CO and HU plots with environmental variables, based alpha diversity regression analyses (linear mixed modelling), selecting statistically significant and marginally significant variables. Each point represents a CO-subplot, and the triangles are representing HU-subplots. The northern orientation is marked in green and the southern in yellow. Metadata: preca = precipitation annual [mm]; tmincol = average temperature of the coldest month [°C], ta = average annual temperature [°C]; hamsl = height above mean sea level [m]; OM = organic matter content [%]; slp = plot slope [degrees]; clay = soil clay content [%], Ca = Assimilable calcium Ca^{2+} [ppm]; CO_3 = total carbonate [%]; microS = electrical conductivity [S/cm]; RICH = herbaceous species richness [non-dimensional]; REGHU = Huelva region [non-dimensional]; REGCO = Córdoba region [non-dimensional, Pc1 = *P. cinnamomi* presence, Pc0 = *P. cinnamomi* absence.

and clay content were strongly related to the NMDS axes (Table A4). Plots in Córdoba exhibited higher electrical conductivity and elevation above sea level (Table A4).

Fifty-three (morpho-)species from the 'constant group', occurring more than 17 times per subplot, were included in the NMDS ordination, along with CO and HU plots and subplot orientations (Fig. 6). Contrary to our expectations, the NMDS did not reveal significant grouping or composition patterns among the (morpho-)species. However, notable differences between the two regions were observed (Fig. 6). The five most frequent species (and plant families) differed between regions, with only one species, *Ornithopus compressus*, shared (Fig. 6 and Table A5).

3.5. Tree health and Phytophthora cinnamomi influence

Phytophthora cinnamomi was detected in 66.6 % of trees, with a higher prevalence in Huelva (70 %), compared to Córdoba (63 %). DNA of the oomycete was found in all but one plot (CO1032). In five plots, including two in Huelva, visually unaffected by decline, the pathogen was detected in all sampled trees. Other plots had between 2 and 5 trees with *P. cinnamomi* DNA, with no significant difference between declining and non-declining plots (Table A6).

The presence of *Phytophthora cinnamomi* did not show significant relationships with alpha diversity indices, biomass, or richness (Table 4, Table A1). However, in terms of beta diversity, the occurrence of *P. cinnamomi* significantly influenced subplot separation in the NMDS analysis by region, with a more pronounced effect in Huelva (Fig. 5).

4. Discussion

Mediterranean *dehesas*, a unique agroforestry ecosystem, are known for their high herbaceous diversity. Despite this, the drivers shaping this plant variety and the intricate interactions between the herbaceous layer, tree layer, and environmental gradients are not well understood. To explore these patterns, we studied alpha and beta biodiversity of the herbaceous layer in holm oak *dehesas*, focusing on spatial scales and macro-scale environmental factors. Our findings indicate that water availability, a key limiting factor in Mediterranean climate, primarily determines alpha diversity, while temperature influences herbaceous plant biomass. However, a range of factors operate at different scales. We observed that herbaceous communities under similar environmental conditions tend to have comparable species compositions. Beta diversity analyses confirmed this, revealing clear differences in species composition

