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Short communication

Short-term effects of red deer overabundance on herbaceous communities in Mediterranean woody ecosystems

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ABSTRACT

Herbaceous communities are vital for biodiversity in forests and scrublands. Herbivory influences their cover, richness, and diversity. Overabundant herbivores disrupt these communities and ecosystem processes. In recent decades, vast territories (e.g., North America, Europe) have experienced a remarkable increase in deer (Cervidae) populations. However, few studies have examined the effects of increasing ungulate densities in different Mediterranean habitats. This study explores the short-term impacts of red deer overabundance on the cover, richness, and diversity (taxonomic and functional) of herbaceous layers in Mediterranean scrublands and forests to guide management. In three enclosures across two habitats (scrubland and oak forest), we manipulated deer densities: control (no deer), high density (18–63 deer/km^2), and hyper density (58–113 deer/km^2). Herbaceous species occurrence and cover were recorded in 90 quadrats (50 × 50 cm), alongside bibliographic data for six functional traits. Herbaceous cover, richness, and diversity (taxonomic and functional) were analysed with Generalized Linear Mixed Models. Hyper deer density negatively affected herbaceous cover, taxonomic richness, and diversity in both forests and scrublands. The high density treatment already showed a clear trend towards reducing these three variables that were heavily increased for the hyper density scenario (e.g. 84.2 % cover loss in the scrubland and 64.2 % in the forest). Functional diversity remained unchanged, likely due to a $>$ 40-year legacy of deer herbivory favoring traits typical of grazing areas. Deer overabundance is causing rapid, drastic changes in herbaceous communities, even in short term. Managers should reduce deer populations to protect these communities, which offer high-quality forage and essential ecological roles.

1. Introduction

Large herbivores modify species composition, seed dispersal and regeneration of different plant species through their food preferences, droppings, urine, and trampling, (Olff and Ritchie, 1998; Côté et al., 2014). They exert an engineering role in ecosystems by changing the structure, species richness, and functional and taxonomic diversity of vegetation that, in turn, alter animal populations and ecological processes (Hobbs, 1996; Díaz et al., 2007; Côté et al., 2014; Jia et al., 2018; Pringle et al., 2023). However, the intensity of their effects depends on the number of individuals grazing within a specific area over a given period, as demonstrated by observational (Horsley et al., 2003), experimental (Lecomte et al., 2016), and modelling studies (Ferraro et al., 2021).

The overabundance of large herbivores leads to overgrazing —defined as a scenario where forage species cannot sustain themselves

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over time due to excessive herbivory or associated processes (Mysterud, 2006)— that compromises the ecological integrity and resilience of ecosystems (Olofsson, 2006; Côté et al., 2004; Nishizawa et al., 2016). Among large herbivores, wild ungulates are currently gaining relevance due to their continuous population increase in vast territories of the Northern Hemisphere (Côté et al., 2004; Apollonio et al., 2010; Pascual-Rico et al., 2021). The red deer (*Cervus elaphus* L.), considered a mixed-feeder as it consumes both woody and herbaceous plants (Álvarez and Ramos, 1991; Gebert and Verheyden-Tixier, 2001), is experiencing a strong population growth (Côté et al., 2004; Carpio et al., 2021) also observed in the Iberian Peninsula since the mid-20th century. This trend is favoured by the absence of natural predators, rural abandonment, an increase in the number of protected areas, and, most notably, big game management in both protected and non protected areas (Charco, 2002; Putman et al., 2011; Perea et al., 2014).

Hunting is a widespread activity globally (Apollonio et al., 2010). Spain ranks among countries with the highest hunting demand worldwide (Hofer, 2002), with 85 % of its land used for hunting activities, especially big game (Gallego, 2009; Ministerio para la Transición Ecológica y el Reto Demográfico [MITECO], 2021; Gallego et al., 2022). In this context, the red deer exhibits remarkably high population densities, often reaching 30 individuals/km^2 and, in some cases, hyper densities of 60–98 individuals/km^2. This overabundance promoted by big game hunting is observed across diverse landscapes, such as scrublands and forests (Azorit et al., 2002; Charco, 2002; Fernández-Olalla et al., 2006; Vicente et al., 2007; Acevedo et al., 2008; Nugent et al., 2011; Azorit et al., 2012; Perea et al., 2014; Carpio et al., 2015). These areas dedicated to big game hunting include public and private fenced lands ranging from 500 to over 5000 ha, where herbivores mobility is limited (Charco, 2002; Vicente et al., 2007; Azorit et al., 2012; Perea et al., 2014). Compared to natural densities (10 individuals/km^2, Morales-Molino et al., 2019), these elevated densities can surpass the carrying capacity of many ecosystems, raising significant ecological concerns (Carpenter et al., 2000; Putman et al., 2011).

