Landsc Ecol (2023) 38:3463–3478
https://doi.org/10.1007/s10980-023-01676-0

RESEARCH ARTICLE

Contrasting effects of wild and domestic ungulates on fine-scale responses of vegetation to climate and herbivory

M. Velamazán · J. A. Sánchez-Zapata · R. Moral-Herrero · E. G. Jacquemin · J. A. Sáez-Tovar · J. M. Barbosa

Received: 26 January 2023 / Accepted: 30 April 2023 / Published online: 21 May 2023

Abstract
Context Wild ungulates and livestock modify a large range of vegetation patterns and processes at the landscape scale. However, we still lack studies that address how changes in herbivores' type and management can determine small-scale ecosystem functioning.
Objectives We compared landscape vegetation processes within a traditional livestock grazing (transhumant) and a system consisting exclusively of wild ungulates. We also investigated methodological approaches to map very fine spatial-scale changes in vegetation structure and functioning over time in a mountainous Mediterranean system (Iberian Peninsula).
Methods We performed different UAV flights per season over exclusion fences, within these two long-term grazing contexts. Later, we processed images to obtain spatially explicit data on vegetation structure (vegetation cover and mean vegetation patch area) and vegetation greenness (NDVI).
Results Very high spatial-resolution images provided key information on the spatial distribution and seasonal oscillation of small vegetation patches. Mean annual NDVI showed similar values in both grazing contexts albeit seasonal and annual differences in NDVI between grazed and ungrazed areas. Vegetation cover remained rather constant across seasons but differed between grazing contexts and fencing. The mean vegetation patch area changed seasonally according to the grazing context, without significant differences in mean annual values in fenced and non-fenced areas.
Conclusions Accurate image classification helped to uncover differences in vegetation functioning in presence of wild ungulates and livestock. Multi-temporal studies at this fine-scale level improve the detection of ephemeral vegetation patches and increase the comprehension of cascade processes mediated by both ungulate groups, such as vegetation response to climate. The temporal and spatial vegetation patterns should be considered before the implementation of management measures, especially in landscapes within potential rewilding processes.

Keywords Rewilding · Traditional grazing · NDVI · Vegetation cover · Unmanned aerial vehicle

---

Supplementary Information The online version contains supplementary material available at https://doi.org/10.1007/s10980-023-01676-0.

M. Velamazán (✉) · J. A. Sánchez-Zapata ·
E. G. Jacquemin · J. M. Barbosa
Department of Applied Biology, Miguel Hernández
University, Avda. Universidad, s/n. Edf. Vinalopó,
03202 Elche (Alicante), Spain
e-mail: mvelamazan@umh.es

R. Moral-Herrero · J. A. Sáez-Tovar
Department of Agrochemistry and Environment, Miguel
Hernández University, Avda. Universidad, s/n. Edificio
Alcudia, 03202 Elche (Alicante), Spain

Introduction

Spatial and temporal changes in primary productivity and vegetation cover are key information to understanding how ecosystems function (Gaitán et al. 2013; Sanaei et al. 2018; Regos et al. 2021). For instance, temporal changes in vegetation productivity and structure indicate how climate determines food resources availability (e.g. biomass and nutrient) for different trophic levels (Hamel et al. 2009; Royo et al. 2017; Johnson et al. 2018), how vegetation cover and patch area can reveal habitat availability (Zweifel-Schielly et al. 2009; Hughey et al. 2021) and what spatiotemporal patterns of primary productivity can give evidence on how species interact (Odadi 2011). Although primary productivity and vegetation cover have already been used in different studies to disentangle climate-vegetation-herbivory interactions in terrestrial ecosystems (e.g. Giralt-Rueda and Santamaria 2021; Keyserlingk et al. 2021), we still lack studies that contrast the effects of wild and domestic ungulates on very fine-scale vegetation functioning in a spatially explicit framework. Understanding how domestic and wild ungulates modulate very small-scale responses of vegetation to seasonality can help us to better manage ecosystems based on the mechanisms that mediate resilience in grazed ecosystems (Murray et al. 2013).

Abiotic factors, such as water availability or temperature, are frequently highlighted as key drivers of seasonal changes in primary productivity and vegetation cover (Augustine and McNaughton 2006; Wang et al. 2020). Using satellite-based vegetation indexes as a proxy for primary productivity, some studies have disentangled the susceptibility of ecosystems to drought, seasonality anomalies, or changes in rainfall patterns at large spatial scales (Lohmann et al. 2012; Grant et al. 2017). Moreover, anthropogenic factors are also indicated as key drivers of vegetation cover and productivity (e.g. agriculture, livestock production or land abandonment) (Khorchani et al. 2021; Ibáñez-Alvarez et al. 2022) and consequently determine their responses to climate. However, biotic factors, such as species interaction, herbivory or diseases can determine vegetation functioning throughout time (Barbosa et al. 2020). Therefore, the presence of domestic or wild ungulates may increase primary productivity and decrease vegetation cover (Manier and Hobbs 2007; Charles et al. 2017) by affecting physiological conditions and species distribution and occurrence (Espunyes et al. 2019; Desforges et al. 2021).

Indeed, abiotic, biotic and anthropogenic landscape-scale drivers occur simultaneously, diversifying the response of vegetation and creating complexity in how grazed ecosystems function. For instance, rural land abandonment (anthropogenic driver) can lead to rewilding processes that consequently may replace livestock with wild ungulates and change animal foraging patterns (biotic driver) and ecosystem functioning (Svenning et al. 2016; Linnell et al. 2020). Besides, the complexity in the responses of ecosystems to rewilding processes can increase when climate change (abiotic driver) alters seasonal vegetation patterns. Grazing intensity from medium-sized ungulates could also control the responses of ecosystems to climate change (Biuw et al. 2014). The effects of replacing domestic or wild ungulate remain unknown especially in grazing-adapted habitats, such as in grasslands under traditional grazing systems or in shrublands with a long-term presence of wild and domestic ungulates (Newman et al. 2014; Ramirez et al. 2019; Vuorinen et al. 2021). Taking into account the complexity of the rewilding framework described, we still need to deepen our knowledge on what are the differences among grazing intensities and ungulate species to determine vegetation functioning in different climate conditions and land management contexts (Forbes et al. 2019; Carpio et al. 2021; Laguna et al. 2021).

Numerous studies evaluate climate-vegetation-herbivory interactions using plot- or large-scale approaches (e.g. Lohmann et al. 2012; Giralt-Rueda and Santamaria 2021). However, there is a lack of research at the intermediate scale, i.e. medium to small spatial-scale remote sensing approaches that provide fine-scale and spatially explicit information on vegetation communities and soil processes to understand ecosystem functioning (Cunliffe et al. 2020; Sankey et al. 2021). This intermediate framework can allow conservation measures for particular threatened species and environments (Velamazán et al. 2017; Kerby et al. 2022). Multispectral sensors attached to Unmanned Aerial Vehicles (UAVs) have been appointed as key tools to fill this knowledge gap because they can provide information on vegetation cover and productivity at an intermediate spatial scale (that is, between satellite- and plot-based studies) (Klosterman et al. 2018; Ren et al. 2021; Kolstad et al. 2022), which allow us to study climate-vegetation-herbivory interactions at varying spatial and temporal scales. UAV sensors provide a singular and useful perspective of the landscapes at a centimeter-level (Riginos et al. 2009; Stavi et al. 2021) with a multi-temporal perspective (Ecke et al. 2022), helping to estimate the productivity and biomass of ephemeral vegetation patches. It is also important to note that several technical challenges regarding image processing from UAV sensors should be addressed, such as the management of shaded areas or cloud effects on image brightness.