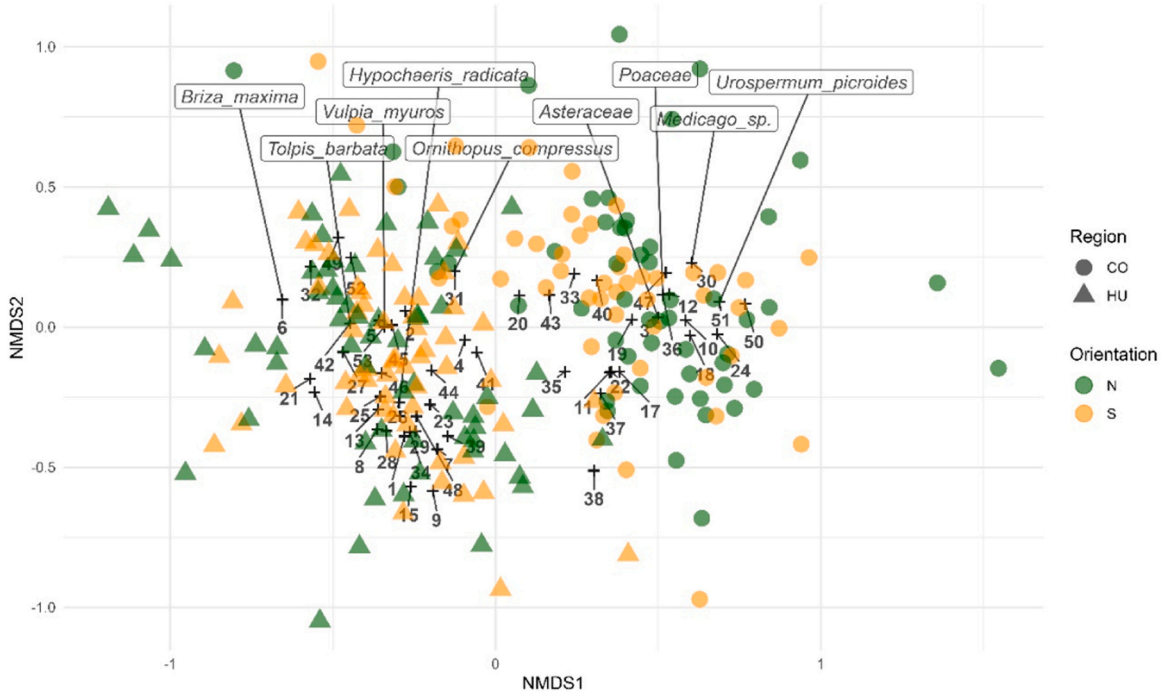

Fig. 6. | Subplots (samples) ordination of herbaceous plant data in the NMDS analysis. Points represent CO-subplots, and triangles represent HU-subplots. Northern orientations are marked in green and the southern in yellow. The most frequent 53 (morpho-)species (or families) according to the Rodwell's Method with presence in more than 17 sampling units (subplots/quadrats) across the entire study area are shown as crosses (+) with corresponding numbers. Additionally, the most frequent plant species are labelled with their names, highlighting the 5 most frequent species from each region.

between the two regions studied. As with alpha diversity, community differences were mainly driven by precipitation, with additional significant contributions from plot and tree factors.

4.1. Floristic composition and species richness

Herbaceous layer of the *dehesa* plots included in this work, were mostly composed of therophyte plants with almost exclusively annual species. Herbaceous and perennial plants are considered the most important resources in the *dehesa*, as they constitute the majority of the diet for livestock and complement other food sources throughout the year (Costa Pérez et al., 2006). The species found belonged mainly to five plant families: *Asteraceae, Poaceae, Fabaceae, Plantaginaceae*, and *Geraniaceae*. The *Fabaceae, Asteraceae*, and *Poaceae* families were considered in previous works as the most dominant herbaceous plant families in the *dehesa* ecosystem (Burzaco et al., 1992). In both Córdoba and Huelva region, forbs were the most prevalent functional group, followed by grasses and legumes, which are crucial for livestock forage (Devesa Alcaraz, 1991; Marañón, 1986). Gramineous plants were the second most abundant functional group in our *dehesa* stands. Besides providing fodder, the main advantages of grasses include preventing soil erosion, binding soil particles with the help of fibrous root systems, maintaining the soil structure and reducing water loss (Carrasco Martín, 2010). Although legumes made up only 16 % (Córdoba) and 21 % (Huelva) of species, they are vital for livestock due to their high protein content (Moreno, 2015). The lower richness of legumes in our study can be explained by the location of our samples in the transition zone of the oak crown projection,where lower radiation levels may competitively weaken these light-depending plants (Gea-Izquierdo et al., 2009; López-Carrasco et al., 2015). However, López-Carrasco et al. (2015) reported the highest legume yields near the edges of the tree crown and outside the canopy. Moreover, soil nitrogen and nitrogen mineralization rate increase beneath oak canopy (Moreno, 2015). As legumes, due to the symbiotic relationship with *Rhizobium* bacteria, are capable of nitrogen fixation, they might exhibit greater competitive advantage in less fertile soils outside the oak canopy projection (Moreno, 2015; Marañón 1986).