The increase in ungulate populations, including red deer, has led to different studies about their effects on vegetation (Bugalho et al., 2011; Boulanger et al., 2017; Unsgård et al., 2024). The most recent meta-analysis (Jia et al., 2018) reveals that effects on richness, and biomass are highly site-specific. Furthermore, most studies use exclusion-control comparisons (Farris et al., 2010; Jia et al., 2018; Riesch et al., 2020) to contrast vegetation metrics. Thus, the precise quantification of the number of grazing individuals outside the exclusions, and consequently the attribution of grazing effects to individual ungulates, remains largely unexplored (Herrero-Jáuregui and Oesterheld, 2017; Jia et al., 2018; DeYoung et al., 2019). In the case of the Mediterranean areas, this knowledge gap is further exacerbated by the fact that most studies have been conducted in *dehesas* or grassland ecosystems (Carmona et al., 2012; López-Sánchez et al., 2016; Rota et al., 2016). Therefore, the effects of ungulate overabundance on the herbaceous layer in scrublands and forests remain significantly understudied despite its ecological relevance at the ecosystem level (Gilliam, 2007; Thiemann et al., 2009; Spicer et al., 2022).

Herbaceous plants are crucial in different ecosystems, contributing significantly to their biodiversity, ecological functioning, and resilience (Gilliam, 2007; Spicer et al., 2022). The significance of the herbaceous community requires the examination of taxonomic and functional parameters of the herbaceous layers to facilitate the acquisition of comprehensive insights into the community's response to explicit herbivore densities (Díaz et al., 2007; Peco et al., 2012; Nishizawa et al., 2016). Furthermore, the increasing frequency of drought periods in the Mediterranean region poses a significant threat to herbaceous plants (Fernández-González et al., 2005; Lens et al., 2016), which are highly palatable for red deer. Consequently, there is a need for further research into the impacts of ungulate overabundance with very limited mobility on herbaceous plant communities to inform effective management strategies (Charco, 2002; Vicente et al., 2007; Apollonio et al., 2010; Kauffman et al., 2021; Pringle et al., 2023).

Our work focuses on the study of the effects of deer overabundance (high density 20–60 deer/km^2 and hyper density > 60 deer/km^2) on the cover, taxonomic richness, taxonomic diversity, and functional diversity of herbaceous understory communities of two distinct habitats, forest and scrubland, in an unmanaged but fenced Mediterranean environment. This scenario is quite common across vast territories of Spain. We, therefore, aim to evaluate the short-term effects after three months of increasing red deer densities under the same ecological conditions (adjacent enclosures) as a basic step to study the cascading consequences towards the rest of the components of Mediterranean ecosystems. We hypothesise that herbaceous cover, richness, and taxonomic and functional diversity will be reduced for hyper deer densities compared to high densities and control situations (no deer). We expect a similar response in both diversity facets to increase deer densities regardless of the overstory habitat type (scrubland vs forest).

2. Material and methods

2.1. Study area

The study area is in Los Quintos de Mora, in the southeastern region of Montes de Toledo range, Toledo province, central Spain (39°26′48.57”N, 4°5′57.38”W, 907–950 m. a. s. l). The climate is Mediterranean continental (mean annual temperature: 14 °C; average annual rainfall: 622 mm) (San Miguel et al., 2011). Soils are poorly developed and acidic, derived from sandstones, slates and quartzites (León Gómez et al., 1981). The landscape is dominated by two distinct plant communities: scrublands co-dominated by *Cistus ladanifer* L., *Rosmarinus officinalis* L. and the genus *Erica*, and forests dominated by *Quercus pyrenaica* Willd with a scattered understory dominated by *Erica* spp. and *Arbutus unedo* L. Herbaceous communities are mostly dominated by annual (therophytes) and oligotrophic taxa (*Bromus, Crepis, Filago, Hipochaeris, Tolpis, Tuberaria, Vulpia*) with an ephemeral life cycle that is completed in May–June.

2.2. Experimental design

To the best of our knowledge, this is the first large-scale experimental study involving the manipulation of wild herbivore densities, specifically red deer, within woody Mediterranean ecosystems.

The experiment was conducted in a ~ 17-ha enclosure that had experienced low deer densities (~10 individuals/km^2; DeYoung et al., 2019) over the last decades until they were removed just before our study. In 2020, the enclosure was divided into three adjacent sub-enclosures measuring 2.6, 7.1, and 7.4 ha, each separated by 2-m-high wire fences. All sub-enclosures shared similar environmental features with comparable proportions of vegetation types, including oak forests and scrublands.

Red deer (*Cervus elaphus*) were introduced in March 2021, only females due to their ease of handling: control (2.6 ha) without red deer (and any other large herbivore); high density treatment (2–7 individuals in 7.4 ha, equivalent to 18–63 deer/km^2); and hyper density treatment (6–12 individuals in 7.1 ha, equivalent to 58–113 deer/km^2). The last two scenarios were compared to the control enclosure without deer since ungulate exclosures are a common conservation measure to preserve vegetation in protected areas (Török et al., 2024). The presence of other possible herbivore taxa was discarded by photo-trapping (3–6 cameras per enclosure, Strike Force HD ProX 20MP, Browning). The scale of the experiment made it unfeasible to generate spatial replicates.