Here, we investigated methodological approaches to map very fine spatial-scale changes in vegetation structure and primary productivity over time in a mountainous Mediterranean system. Using three grazing contexts (wild, domestic and exclusion plots), we also examined spatiotemporal changes in these vegetation properties (productivity, cover and mean patch area), with a particular focus on evaluating the relationship of abiotic (seasonality), biotic (herbivory) and anthropogenic (ungulate management) factors with micro- to meso-scale vegetation patterns. We hypothesized that seasonality is the main driver of intra-annual vegetation changes (productivity, cover and patch area) because seasonal rainfall and temperature strongly drive semi-arid ecosystems (Augustine and McNaughton 2006; Lohmann et al. 2012). However, we also expect that grazing/browsing pressures play an important role to modulate these responses because herbivory affects plant leaf area (Gorné and Díaz 2022) and dung from medium-sized ungulates can change the nutrient balance in ecosystems (Valdés-Correcher et al. 2019). In particular, we expect higher intra-annual changes in ecosystem productivity where domestic ungulates are present because a monospecific and higher herbivory pressure can favour herbaceous plants resistant to herbivory (Beguin et al. 2022) and consequently can show a faster response to changes in climate conditions (Wang et al. 2020). We also expect seasonal dissimilarities in the response of vegetation to climate and herbivory because transhumant livestock changes foraging locations following seasonal patterns (Hevia et al. 2013). In this context, we first searched for methodological approaches to standardize imagery obtained from different UAV flights. Using these data, we then explored similarities and differences in mechanisms by which wild ungulates and extensive livestock mediate temporal changes in vegetation structure and functioning in grazed ecosystems.

Materials and methods

Study areas

We performed the study in two areas with herbivore exclusion fences (Fig. 1) in the Cazorla, Segura and Las Villas Natural Park (Jaén, southern Spain). Exclosure plots were constructed to protect threatened plant species more than 20 years ago. Both study areas are located between 1700 and 1800 m of altitude, presenting a sub-humid cold Mediterranean high mountain climate. This Mediterranean climate shows significant seasonal changes. It is characterized by higher precipitation in autumn–winter, with frequent snowfalls, but an important percentage of annual precipitation in spring and convective rainfalls in June–August (100 mm approx.). It shows high insolation but a relatively low temperature in Summer and an important annual number of frost days. Yearly mean temperature varies between 7.3 and 15.3 °C, with yearly minimum and maximum temperatures between 1.6 and 7.5 °C and 13.1 and 20.2 °C respectively (Gómez-Zotano et al. 2015; Espín-Sánchez et al. 2018). We compared monthly temperature and precipitation during the study period and the monthly climatic data for the period between 1990 and 2020 (Fig. S1) to evaluate the representativeness of the study period regarding historical climate seasonality (Muñoz Sabater 2019). Their vegetation is therefore located within the supra- and oro-Mediterranean bioclimatic floors (REDIAM 2012a, b).

The study areas present calcareous substrates, mainly dolomites (Gómez-Mercado 2011). Using field observations and satellite images, we observed great similarities in vegetation characteristics between both study areas and the most representative vegetation (herbaceous and scrub) of the natural park. Both study areas show the same grassland-scrub habitats inside and outside fences. These habitats are characterized by perennial xerophilous grasslands of class *Lygeo-stipetea* and other short

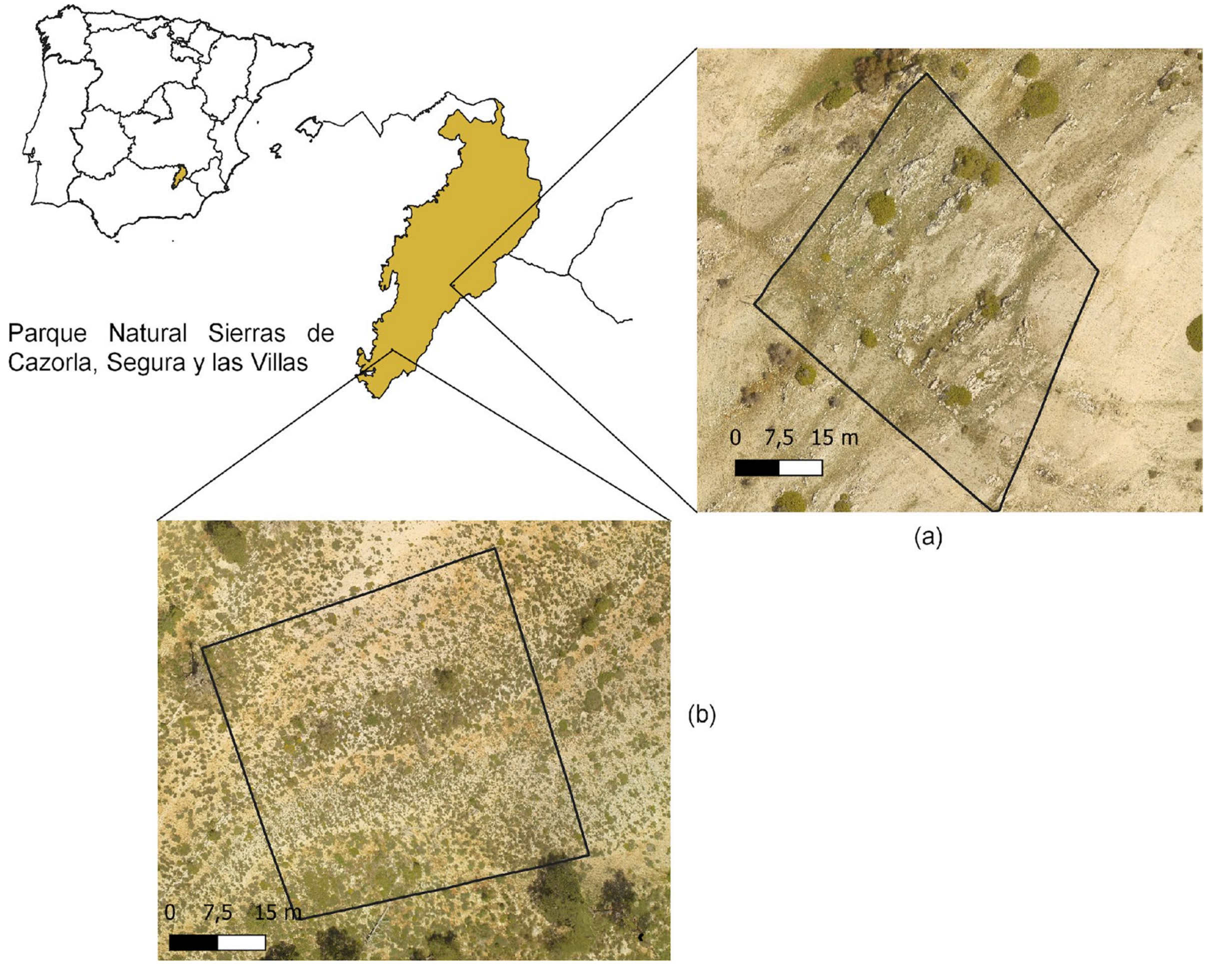


Fig. 1 Study areas are located in the Natural Park "Sierras de Cazorla, Segura y las Villas" where exclosure plots were built to protect rare plant species from medium-size herbivores. UAV-RGB images of the exclosures plots with presence of **a** extensive transhumant livestock and **b** wild ungulates and in Sierra de Cazorla