4.2. Drivers of plant alpha diversity and herbaceous biomass in dehesas

Plant diversity and richness of the herbaceous layer in Iberian *dehesas* is usually high (Moreno et al., 2016), and our results confirm this statement. We recorded an average of 12.0 ± 0.7 (morpho-)species per quadrat, similar to Marañońs (1986) report of 16.5 species per 4 m^2. Other studies have found even higher richness (spring sampling as well), with up to 37 ± 2.5 species per 100 m^2 (Moreno et al., 2016), which aligns with our maximum of 36 species per quadrat in one subplot from Huelva.

Our results indicate that the herbaceous communities differ markedly in structure and species composition, primarily due to

topographic and edaphic factors. Vegetation cover in agroforestry ecosystems vary in space and time due to differences in soil, topography, climate, weathering processes, and microbial activities (Manral et al., 2022, 2023; Paudel and Sah, 2003). In semi-arid *dehesas* ecosystem, higher clay content can help moisture retainage by the higher water holding capacity of clay (González González et al., 2012). Moreover, high clay content may be positively linked to soil electrical conductivity, which also showed strong correlation with richness in our study. Clay particles contribute to higher soil conductivity (Tabbagh and Cosenza, 2007) and therefore to higher presence of dissolved ions (Maathuis, 2009). Interestingly, calcium had a notable but negative impact on plant richness. In some cases, nutrient excess can lead to decline in plant species diversity and significant changes in the community composition, (Bedford et al., 1999). In the highly fragmented landscapes of disturbed ecosystems bioclimatic conditions change rapidly and may vary within short distances, resulting in a pronounced heterogeneity of soil types and vegetation (Bargali et al., 2018; Bäumler, 2015).

The Shannon and Simpson's indices showed higher biodiversity in Huelva compared to Córdoba. These differences are likely attributable to climatic variations: Huelva experiences milder summer temperatures and significantly more annual precipitation than Córdoba. These favorable conditions in Huelva support better plant growth and diversity within the semi-arid Mediterranean climate. The positive correlation between annual precipitation and biodiversity, particularly evident in the Simpson's Index, supports this observation. Chang (2000) similarly found that increased precipitation in fixed-dune grasslands led to higher species diversity, aligning with our findings. In semi-arid climates,precipitation is crucialas it affects soil moisture and plant growth. Variations in precipitation enable different plant species, both short-lived and long-lived, to complete their life cycles and contribute to overall community diversity. Fieldwork in Córdoba was conducted from March to mid-April, while sampling in Huelva occurred from late April to May. This sampling time was carefully scheduled attending to the different phenotypic characteristics of both zones, aiming to start in areas where herbaceous species were anticipated to proliferate earlier. We believe these differences may create discrepancies in relative abundance values, but not in richness and species composition, as the identification was carefully checked across the different stages of plant development.

We also identified plot slope as significant factor positively correlating with Simpson's Index and marginally significant with Shannon Index. This finding contrasts with other studies, which typically report increased plant cover and species richness with decreasing slope angles (Nadal-Romero, 2014). The opposing result in our study may be attributed to the influence of moderate slope levels of local conditions and habitats due to microtopography and microclimate variations. In terms of geophysical effects, slope angle can influence soil stability and erosion patterns, with steeper slopes potentially causing greater soil erosion and nutrient redistribution.

Statistical analysis revealed no significant differences in the biomass of herbaceous plants between the two regions according to the multivariate analysis. However, climatic variables emerged as crucial factors influencing biomass. Research by Díaz de León-Guerrero et al., (2021) in the Mediterranean-climate shrubland in Baja California (Mexico), suggested that environmental controls played a crucial role in shaping properties of plant communities, with biomass being strongly linked to water availability (Díaz de León--Guerrero et al., 2021). In our study, annual temperature and annual precipitation were strongly positively correlated with biomass, while the average minimum temperature of the coldest month showed a negative correlation. In semiarid regions, adequate precipitation ensures a steady water supply, which is a limiting factor in Mediterranean climates (Jacobsen et al., 2012). As long as water supply is not limited, the combination of warmth and sunshine create ideal conditions for plant development, since higher temperatures often fall within the optimal growth range of many plant species adapted to semi-arid conditions. Additionally, herbaceous biomass was positively influenced by plot characteristics such as height above mean sea level. Higher altitudes, especially in summer, typically offer milder temperatures and greater winter precipitation, which can enhance plant growth and biomass production compared to the more extreme climates of lowlands. Furthermore, soil clay content exhibited a positive linear correlation with biomass.