The sampling campaign was conducted in June 2021, when most herbaceous plants (mostly therophytes) completed their life cycle and exhibited their diagnostic characteristics (regarding flowers, fruits and seeds). In each treatment, 10 transects (30 m long) were randomly distributed, five in the forest and five in the scrubland. Within each transect, three 50 × 50 cm quadrats were placed, preferably at metres 7, 14 and 21, and the ground cover (%) of each species was recorded (**Table S1**). The efficiency of this methodology was assessed using rarefaction curves (**Fig. S1)**.

The short-term (three-month) effects of different deer densities on the herbaceous layer of scrubland and forests were evaluated by analysing herbaceous coverage, species richness, taxonomic diversity, and functional diversity.

Before the 2021 sampling campaign, an initial survey was conducted in June 2020 to ensure that the herbaceous strata of the scrubland and forests were similar in the three sub-enclosures before the manipulated deer entry. Specifically, cover and species richness were sampled in the same transects and plots considered later in 2021.

2.3. Data collection for functional diversity

Six functional traits were considered: Biotype (therophyte, cryptophyte, chamaephyte or hemicryptophyte), Dispersal Mode (barochory, anemochory or zoochory), Height (cm), Seed Weight (mg), Leaf Area (mm^2), and Specific Leaf Area (SLA) (mm^2/mg). The Biotype follows Raunkiaer's criteria (Raunkiaer, 1934) and the Dispersal Mode reflects the most basic types (Ridley, 1930). The main source of information to build a matrix of 80 taxa (from the 84 total taxa found in the study area) and six functional traits was BROT (Tavşanoğlu and Pausas, 2018) but the final matrix had to be completed with different Iberian floras (Castroviejo, 1986-2021; Valdés et al., 1987; Devesa, 1995) and scientific articles (Azcárate et al., 2002; Peco et al., 2009; Silvestre et al., 2019; de Bello et al., 2021) (**Table S2**).

2.4. Statistical analyses

We developed Generalized Linear Mixed Models -GLMMs- to evaluate the pre-treatment scenario, using data form 2020, and to evaluate the short-term effects of deer overabundance on herbaceous communities of two distinct habitats (forest and scrubland) at increasing deer densities, using data from 2021 (Dobson, 2002). The analyses considered plots nested within transects as a random effect for all models.

For each sample unit (50 × 50 cm quadrat), the response variables were the percentage of total herbaceous cover, taxonomic richness, taxonomic diversity and functional diversity. Richness was calculated by counting taxa, and taxonomic diversity was estimated through the Shannon-Wiener index ($H' = -\Sigma\, Pi \log2\, Pi$; where Pi = relative abundance of the taxon; Shannon, 1948), using the relative cover of each herbaceous taxon. For functional diversity comparisons, we log-transformed the Height, Leaf Area and Seed Weights. The functional diversity was then calculated using the Rao index ($\text{Rao} = \sum_{i=1}^{S} \sum_{j=1}^{S} d_{ij}\, p_i\, p_j$; d_{ij} expresses the dissimilarity between i and j pairs of species; p_i and p_j refer to the relative abundances of species i and j) from the Gowdis distance matrix, as supported by other authors (Carmona et al., 2012; Peco et al., 2017; de Bello et al., 2021). Due to the non-Euclidean nature of the dissimilarity matrix (Gowdis distance), the cailliez correction was applied to avoid negative values (Cailliez, 1983).

The explanatory variables considered in the models are two: Treatment, which consists of three categories corresponding to red deer densities (null, high and hyper) and Habitat, which comprises scrubland and forest. The response variables were fitted to: a) gamma distribution for vegetation cover of 2021 and 2020, using the Box-Cox transformation in order to calculate the power lambda link that maximises the likelihood (Box and Cox, 1964); b) negative binomial distribution for taxonomic richness of 2020; c) negative binomial zero-inflated distribution for taxonomic richness of 2021; d) gaussian distribution for taxonomic diversity and the logarithm of functional diversity. In each of the analyses, different GLMM were considered depending on the explanatory variables: i) Treatment; ii) Habitat; iii) Treatment and Habitat; iv) Treatment, Habitat and their interaction. Model averaging was applied and only the best-fitting models (hereafter top models) wit Δ *AIC* below 3 needed to reach a total *AIC* weight at least equal to 80 % were retained Δ *AIC* is the difference between Akaike's Information Criterion of the model and the model with minimum *AIC* (Akaike, 1974; Burnham and Anderson, 2002). The *AIC* weights were also used to calculate the relative importance of each predictor, from 0 to 1. The explained deviance and the dispersion parameter were calculated to confirm their validity and the absence of overdispersion (McCullagh and Nelder, 1983).