mesophite and xero-mesophite grasslands where small camephites (*Helianthemum* sp., *Astragalus* sp.) and cushion scrubs (e.g. *Erinacea anthyllis*, *Genista longipes*) are abundant. A scattered shrub stratum is mainly integrated by arborescent *Juniperus* sp. and thorny species in the wetter areas, such as *Berberis vulgaris* or *Crataegus monogyna*. Few pines (*Pinus nigra*) appear in the study areas, which also constitute the main tree species in the surrounding forests (Benavente 2008; Gómez-Mercado 2011).

Despite their similar vegetation, the two study areas represent two different grazing systems (Fig. 1). The first area is located in the Campos de Hernán Perea (municipality of Santiago-Pontones) which constitutes a plateau with 1697 m of average altitude, in which numerous herds of extensive transhumant livestock (mainly sheep) graze in Summer (131–133 individuals/km^2) and scarce wild ungulates use pastures continuously throughout the year, mainly mouflon—*Ovis orientalis musimon*—at approximately 4 individuals/km^2 (Aguilera-Alcalá et al. 2022). In the wintertime, the transhumant livestock moves to Sierra de Andujar (approximately 130 km away). Although there still exists a very small proportion of extensive sedentary livestock in the region, only transhumant herds graze the study area. The second study area is located in the municipality of Cazorla, which has resident populations of Spanish ibex (*Capra pyrenaica*), fallow deer (*Dama dama*), mouflon (*Ovis orientalis musimon*) and

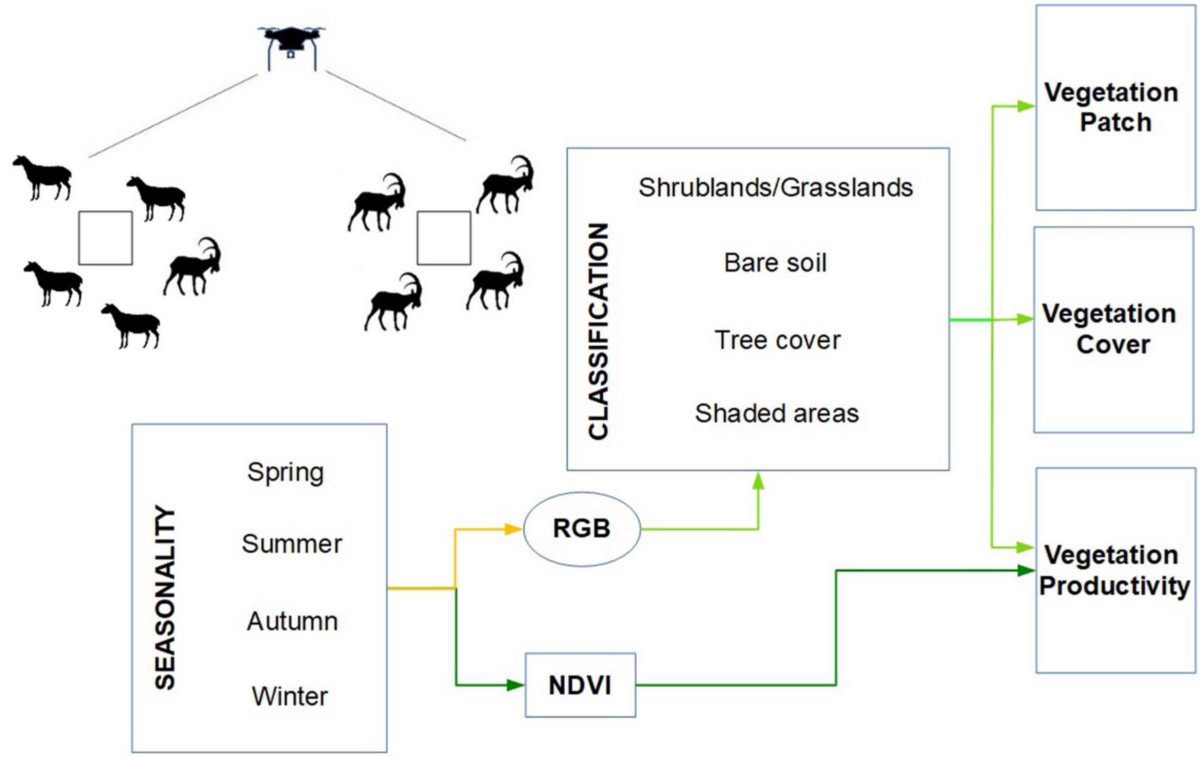


Fig. 2 Workflow overview. RGB and vegetation greenness (NDVI) images from different season were used to analyze the effects of seasonality and wild/domestic ungulate herbivory on vegetation cover, vegetation productivity and vegetation patch area

red deer (*Cervus elaphus*) (Martínez 2002). Total wild ungulate populations in Cazorla vary from 6 to 13 individuals/km^2 and the four wild ungulate populations show similar densities according to the information provided by the Junta de Andalucía of the hunting censuses carried out in the Reserva Andaluza de Caza de Cazorla. Though wild boar (*Sus scrofa*) is evenly distributed in both study contexts there are no population assessments in the study area.

UAV data acquisition and processing

We performed multi-temporal UAV flights over two exclusion fences and their surroundings (Fig. 2): *Campos de Hernán Perea* (2318 m^2 fenced and 15,073 m^2 with herbivore presence) and *Cazorla* (2294 m^2 fenced and 8246 m^2 with herbivore presence). We captured UAV images in four different dates once by season, from spring 2021 to winter 2022. The flights were conducted at low wind speeds and good sky visibility (Table S1). We carried out perpendicular flights to create a grid covering each plot and its surroundings (90% overlapping between flight lines). Pictures were taken with a Zenmuse X3 RGB integrated into an Inspire 1 UAV. It utilizes wavelengths in the visible spectrum (RGB range) with 12.4 megapixel and 3.6 mm focal length. Simultaneously we collected multispectral (MS) information on five bands: Near Infrared (842 nm); Red edge (717 nm); Red (668 nm); Green (560 nm) and Blue (475 nm). We used a Micasense RedEdge sensor with 5.2 Megapixel and 5.4 mm focal length. According to height flight, pixel resolution in raw images varied between 1.0 and 6.5 cm. Later, we processed RGB and MS images with software pix4d v4.6.4®. We also used this software for the later processing of MS images to translate the digital data into radiance and reflectance. The calibration of the MS images was carried out from the standard white reflectance panel of the camera. After radiometric calibration, we aligned MS and RGB images using the QGIS Geographic Information System (QGIS 2022).