Clay is one of the main factors in retaining moisture in dryland soils (Kramer and Boyer, 1995). Its high fertility also promotes crop production (Hoekstra et al., 2005). In heavy rainfall conditions, clay-rich soils can enhance woody plant biomass due to their high water-holding capacity (Laurance et al., 1999).

4.3. Beta diversity patterns

Our results indicated that nestedness contributed significantly less to total beta diversity than turnover, both within and between regions. This suggests that species assemblages across subplots are notably distinct and do not commonly overlap. High beta diversity reflects substantial variation within communities, likely driven by considerable environmental differences among the locations studied (Nekola and White, 1999).

Beta diversity partitioning revealed that plot level was the primary driver of dissimilarities among samples, with smaller contributions from tree-level factors within plots. Given that *Phytophthora cinnamomi* was present in all but one plot, differences in plant communities are more likely attributed to tree and microsite characteristics rather than the tree health alone.The findings from alpha diversity support this, suggesting that varying sampling positions within plots, which provide different microhabitats, are more critical than phytosanitary state in explaining community differences.. Considering the combined effect of plot and tree levels, we infer that the geographical and climatic factors at larger, regional scale are equally important as the microsite characteristics and features. Plant communities often exhibit spatial heterogeneity, by altering the composition and abundance of species across different microsites within a plot (Chesson, 2000; Levins, 1979). Hence, sampling localities may affect the plant community compositions by capturing broad range of species due to microenvironmental gradients, different degrees and types of species interactions, microclimatic differences, or variations in soil conditions (Liu et al., 2020; Xu et al., 2000).

We observed significant regional and local heterogeneity among *dehesa* plots, influenced by various ecological factors at both scales. The NMDS clustering analysis revealed that samples were predominantly separated by region, reflecting the milder and wetter

conditions in Huelva compared to Córdoba, likely due to Huelva's maritime influence. At a finer scale, edaphic variables played a crucial role, with Córdoba plots showing less organic material and higher soil conductivity. In summary, regional differences in herbaceous diversity were strongly influenced by water availability and soil quality, with a gradient from the wetter West (Huelva) to the drier East (Córdoba).

4.4. Tree health and Phytophthora cinnamomi presence

The soil-borne pathogen *Phytophthora cinnamomi* Rands is a severe threat to plant health worldwide and is a major driver of tree loss in *Quercus ilex* and *Quercus suber* forests in the Iberian Peninsula (Hardham and Blackman, 2018; Sena et al., 2018; Ruiz-Gómez et al., 2019). We hypothesized that its presence in dehesas would influence herbaceous layer composition, either directly or through effects on tree health. However, our analysis revealed no significant relationship between *P. cinnamomi* presence, tree characteristics (such as size or defoliation), and herbaceous diversity or biomass.

We were surprised to find that *Phytophthora cinnamomi* was present in all but one of the plots deemed healthy for our study. This suggests that *P. cinnamomi* may not be the primary cause of tree decline but rather a contributing factor, consistent with the concept of forest decline as a syndrome involving predisposing, inciting, and triggering factors (Manion and Lachance, 1992). Our experimental design relied on expert assessments based on visual symptoms. Consequently, *P. cinnamomi* may be present in plots without apparent symptoms until a clear decline becomes evident. This finding indicates that the pathogen's spread is more extensive than previously understood and poses a threat to the sustainability of holm oak *dehesas*.

Although there were no differences in *P. cinnamomi* prevalence between the plots, the varying levels of defoliation might have affected herbaceous diversity. The choice of quadrat locations at the tree crown edges might have created a mixed community of open and shade-adapted species, potentially diminishing the impact of tree shade changes on herbaceous diversity. Alternatively, *P. cinnamomi* might primarily affect specific plant species or *Quercus ilex* roots, leaving other species unaffected. If the herbaceous community primarily consists of species resistant to or less affected by the oomycete, their diversity might remain largely unchanged, with these species potentially acting as symptomless hosts (Crone et al., 2013a; Wills, 1993).