Data processing and statistical analyses were performed using R 4.2.2 (R Core Team, 2022) and RStudio (RStudio Team, 2022). The packages required were: “vegan” (Shannon-Wiener index) (Oksanen et al., 2018), “FD” (Gowdis and Rao index) (Laliberté et al., 2014), “MASS” (GLMM) (Venables and Ripley, 2002), “MuMIn” (model averaging) (Barton, 2022), “caret” (Box-Cox transformation) (Kuhn, 2022) and “DHARMa” for checking model assumptions (Hartig et al., 2024).

3. Results

3.1. Pre-treatment scenario

The survey conducted in 2020 yielded a total of 83 herbaceous taxa. The analyses showed a great similarity in terms of herbaceous layer coverage and species richness across the three enclosures before the introduction of deer ($p_{\text{Hyper-High}} = 0.078$ and $p_{\text{Hyper-High}} = 0.349$ respectively; Table 1). The results also reflected higher values of herbaceous cover and species richness in the forest patches than in the scrublands (Table 1).

3.2. Effect of ungulate overabundance on vegetation cover

The top GLMM for herbaceous cover considered Treatment, Habitat and their interaction as explanatory variables (Table 2). However, only Treatment and interactions showed significant differences. Hyper density treatment showed significantly lower values of cover than those of the high density treatment ($p_{\text{Hyper-High}} = 0.006$) and the control (Table 2). The high density and the control treatments showed similar cover values (Table 2). The analysis also revealed a significant effect of the interaction between Habitat and Treatment. The scrubland with hyper density treatment has lower cover compared to any habitat without deer and the forest with high density treatment ($p_{\text{Scrubland:Hyper-Scrubland:Null}} = 0.009$, $p_{\text{Scrubland:Hyper-Forest:Null}} = 0.002$, $p_{\text{Scrubland:Hyper-Forest:High}} = 0.005$).

Herbaceous cover in the scrubland decreased from the 23.4 % found in the control to 16.1 % in the high density treatment and nearly disappeared with hyper density of red deer where only 3.7 % remained. The reduction in the forest was also notable, with cover dropping from 32.1 % in the control to 26.4 % in the high density treatment and to less than a half, 11.5 %, in the hyper density scenario (Fig. 1A).

3.3. Effect of ungulate overabundance on taxonomic richness

After three months of treatment implementation, a total of 83 herbaceous taxa were identified in the study area. The lowest richness values were observed in the hyper density deer treatment, followed by the high density deer treatment and the control. In the scrubland, the numbers of taxa were 18, 28, and 44, respectively. In the forest, the numbers of taxa were 25, 36, and 41, respectively. The top GLMMs included the effect of the variables Treatment and Habitat but discarded the interaction between them (Table 2). Significant differences were observed between the hyper density and the other two treatments ($p_{\text{Hyper-Control}} < 0.001$; $p_{\text{Hyper-High}} = 0.006$), but not between habitats ($p = 0.358$) (Fig. 1B). Richness in the high density and control treatments showed marginal differences ($p_{\text{High-Control}} = 0.062$).

Table 1

Summary of the Model averaging of the top Generalized Linear Mixed Models fitted for response variables (% cover and taxonomical richness) comparing the red deer (*Cervus elaphus*) density treatments (Control, High and Hyper) and habitats (Scrubland and Forest) in Los Quintos de Mora (central Spain). ED: Error distribution. Importance: predictor contribution in the selected models ranging from 0 to 1. High and Hyper treatments are compared against control, and forest habitat against scrubland.

Response variable	ED	Predictor	Impor-tance	Level	Coeff.	SE	t value	*p*-value
Taxonomic richness 2020	Negative binomial	(Intercept)			0.999	0.174	5.661	<0.001
		Treatment	0.26	High	0.023	0.253	0.090	0.929
				Hyper	0.260	0.250	1.026	0.305
		Habitat	0.86	Forest	0.051	0.211	2.374	0.018
% Cover 2020	Gamma	(Intercept)			1.904	0.181	10.403	<0.001
		Treatment	0.54	High	0.416	0.243	1.686	0.092
				Hyper	−0.030	0.224	0.131	0.895
		Habitat	0.99	Forest	0.595	0.211	2.784	0.005

Table 2

Summary of the Model averaging of the top Generalized Linear Mixed Models fitted for response variables (% cover, taxonomical richness, taxonomical diversity and functional diversity) comparing the red deer (*Cervus elaphus*) density treatments (Control, High and Hyper) and habitats (Scrubland and Forest) in Los Quintos de Mora (central Spain). ED: Error distribution. Importance: predictor contribution in the selected models ranging from 0 to 1. High and Hyper treatments are compared against control, and forest habitat against scrubland.