To evaluate multi-temporal biomass/primary productivity fluctuations and spatial changes in vegetation structure under different seasons and grazing contexts, we calculated vegetation greenness using three metrics: Normalized Differential Vegetation Index (NDVI), total vegetation cover (%) and mean vegetation patch area (m^2). To make seasonal image sizes equal, we masked them to the minimum overflown area that was from the Spring season.

We masked the images to perform the subsequent analysis on the effects of wild ungulates and livestock on the vegetation strata focus of this study: herbaceous and scrub vegetation. We performed a supervised classification using the SCP plug-in (Semi-automatic Classification Plugin) of QGIS (Congedo 2021) to differentiate shaded areas, vegetation and bare soil. After different attempts, we selected RGB information (pixel size 1.0–6.5 cm) with Minimum Distance Classification Algorithm, as this procedure resulted in a suitable way to distinguish these three strata. We distinguished shaded areas to minimize the effects of shadow on the vegetation index and vegetation boundaries. We assessed classification accuracy through the overall accuracy (ratio between the number of samples that are correctly classified and the total number of sample units) and Cohen's kappa index to address class distribution. Afterwards, we also masked vegetation located under the tree cover. We delineated the tree boundaries within the images using vegetation height information estimated through the difference between Digital Surface Model (DSM) and Digital Terrain Model (DTM) from the RGB sensor (Fig. 3).

Secondly, we randomly created circular subplots of 78.5 m^2 (5 m of radius) located inside (N = 20) and outside (N = 20) the fences to compare the vegetation variables in the presence or absence

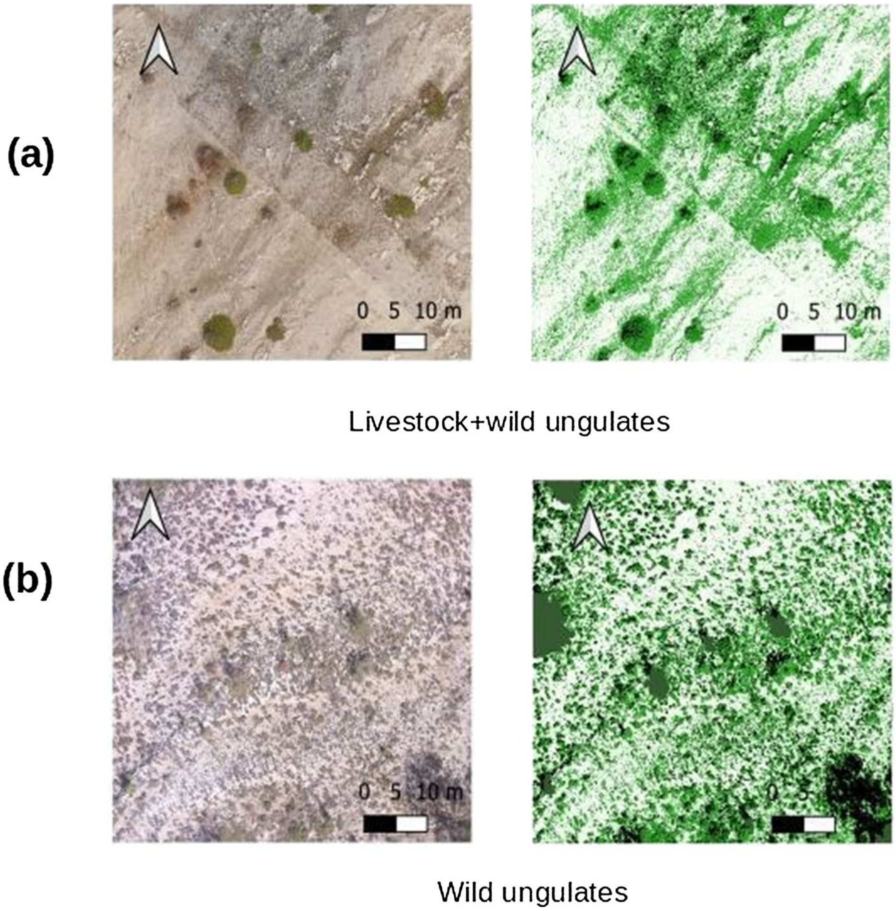


Fig. 3 Autumn RGB images and cover classification, in livestock and wild ungulates (**a**) and only wild ungulates (**b**) grazing systems. Colors in both lower panels refer to shrub and herbaceous vegetation (green), trees (dark green), bare soil (white) and shadow (black)

of herbivores. We used this subplot approach to reduce errors derived from differences in flight areas through fences (inside/outside) and seasons (Spring, Summer, Autumn, and Winter). A subplot of 5 m corresponds to the minimum area required to represent vegetation communities in the study areas (Fernández-Olalla et al. 2016; Perea et al. 2016). Subplot centres were randomly selected for each context and season ($N_{total} = 320$) through "R spatstat" package (Baddeley and Turner 2005), defining 5 m as the minimum distance between centres to reduce overlapping and to permit the use of a higher number of subplots in the analysis (Fig. S2).

After excluding pixels with shaded areas, bare soil and tree cover, we used the mean data of all pixels within subplots inside and outside the exclusion fences to compare vegetation greenness throughout grazing contexts and seasons. We calculated the Normalized Difference Vegetation Index (NDVI) from MS images as "(Near-infrared − Red)/(Near-infrared + Red)" with the QGIS Geographic Information System (QGIS 2022). We increased MS pixel size to the maximum one (6.5 cm) to compare seasonal NDVI.

The vegetation greenness (NDVI) is a common proxy of primary productivity that can be calculated from multispectral images. It is linked to ecosystem structure and functioning (Gaitán et al. 2013) and its evolution throughout time can be used to calculate important ecosystem parameters, such as resistance or resilience (Keyserlingk et al. 2021). Regarding ungulate-ecosystem interactions, NDVI can indicate the effects of ungulates on ecosystems throughout grazing and browsing pressure (Pringle et al. 2007; Rueda and Rebollo 2013). Besides, NDVI also indicates pasture quality and availability for herbivores (Hamel et al. 2009). This index is often related to vegetation photosynthetic activity (Cunliffe et al. 2020), varying with habitat conditions and seasonality (Borowik et al. 2013). NDVI is, therefore, a common index for estimating both vegetation activity and resource availability.

Based on the previous classification procedure, we also analyzed the proportion of shrubland/grassland cover and bare soil within the 320 subplots. We calculated the total vegetation cover (%) and mean vegetation patch area (m^2) per subplot. We managed images with R software and R packages "raster" and "terra" (Hijmans 2022a, b) and we used the R package "landscapemetrics" (Hesselbarth et al. 2019) to calculate both fine landscape parameters.