Despite evidence of *P. cinnamomi* presence in various herbs (Crone et al., 2013b; Serrano et al., 2010, 2012), research on its pathogenicity to herbaceous plants remains limited. Further studies are needed to fully understand these interactions. Nonetheless, the correlation between the presence of pathogen DNA in the soil rhizosphere and the separation of CO and HU plots—particularly the higher prevalence in HU—supports previous findings. This suggests that while environmental factors modulate the pathogen's impact on trees (Sánchez-Cuesta et al., 2021), *P. cinnamomi* plays a significant role as a triggering factor in forest decline. Moreover, it has been shown, that in various Mediterranean ecosystems, the presence of trees and woody species negatively impacts the diversity of herbaceous communities. Madrigal-González et al., (2010) demonstrated that the understory of *Pinus pinaster* mediterranean forests vary significantly, as well in evergreen maquis (Agra and Ne'eman, 2009). Despite the evidence that in most of the Mediterranean forests herbaceous vegetation is strongly modulated by canopy cover, it seems that in agroforestry systems like dehesa, this effect is low or even negligible.

5. Conclusions

Our results showed that herbaceous plant communities in dehesa stands are affected by both climatic conditions and microsite characteristics. At the regional scale, annual precipitation significantly impacts herbaceous biomass and diversity, reflecting its role as a limiting factor in Mediterranean climate. At the site scale, factors like soil clay content and plot slope positively correlate with plant biodiversity, richness, and growth, though these effects vary by diversity index. Small-scale variations in resource availability significantly affect floristic composition and productivity of annual plants in semi-arid environments (Haase et al., 1996). Limited nutrient availability may reduce competition and enhance positive species interactions under environmental stress. Although *P. cinnamomi* did not appear to impact herbaceous diversity or composition, its widespread presence across the study area suggests that further research is needed to confirm its effects. Overall, climate, local environmental conditions, and plant adaptations are crucial in shaping herbaceous community structures beneath holm oak canopies.

Our study's findings have direct implications for the sustainable management of dehesa ecosystems. The critical role of annual precipitation suggests that water conservation practices, such as mulching and water-retaining structures, are vital to mitigate drought impacts and enhance plant diversity. Improving soil health through reduced tillage, cover cropping, and organic amendments can increase water retention and nutrient availability, thereby fostering herbaceous diversity (Lal, 2015). Given the positive impact of soil clay content, amending sandy soils with clay or organic matter could be beneficial. Maintaining microsite heterogeneity is crucial and can be achieved by preserving tree cover, promoting natural tree regeneration, and integrating agroforestry practices to create diverse microhabitats (Jose, 2009). Although tree health did not significantly affect herbaceous diversity, monitoring it remains important for overall ecosystem resilience and sustainability (Plieninger et al., 2003).

CRediT authorship contribution statement

Conceptualization, P.G.M. and F.J.R-G.; methodology, P.G.M, F.J.R-G. and A.L.G; formal analysis, K.O., P.G.M. and L.L.; resources, K.O., P.G.M. data curation, K.O.; writing—original draft preparation, K.O. and P.G.M.; writing—review and editing, all the authors; supervision, P.G.M. and F.J.R-G.; All authors have read and agreed to the published version of the manuscript.

Declaration of Competing Interest

The authors declare the following financial interests/personal relationships which may be considered as potential competing interests: Francisco Jose Ruiz Gomez reports financial support was provided by Life FAGESOS project (101074466-LIFE21-CCA-IT-LIFE FAGESOS). Francisco Jose Ruiz Gomez reports financial support was provided by Spain Ministry for the Ecological Transition and Demographic Challenge. Pablo Gonzalez Moreno reports financial support was provided by Ramon y Cajal School. Francisco Jose Ruiz Gomez reports financial support was provided by Government of Andalusia. Pablo Gonzalez Moreno reports financial support was provided by IES Juan de la Cierva y Cordorniú. Francisco Jose Ruiz Gomez reports financial support was provided by European Social Fund 2014–2020. Katherine Onoszko reports financial support was provided by CeiA3 Excellency Campus. If there are other authors, they 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.gecco.2024.e03162.

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