Response variable	ED	Predictor	Impor-tance	Level	Coeff.	SE	t value	p-value
% Cover	Gamma	(Intercept)			2.575	0.279	9.239	<0.001
		Treatment	1.00	High	−0.275	0.374	−0.735	0.462
				Hyper	−1.089	0.322	−3.385	<0.001
		Habitat	1.00	Forest	0.255	0.414	0.616	0.538
		T:H	0.99	High:Forest	0.114	0.563	0.203	0.839
				Hyper:Forest	0.342	0.498	0.686	0.492
Taxonomic richness	Negative binomial zero inflated	(Intercept)			2.181	0.190	11.318	<0.001
		Treatment	0.99	High	−0.449	0.237	1.863	0.062
				Hyper	−1.151	0.253	4.486	<0.001
		Habitat	0.42	Forest	−0.185	0.198	0.920	0.358
Taxonomic diversity	Gaussian	(Intercept)			1.747	0.188	9.180	<0.001
		Treatment	0.97	High	−0.422	0.212	1.956	0.051
				Hyper	−0.858	0.212	3.969	<0.001
		Habitat	0.52	Forest	−0.322	0.168	1.878	0.06
Log Functional Diversity	Gaussian	(Intercept)			−3.299	0.124	26.124	<0.001
		Habitat	0.31	Forest	−0.195	0.206	0.934	0.35

3.4. *Effect of ungulate overabundance on taxonomic diversity*

The top GLMMs included Treatment and Habitat as explanatory variables (Table 2). Taxonomic diversity was significantly lower in hyper deer density compared to control and to the high density ($p_{\text{Hyper-Control}} < 0.001$; $p_{\text{Hyper-High}} = 0.042$). The high deer density treatment showed lower taxonomic diversity than the control with marginal differences ($p_{\text{High-Control}} = 0.051$). A general trend of inverse relationship between diversity and deer density **(**Fig. 1C**)**.

3.5. *Effect of ungulate overabundance on functional diversity*

The functional diversity in both habitat types was unaffected by red deer overabundance. The two top GLMMs for functional diversity included: 1) no variables (model weight = 0.686); and 2) Habitat (model weight = 0.203), as explanatory variables (Table 2). The functional diversity showed no significant differences between habitats (Fig. 1D).

4. Discussion

4.1. *Effects of ungulate overabundance on vegetation cover*

The results revealed that the hyper abundance of red deer reduced the cover of the herbaceous layer in both habitats (Fig. 1A). According to Côté et al. (2004), deer can enhance herbaceous cover, but when they become overabundant, they reduce the herbaceous layer. The loss of ground vegetation can significantly impact the entire ecosystem despite its shorter stature than the tree or shrub canopy (Gilliam, 2007). The relevance of ground vegetation extends beyond providing food for herbivores and pollinators. While they are naturally crucial in ecosystems dominated by herbaceous taxa (e.g., steppe grasslands and savannas), they also play an essential role in the structure and function of woody ecosystems. For instance, they contribute to energy flow and nutrient cycling by producing high-quality foliar litter and reducing potential nutrient loss (Gilliam, 2007).

The impact that we detected in the scrubland was so significant that it nearly caused the disappearance of the herbaceous community (Fig. 1A). Müller et al. (2017) highlights the preference of herbivores for elevated areas with greater visibility, which in our study system correspond to the scrubland. However, deer are expected to spend more time in the forest due to their preference for specific characteristics, such as hiding places, greater water availability or the high-quality forage from young deciduous trees (Torres et al., 2013; Müller et al., 2017). Thus, the limited mobility of herbivores in the study area may alter their natural behaviour, as frequently occurs in fenced areas (Boone and Hobbs, 2004). Moreover, the impact on the herbaceous layer of the scrubland could also be due to the higher abundance of small therophytes (e.g., *Filago gallica* L. or *Galium parisiense* L.), which are entirely consumed, compared to the abundance of perennial hemicryptophytes (e.g., *Doronicum plantagineum* L. or *Festuca* spp.) in the forest, which are typically grazed only on their scapes, thereby preserving some degree of cover (basal or rosulate leaves).

The results of this study clearly demonstrate that such overabundance can drastically reduce the cover of the herbaceous layer, especially in fenced scrubland ecosystems. Thus, these findings highlight the potential for the current hyper abundance of red deer, observed in vast territories (either protected or unprotected), to have significant and detrimental consequences on the ecological integrity of these