Data analysis

First, we used the R package glmmTMB (Magnusson et al. 2017) to evaluate the relative effect of abiotic, anthropogenic and biotic factors on vegetation productivity, cover and mean vegetation patch area. Predictor variables were ungulate management context (livestock + wild ungulate or wild ungulate), season (spring, summer, autumn or winter) and fences (inside or outside the exclosure), with the subplot identity included as a random intercept to fit the models. Because transhumant livestock change foraging locations following seasonal patterns and we were interested in evaluating seasonal dissimilarities in the response of vegetation to herbivory, we evaluated models that consider the interaction of season and herbivore exclosure. We compared these models with others that take into account the independent effect of each variable and with a null model using Akaike information criteria (AIC). We present the results for the retained models with the lower AIC values. We calculated mean NDVI values for all subplots to understand annual variation in each grazing context inside and outside fences. Later, we represented data from each season separately. We repeated the procedure to visualize annual and seasonal changes in vegetation cover and mean vegetation patch area inside and outside exclosures. In all cases, we created boxplots with "ggplot2" (Wickham 2016) and "ggpubr" (Kassambara 2020).

To assess the degree of difference in vegetation factors between inside/outside fences in each context, we calculated mean differences for NDVI, vegetation cover and mean vegetation patch area using the subplots. In the output of this difference, positive values mean higher values inside the exclosure and negative values indicate higher values outside the exclosure. The differences were expressed according to the units of each parameter. To obtain the statistical significance of these differences inside/outside we performed a bootstrapping analysis that allowed us to calculate the p-value, through a pseudo sample with replacement, and the confidence interval with "bootES" function within R "bootES" package

(Gerlanc and Kirby 2021). Firstly, we analyzed data of all subplots in the *livestock + wild ungulate* context (N = 160) and the *wild ungulate* context (N = 160) to estimate the annual variation of NDVI, vegetation cover and mean vegetation patch area. Subsequently, we repeated the process for each season and grazing context (e.g. N = 40 for Spring in the *wild ungulate* context).

Results

We obtained high accuracy in mapping shaded areas and creating a vegetation mask in both study areas (Table 1). This procedure was crucial for calculating NDVI exclusively from focal vegetated areas (16.17×10^6 pixels) by excluding shaded areas, bare soil and trees. This procedure allowed us to evaluate 5.74×10^6 remaining pixels from grasses and shrubs within subplots (N = 320).

Although ungulate management context and seasonality were the main drivers of temporal and spatial changes in NDVI, we also found that the interaction between ungulate exclusion and seasonality was key to determining NDVI (Table 2-A). Vegetation cover was only affected by ungulates context, Spring season and exclusion (Table 2-B). The vegetation patch area was mainly determined by the interaction between seasonality and ungulate exclusion, indicating a similar spatial and temporal pattern of patch area between ungulate contexts (Table 2-C).

Table 2 Results of the generalized linear models showing the effect of the explanatory variables on our 3 response variables (NDVI, vegetation cover and mean patch area)

Parameters	Estimate	Std. error	p-value
(A) Response variable: NDVI			
Intercept	− 1.24848	0.03382	< 2e−16 ***
Wild ungulate context	0.24864	0.02242	< 2e−16***
Season_Spring	0.29992	0.04460	1.75e−11***
Season_Summer	− 0.16913	0.04465	0.000152***
Season_Spring:Fence out	− 0.14695	0.06307	0.019815*
(B) Response variable: vegetation cover			
Intercept	− 0.36476	0.11159	0.00108**
Wild ungulate context	0.58275	0.09138	1.81e−10***
Season_Spring	0.27697	0.12892	0.03168*
Fence out	− 0.49441	0.09128	6.07e−08***
(C) Response variable: mean vegetation patch			
Intercept	− 1.80545	0.19001	< 2e−16***
Season_Summer: fence out	− 0.68521	0.31703	0.0307*
Season_Winter: Fence out	− 0.65456	0.30716	0.0331*

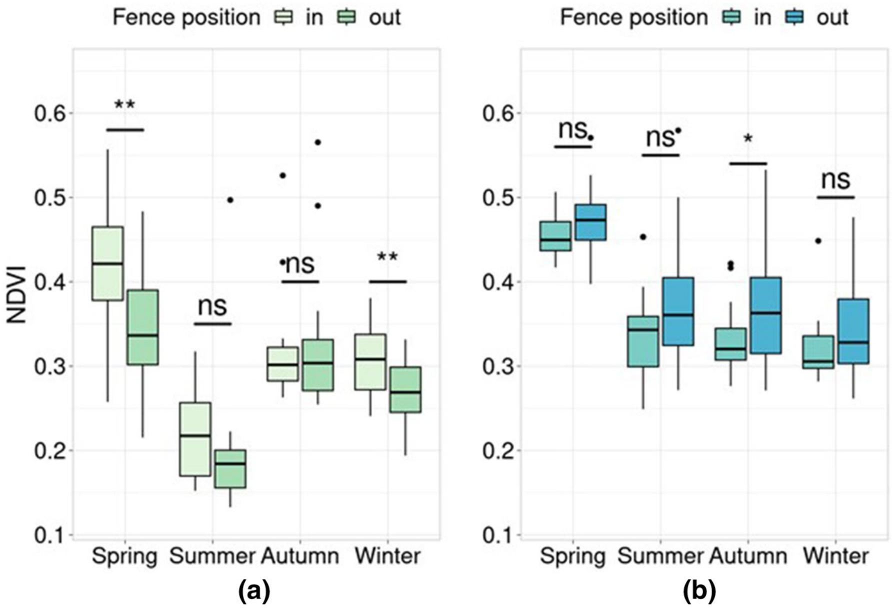
In the NDVI model (family = Gamma; link = log), predictors are ungulate management context (livestock + wild ungulate or wild ungulate) and interactions between season (Spring, Summer, Autumn or Winter) and fences (inside or outside the exclosure). In the vegetation cover model (family = beta; link = logit), predictors are ungulate management context, season and fences. In the mean patch area model (family = Gamma; link = log) the predictors are ungulate management context and interactions between season and fences. The subplot identity is included as a random intercept in the three models

We found that NDVI decreased by 3.52% outside of exclosures (Table S2) within the *livestock + wild ungulate* context (Fig. 4a). On the contrary, the opposite was true in the context of wild ungulates, where NDVI increased by 3.44% (Table S2; Fig. 4b). NDVI fluctuated sdifferently throughout seasons according to the ungulate context (Table S2). Maximum NDVI values were recorded in spring in both cases (Fig. 4) but minimum productivity was recorded in summer in the *livestock + wild ungulate* context (Fig. 4a). The minimum NDVI values were recorded in winter in the *wild ungulate* context (Fig. 4b). Differences in NDVI inside/outside exclosures also changed during the year according to the ungulate context. These differences were stronger in areas with livestock, where differences were significant in spring and winter and annual

Table 1 Overall precision (P, values in %) and Kappa classification index (K, values between 0 and 1) for each flight and grazing scenario

	Spring		Summer		Autumn		Winter	
	P (%)	K	P (%)	K	P (%)	K	P (%)	K
Livestock and wild ungulates	89.85	0.85	95.17	0.90	96.85	0.93	94.92	0.92
Wild ungulates	97.19	0.95	89.15	0.84	89.03	0.83	93.72	0.90