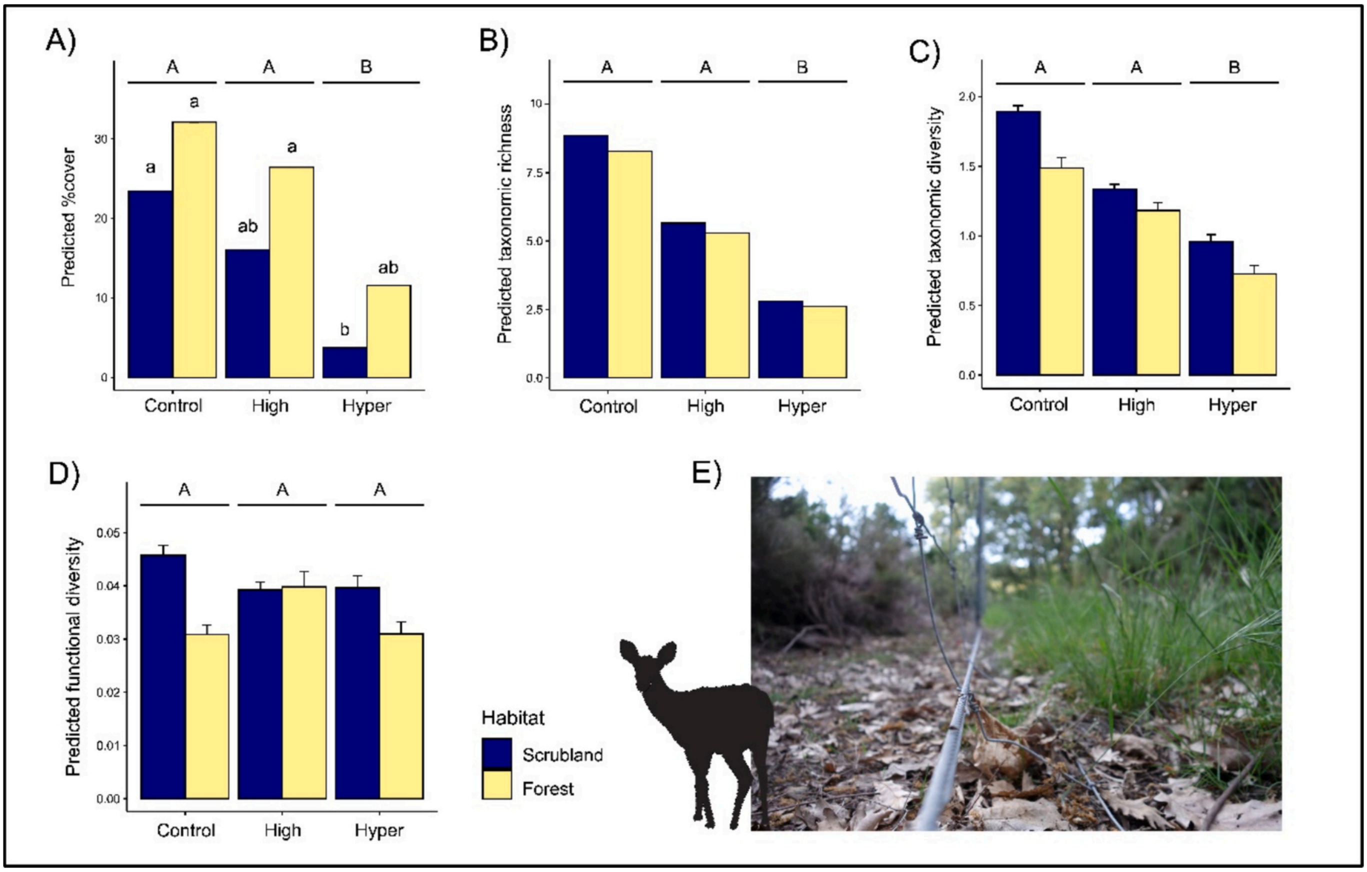

Fig. 1. Mean values of predicted percentage cover (A), taxonomic richness (B), taxonomic diversity (C) and functional diversity (D) in the red deer (*Cervus elaphus*) density treatments (Control, High and Hyper) and habitats (Scrubland and Forest) in Los Quintos de Mora (central Spain). Bars represent standard errors. Identical letters (A, B, a, b) above bars indicate no significant differences in the response variables, while different letters indicate significant differences. E) Limit between high deer density treatment and control in the forest of the study area. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

ecosystems.

4.2. Effects of ungulate overabundance on taxonomic richness and diversity

The results of this study show a decreasing trend in both taxonomic richness and diversity of herbaceous plants after three months of red deer overgrazing with limited mobility. This fast decline culminates in very low and significantly different values at hyper overabundance, in which the total richness is reduced by almost 2/3 compared to the control.

Previous works support the positive effects of ungulates on the richness and diversity of herbaceous plant communities in different environments (e.g., by increasing environmental heterogeneity at the local scale) (Olff and Ritchie, 1998; Tschöpe et al., 2011). It is also argued that some ecosystems (e.g., Mediterranean) exhibit a high resilience, largely promoted by prolonged historical exposure to anthropogenic and natural disturbances such as fires and herbivore grazing (Gutman et al., 1999; Blondel et al., 2010; Sternberg et al., 2015; Pringle et al., 2023). However, most of the previous works do not evaluate the effects of strong levels of overabundance of wild ungulates, such as those registered in private or public lands devoted to big game or even within National Parks in Mediterranean ecosystems (Charco, 2002; Nugent et al., 2011; Perea et al., 2014; Morales-Molino et al., 2019; Carpio et al., 2021).

The experimental densities considered in our study mimic the high densities commonly found in many natural areas (including protected territories) across vast regions of the Iberian Peninsula (> 30 deer/km^2; Charco, 2002; Fernández-Olalla et al., 2006; Vicente et al., 2007; Perea et al., 2014; Carpio et al., 2015). In addition, they reflect the hyper-densities typically observed in commercial and intensively managed game estates in Central and Southern Iberia (> 90 deer/km^2; Acevedo et al., 2008; Azorit et al., 2002, 2012). These extremely high red deer densities are not geographically exceptional, with similar values reported in other European regions (e.g., Gobbi et al., 2018) and in other continents where the species has been introduced, such as South America (Charro et al., 2018) and Oceania (Forsyth et al., 2007). Comparable high densities of other deer species have also been recorded in North America (e.g., Williams et al., 2013). These densities clearly exceed the values proposed to foster taxonomic richness and diversity (Virtanen et al., 2002; Riesch et al., 2020). Therefore, the current overabundance of red deer in our study area markedly reduces herbaceous species richness and diversity in the short term, compromising herbaceous community integrity. Similar comparable and proportional changes were observed in both woody systems, scrublands and forests. This reinforces the idea of plant diversity loss at increasing deer densities in overabundance scenarios (Côté et al., 2004; Tanentzap et al., 2009; Côté et al., 2014).

4.3. Effects of ungulate overabundance on functional diversity

The overabundance of red deer caused no significant effect on functional diversity. These results could be linked to functional redundancy related to a legacy effect (Royo et al., 2010; Nuttle et al., 2013). Mediterranean ecosystems have historically been exposed to herbivores, which has played a key role in shaping their vegetation (Perevolotsky and Seligman, 1998). The vegetation of the study area has been grazed and browsed for decades by red deer before the treatments (Quintos de Mora has been fenced for 40 years with approximately 10 individuals/km^2). This long-standing interaction between herbivory and plants provides an important context for understanding the characteristics of herbaceous vegetation, which may have already been filtered.

The legacy effect may have promoted the presence of multiple plant species with shared functional traits. For example, small size therophytes with reduced leaves dominate the study area, abundant in the control but also highly persistent in both treatments (**Table S2**). This pattern indicates that the current prevalence of small annual species could be the legacy of an herbivore-driven filtering process, as previously documented in grasslands (Díaz et al., 1992; Peco et al., 2012) and forest understories (Lecomte et al., 2024). Small therophytes complete their life cycle within a single growing season, so their fitness depends on rapid seed production rather than longevity or biomass accumulation. This fast-cycle strategy is advantageous under herbivory, allowing plants to divert resources to reproduction despite biomass loss (Díaz et al., 1992). Additionally, multiple species within the same genus that share several functional traits contribute to functional redundancy, e.g., *Bromus, Crepis, Galium, Trifolium* and *Vulpia*. These genera exhibit species loss under high and hyper density treatments, yet other, more abundant species within these genera persist (**Table S2**). This redundancy may explain why the overabundance of red deer causes a clear decrease in taxonomic richness and diversity, but functional diversity remains unaffected.

Other relevant factors, such as the typical Mediterranean summer drought (3–5 months), might be an independent filter that could homogenise the traits of the herbaceous communities (Coughenour, 1985), promoting functional redundancy (Mayfield et al., 2010; Carmona et al., 2012). Moreover, this functional redundancy, derived from herbaceous species showing similar traits, could provide the ecosystem with high resilience (Lipoma et al., 2024).

Alternatively, functional shifts may have escaped detection because of the study's short temporal window or because they occur at the individual rather than the community level (Gordaliza et al., 2025). Similarly, unaccounted interannual climatic variability can exert a stronger influence on functional diversity than herbivory (Cera et al., 2024; Klope et al., 2025). Hence, herbivore overabundance in the study area may not, by itself, translate into community-level changes in functional diversity.

In scenarios of herbivore overabundance, as observed in this study, the ecosystem is impacted by a loss of herbaceous cover, richness and taxonomic diversity, which contrast with the pattern observed in functional diversity. This disparity underscores the need to assess a broad set of metrics to accurately evaluate herbaceous layer condition and overall ecosystem integrity (Carpio et al., 2021).

4.4. *Consequences of overabundant deer populations on herbaceous layers*

Our results indicate that impacts are most severe in the short term under extreme (hyperdensity) ungulate populations. However, similar effects may arise under our scenario of high density if the treatment persists over time. Cumulative damage and negative synergies on plant species composition, richness and regeneration are expected after several years of sustained ungulate overabundance (Côté et al., 2004; Mysterud, 2006; Putman et al., 2011).