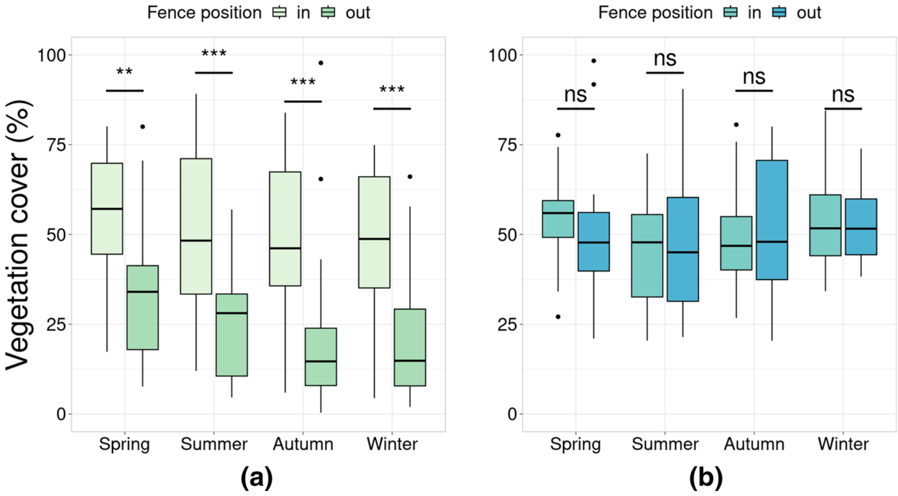
Fig. 4 Boxplot representing vegetation greenness (mean NDVI per pixel) by season. Plots show comparisons between exclosures (left side) and surrounding areas (right side) with livestock and wild ungulates (**a**) or with the only presence of wild ungulates (**b**)



fluctuation was higher within the exclosure (Fig. 4a; Table S2). The *wild ungulate* context presented higher productivity outside of the exclosure every season although the difference was only significant in autumn (Fig. 4b). Annual NDVI fluctuation was similar inside/outside the fenced area in the wild ungulate context (Fig. 4b; Table S2).

Annual vegetation cover was higher within the exclosure in the *livestock + wild ungulate* context (Fig. 5a) and the difference inside/outside remained similar every season (Table S3). In contrast, the *wild ungulate* context showed differences in vegetation cover inside/outside exclosures that were not statistically significant (Fig. 5b; Table S3). In the presence of livestock, the mean vegetation patch area was lower outside the exclosures every season but the difference was only statistically significant in summer (Table S4; Fig. 6a). The *wild ungulate* context showed a decreasing mean vegetation patch area from spring to winter. In addition, patch area differences between inside and outside exclosures were only significant in autumn and winter (Table S4; Fig. 6b).

Fig. 5 Boxplot representing vegetation cover (%) by season. Plots show comparisons between exclosures (left side) and surrounding areas (right side) with livestock and wild ungulates (**a**) or only with wild ungulates (**b**)



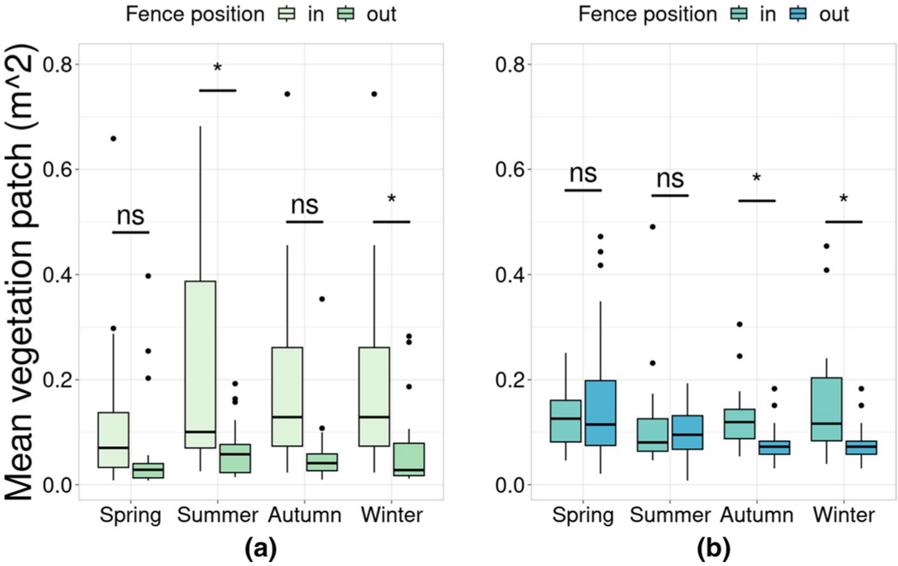


Fig. 6 Boxplot representing mean vegetation patch area (m^2) by season. Plots show comparisons between exclosures (left side) and surrounding areas (right side) with livestock and wild ungulates (**a**) or only with wild ungulates (**b**)

Discussion

Using a time series of very-high spatial resolution imagery from inside and outside exclusion plots, we found that the relative effect of grazing on landscape structure and functioning changes according to particular seasonal periods. Because of the seasonal aspect of the transhumant livestock activity on the landscape, pastures with domestic transhumant livestock seem to have enough time to recover during the Winter period because of the strong reduction in the presence of domestic ungulates. The management patterns of this traditional grazing system seem to reduce differences in vegetation greenness between vegetation located inside and outside exclusion plots. This transhumant management strategy indicates that this pastoral system has been sustainable for centuries and coexisted with wild ungulates (San Miguel-Ayanz et al. 2010; Oteros-Rozas et al. 2013; Fernández-García and Calvo 2023). Our study still highlights that vegetation response to herbivory differs between domestic (traditional transhumant grazing system) and wild ungulate contexts, although these differences reduce in warmer and colder periods of the year. As expected, seasonality was a determinant of the temporal oscillation of primary productivity but it was less important than herbivory context (i.e. wild or domestic ungulates) to define fine-scale vegetation cover. Our results highlight that climate seasonality and herbivory context interacted to determine fine spatial-scale patterns of landscape configuration (grass and shrub cover and patch size) and function (vegetation greenness).

Domestic and wild ungulates have been long present in the study areas. Both grazing contexts present a very long shared evolutionary history in the region and it has been long enough for the vegetation to adapt to herbivory (Augustine et al. 2019; Vuorinen et al. 2021). During this ungulate-vegetation shared history, adaptation processes select species which are resistant to herbivory (Beguin et al. 2022) and ungulates induce changes in community structure and properties, such as relative plant cover and structural complexity (Ibáñez-Alvarez et al. 2022). These ungulate-induced habitat properties may influence the response time of primary productivity and explain therefore why differences in primary productivity inside/outside exclosures vary seasonally. Despite climate seasonality, temperature and precipitation are the main drivers for primary productivity increases and decreases throughout the year (Odadi 2011; Sun & Du 2017), a higher percentage of herbaceous cover would allow a faster response to changes in climate conditions in the *livestock + wild ungulate* context, where differences were significant in spring and winter. On the contrary, the predominantly shrubby vegetation in presence of wild ungulates would respond more slowly to climate seasonality. The spring growth of shrubby vegetation is gradually reduced by wild ungulates outside of the exclosure and the same applies to vegetation patch size, which could increase NDVI and could explain that differences in primary productivity are only significant in autumn in the *wild ungulate* context.