Over time, the loss of herbaceous cover, richness, and diversity has a cascading effect on ecosystem components and their interactions, thereby undermining overall integrity (Côté et al., 2004; Putman et al., 2011). Fences that limit the mobility of ungulates (Boone and Hobbs, 2004; Carpio et al., 2015) exacerbate the degradation of soil properties and nutrient cycle (Liu et al., 2015) and the loss of specialist invertebrates (Gobbi et al., 2018; Hernández-Castellano et al., 2025). This leads to the restructuring of plant–animal networks and disruption to ecological and biological processes such as pollination and plant reproduction (Lecomte et al., 2016), effects that have already been observed in the study area even in the short term (Hernández-Castellano et al., 2025).

Subsequently, the degradation of herbaceous communities also reduces the quality of forage for large herbivores, including red deer (Schaub et al., 2020), which is particularly relevant for conservation authorities and game managers (Putman et al., 2011). The loss of key herbaceous species diminishes pastoral value and the performance of herbivores, often resulting in an increased reliance on supplementary inputs such as additional feeding (Putman et al., 2011; Carpio et al., 2021).

4.5. *Conservation and management recommendations*

Reducing red deer populations to sustainable levels (<10 deer/km^2, as observed in most Mediterranean environments, Morales-Molino et al., 2019), may enhance both herbaceous plant diversity (Fig. 1; Pringle et al., 2023) and regeneration and diversity of woody plants (Perea et al., 2014) as previously reported. It may also increase the quality-adjusted yield (an integrated measure of biomass yield and forage quality), even across varying management intensities (see Schaub et al., 2020 and references therein). Furthermore, it could help reverse or prevent impacts on key ecological processes previously mentioned (Putman et al., 2011; Liu et al., 2015; Valladares-Pérez et al., 2021; Pringle et al., 2023).

Numerous management interventions aim to stabilise ungulate densities (Côté et al., 2004; Carpio et al., 2021). Regulated culling reduces numbers while may also maintain hunting revenue (Nugent et al., 2011). However, to ensure conservation goals, this measure should be supervised by public authorities, particularly when carried out by the hunting sector. Other measures include the selective translocation and the recovery of large carnivores, although public acceptance of predators is inconsistent (Carpio et al., 2021). Supplementary feeding has been also used for two contrasting purposes: eliminating feed drops reduces artificially high densities, whereas diversion feeding steers animals away from vulnerable plant communities (Côté et al., 2004; Nugent et al., 2011). Similarly, exclusion fences are also installed to protect habitats that support sensitive vegetation or threatened species. However, no single measure is fully effective or universally applicable in all ecological and socioeconomic contexts (Carpio et al., 2021). Spain and many other countries lack a nationwide monitoring system to quantify the ecological and economic impacts of wild ungulates (Putman et al., 2011). Nevertheless, in Spanish national parks, any population-control action, including culling, is authorised only when monitoring data confirm ecological damage (MITECO, 2021; Carpio et al., 2024), which highlights the need for rigorous, science-based oversight.

5. Conclusions

This short-term response of herbaceous plant communities to deer overabundance has demonstrated a rapid decrease in cover, taxonomic richness, and diversity of herbaceous communities in both scrublands and forests. However, functional diversity has remained unaffected by different levels of red deer overabundance, probably due to functional redundancy, partially linked to a legacy effect.

The results suggest that the situation is particularly critical in fenced areas with restricted animal mobility, such as National Parks or states under intensive hunting management, where ecological functionality is often overlooked. In this context, long-term studies are needed to better understand the effects of the overabundance of red deer, as they may reveal more pronounced impacts. Such investigations, if conducted with a controlled number of grazing individuals, could provide deeper insights into the cascading effects of herbivores overabundance and offer valuable guidance for management practices.

CRediT authorship contribution statement

Macarena Cuerdo: Writing – review & editing, Writing – original draft, Visualization, Methodology, Investigation, Formal analysis, Data curation, Conceptualization. **David G. del Olmo:** Writing – review & editing, Visualization, Methodology, Investigation, Formal analysis, Data curation, Conceptualization. **David Horcajada:** Writing – review & editing, Investigation, Data curation. **Aída López-Sánchez:** Methodology, Formal analysis. **Francisco M. Azcárate:** Writing – review & editing, Formal analysis. **Ramón Perea:** Writing – review & editing, Resources, Methodology, Funding acquisition, Conceptualization. **Emmanuel Serrano:** Writing – review & editing, Resources, Methodology, Funding acquisition, Conceptualization. **Juan A. Calleja:** Writing – review & editing, Writing – original draft, Supervision, Resources, Methodology, Investigation, Formal analysis, Data curation, Conceptualization.

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.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.biocon.2025.111412.

Data availability

Data will be made available on request.

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