The effect of herbivory on annual primary productivity was intermittent and lower than expected in both contexts. In particular, primary productivity was reduced outside of the exclosures in the *livestock + wild ungulate* context during particular seasons. Recent research, however, found an overall increase in primary productivity with moderate grazing pressure (Jarque-Bascuñana et al. 2022). In our case, we focused our study on the interaction between herbivory and seasonal environmental conditions in a Mediterranean environment, which may explain some of the differences with previous studies. The seasonal presence of livestock in the area indicates a reduction in productive capacity mainly when livestock return to the study region (spring). However, primary productivity increased in the presence of wild ungulates. This increment could be due to low densities of wild ungulate populations and associated to feeding behaviour (i.e. less intense and more randomly distributed) (Charles et al. 2017), as their pressure on shrubs growth reduces plant competition and increases the rate of vegetation activity (Nishizawa et al. 2016). Therefore, the role of wild ungulates in system stability would be more related to the reduction of vertical and horizontal growth of woody vegetation. Similar results were found in vegetation cover inside/outside and a progressive reduction in vegetation patch size outside the exclosure. These results suggest that wild ungulate pressure is strong enough to prevent wood densification in this long-term grazed system but not to prevent shrubland encroachment (Li et al. 2020), except in more preferred areas (Velamazán et al. 2018). Furthermore, the wild ungulate guild in our study area includes species that are predominantly grazers (i.e. mouflon, fallow deer) to browsers (i.e. red deer, Spanish ibex) as derived from stable isotope analysis of ^{13}C and ^{15}N in hair (Donázar, J.A. et al. unpublished data). Thus, the lower density of animals may add to a more diverse diet and also contribute to the more limited effects of these herbivores on the vegetation.

Differences in vegetation cover inside/outside the fence showed low intra-annual fluctuations in both grazing contexts, livestock and wild ungulates, indicating intra-annual stability in species diversity and above-ground biomass (Sanaei et al. 2018). However, livestock significantly reduced vegetation cover outside the exclosure in contrast with the *wild ungulate* context, where vegetation cover remained rather similar inside and outside the exclosure (Manier and Hobbs 2007; Royo et al. 2017). Livestock, therefore, affects vegetation cover to a greater extent than wild ungulates. Furthermore, NDVI fluctuations were lower outside the exclosure throughout the year, where livestock and wild ungulates are present. Indeed, the mean vegetation patch area, related to landscape disturbance and stability (Kéfi et al. 2011; Moreno de las Heras et al. 2011) was lower and more stable outside the exclosure every season. At the spatial and temporal scales of the present study, our results indicate that seasonal livestock grazing reduces fluctuations throughout the year in vegetation cover, vegetation greenness and mean vegetation patch area. Livestock grazing keeps adapted plant species in more suitable areas, where lower vegetation cover and mean vegetation patch area showed seasonal and annual stability.

Previous studies highlight that multi-temporal and fine-scale (cm) UAV imagery has the potential to inform fine-scale vegetation patterns and functioning (Müllerová et al. 2021; Sankey et al. 2021). Multi-temporal flights allowed us, for instance, to determine seasonal patterns in landscape structure and primary productivity. Besides, the spatial resolution of UAV imagery was key to identifying small vegetation patches. In addition, our methodological procedure helped to distinguish and exclude shaded areas, as shadows make it difficult to match temporal UAV images and to analyze vegetation patterns (Mlambo et al. 2017; Forsmoo et al. 2018). The exclusion of shaded areas increased the accuracy of soil/vegetation boundaries, and it also improved measurements of vegetation primary productivity and calculation of landscape metrics. According to the results of our methodological approach, we suggest that appropriate methods to classify land cover from UAV imagery is a crucial first step to distinguishing vegetation from soil and studying related ecological processes involving both parameters. Therefore, the fine adjustment and processing of UAV imagery allow a further comprehension of ecological processes in larger areas when using upscaling procedures (Alonso-Martínez et al. 2020; Cunliffe et al. 2020). Due to their spatial resolution, UAV remote sensing images are especially relevant in shrublands or grasslands where vegetation is dispersed into small patches, such as in semi-arid landscapes. However, certain caveats should be avoided to correctly estimate shrublands or grassland properties. For example, we can combine different remote sensing datasets (UAV and satellite imagery), use higher spectral resolution sensors (e.g. hyperspectral camera) or use LiDAR to obtain precise information on the vertical distribution of the vegetation (Boelman et al. 2016; Prošek and Šímová 2019; Räsänen et al. 2020; Kolstad et al. 2022).

We recognise some limitations in our methodological framework because disentangling the relevant 'treatment' effect of the ungulate management context (i.e. domestic + wild ungulates vs. wild ungulates) on productivity is difficult to define in natural ecosystems and at a landscape scale. However, similarities in environmental conditions, plant composition and land use trajectories between study areas (albeit not equal) helped us to infer the historical effect of different ungulate species on vegetation through changes in plant community structure and consequently on ecosystem functioning (primary productivity). Experimental studies with pure "treatments" (e.g. completely similar vegetation) at the landscape scale are very hard to establish because natural ecosystems are driven by numerous confounding factors (e.g. edaphic characteristics). In particular, we do not know the relative abundance of the relevant plant species in each study area. We understand that a combined analysis of plant species composition, relative abundance and multispectral imagery can provide key information on how different herbivores affect ecosystem functioning. In our *quasi*-experimental approach, we have done our best to find fenced/non-fenced areas with comparable conditions, despite their differences in ungulate composition and grazing pressure. We suggest that this knowledge gap may lead to more studies conducted in different regions and with a larger time series to evaluate and distinguish the effects of wild and domestic ungulates on ecosystem functioning.

Our results disentangle to some extent the relative importance and potential interaction of abiotic (seasonality), biotic (herbivory) and anthropogenic (ungulate management) factors to affect micro- to meso-scale vegetation patterns. While both, herbivory and ungulate management, are key drivers of vegetation cover, climate seasonality was the main driver of primary productivity in the domestic grazing systems. Both ungulate groups differ in terms of their seasonal effects on vegetation structure and functioning, suggesting different mediation mechanisms of wild ungulates and livestock to maintain vegetation processes in long-term grazed systems. These different mediation mechanisms emphasize the need for preserving specific ungulate-vegetation interactions for habitat conservation, such as extensive transhumant pastoralism to avoid grasslands encroachment or wild ungulate management to diminish excessive biomass in shrublands when the biome originally evolved with the presence of medium-sized herbivores. Fine-scale information provided by UAVs and accurate image classification showed to be key tools for detecting ephemeral landscape characteristics (e.g. herbaceous cover and primary productivity) in presence of wild ungulates and livestock. Future studies at this scale can be replicated for other exclusion plots to improve comprehension of the trophic cascade processes mediated by both ungulate groups.

Acknowledgements We would like to thank Paloma Prieto, David Cuerda and Francisco Martinez, and the Sierras de Cazorla, Segura, and Las Villas Natural Park for their support. This study forms part of the AGROALNEXT (2022/038) programme and was supported by MCIN/AEI/10.13039/501100011033 with funding from European Union NextGenerationEU (PRTR-C17.I1) and by Generalitat Valenciana. This study also forms part of the DIGITALPAST (TED2021-130005B-C21) project and was supported by MCIN/AEI/10.13039/501100011033 and European Union NextGenerationEU/PRTR. This study also forms part of the TRASCAR (RTI2018-099609-B-C21) project and was supported by MCIN/AEI/10.13039/501100011033 with funding from European Regional Development Fund (ERDF). JMB was supported by Generalitat Valenciana with the program PlanGenT (CIDEGENT/2020/030).

Author contributions MV, JASZ and JMB contributed to the study conception and design. MV, EJ and JMB collected and processed the images and analyzed the data. All authors contributed to the writing process of the manuscript.

Funding This study forms part of the AGROALNEXT (2022/038) programme and was supported by MCIN/AEI/10.13039/501100011033 with funding from European Union NextGenerationEU (PRTR-C17.I1) and by Generalitat Valenciana. This study also forms part of the DIGITALPAST (TED2021-130005B-C21) project and was supported by

MCIN/AEI/10.13039/501100011033 and European Union NextGenerationEU/PRTR. This study also forms part of the TRASCAR (RTI2018-099609-B-C21) project and was supported by MCIN/AEI/10.13039/501100011033 with funding from European Regional Development Fund (ERDF). JMB was supported by Generalitat Valenciana with the program PlanGenT (CIDEGENT/2020/030).

Data availability The datasets generated during and/or analyzed during the current study are available from the corresponding author on request.

Declarations

Conflict of interest The authors have no competing interests to declare that are relevant to the content of this article.

References

Aguilera-Alcalá N, Arrondo E, Pascual-Rico R, Morales-Reyes Z, Gil-Sánchez JM, Donázar JA, Moleón M, Sánchez-Zapata JA (2022) The value of transhumance for biodiversity conservation: vulture foraging in relation to livestock movements. Ambio 51:1330–1342

Alonso-Martínez L, Ibañez-Álvarez M, Brolly M, Burnside NG, Calleja JA, Peláez M, López-Sánchez A, Bartolomé J, Fanlo H, Lavín S, Perea R (2020) Remote mapping of foodscapes using sUAS and a low cost BG-NIR sensor. Sci Total Environ 718:137357

Augustine DJ, McNaughton SJ (2006) Interactive effects of ungulate herbivores, soil fertility, and variable rainfall on ecosystem processes in a semi-arid savanna. Ecosystems 9(8):1242–1256

Augustine DJ, Wigley BJ, Ratnam J, Kibet S, Nyangito M, Sankaran M (2019) Large herbivores maintain a two-phase herbaceous vegetation mosaic in a semi-arid savanna. Ecol Evol 9(22):12779–12788

Baddeley A, Turner R (2005) Spatstat: an R package for analyzing spatial point patterns. J Stat Softw 12:1–42

Barbosa JM, Pascual-Rico R, Eguia Martínez S, Sánchez-Zapata JA (2020) Ungulates attenuate the response of Mediterranean mountain vegetation to climate oscillations. Ecosystems 23(5):957–972

Beguin J, Côté SD, Vellend M (2022) Large herbivores trigger spatiotemporal changes in forest plant diversity. Ecology 103:e3739

Benavente A (2008) Flora y vegetacion: Parque Natural de las Sierras de Cazorla, Segura y Las Villas. Anuario Del Adelantamiento De Cazorla 50:149–153

Biuw M, Jepsen JU, Cohen J, Ahonen SH, Tejesvi M, Aikio S, Wäli PR, Vindstad OPL, Markkola A, Niemelä P, Ims RA (2014) Long-term impacts of contrasting management of large ungulates in the Arctic tundra-forest ecotone: ecosystem structure and climate feedback. Ecosystems 17(5):890–905

Boelman NT, Holbrook JD, Greaves HE, Krause JS, Chmura HE, Magney TS, Vierling LA (2016) Airborne laser scanning and spectral remote sensing give a bird's eye perspective on arctic tundra breeding habitat at multiple spatial scales. Remote Sens Environ 184:337–349

Borowik T, Pettorelli N, Sönnichsen L, Jędrzejewska B (2013) Normalized difference vegetation index (NDVI) as a predictor of forage availability for ungulates in forest and field habitats. Eur J Wildl Res 59(5):675–682

Carpio AJ, Apollonio M, Acevedo P (2021) Wild ungulate overabundance in Europe: contexts, causes, monitoring and management recommendations. Mamm Rev 51(1):95–108

Charles GK, Porensky LM, Riginos C, Veblen KE, Young TP (2017) Herbivore effects on productivity vary by guild: cattle increase mean productivity while wildlife reduce variability: cattle. Ecol Appl 27(1):143–155

Congedo L (2021) Semi-automatic classification plugin: a Python tool for the download and processing of remote sensing images in QGIS. J Open Source Softw 6(64):3172

Cunliffe AM, Assmann J, Daskalova NG, Kerby JT, Myers-Smith IH (2020) Aboveground biomass corresponds strongly with drone-derived canopy height but weakly with greenness (NDVI) in a shrub tundra landscape. Environ Res Lett 15(12):125004

Desforges JP, Marques GM, Beumer LT, Chimienti M, Hansen LH, Pedersen SH, Schmidt NM, van Beest FM (2021) Environment and physiology shape Arctic ungulate population dynamics. Glob Change Biol 27(9):1755–1771

Ecke S, Dempewolf J, Frey J, Schwaller A, Endres E, Klemmt H, Tiede D, Seifert T (2022) UAV-based forest health monitoring: a systematic review. Remote Sens 14(13):3205

Espín-Sánchez DE, Álvarez VR, Talavera JM, Marín RG (2018) Preliminary study of inversion temperature in the southeast Iberian Peninsular: the case of Hernán Perea Plateau. Pirineos 173

Espunyes J, Bartolomé J, Garel M, Galvez-Ceron A, Fernández Aguilar X, Colom-Cadena A, Calleja JA, Gasso D, Jarque L, Lavin S, Marco I (2019) Seasonal diet composition of *Pyrenean chamois* is mainly shaped by primary production waves. PLoS One 14(1):e0210819

Fernández-García V, Calvo L (2023) Landscape implications of contemporary abandonment of extensive sheep grazing in a globally important agricultural heritage system. Land 12(4):780

Fernández-Olalla M, Martínez-Jauregui M, Perea R, Velamazán M, San Miguel A (2016) Threat or opportunity? Browsing preferences and potential impact of *Ammotragus lervia* on woody plants of a Mediterranean protected area. J Arid Environ 129:9–15

Forbes ES, Cushman JH, Burkepile DE, Young TP, Klope M, Young HS (2019) Synthesizing the effects of large, wild herbivore exclusion on ecosystem function. Funct Ecol 33(9):1597–1610

Forsmoo J, Anderson K, Macleod CJ, Wilkinson ME, Brazier R (2018) Drone-based structure-from-motion photogrammetry captures grassland sward height variability. J Appl Ecol 55(6):2587–2599

Gaitán JJ, Bran D, Oliva G, Ciari G, Nakamatsu V, Salomone J, Ferrante D, Buono G, Massara V, Humano G, Celdrán D, Opazo W, Maestre FT (2013) Evaluating the performance of multiple remote sensing indices to predict the spatial variability of ecosystem structure and functioning in Patagonian steppes. Ecol Indic 34:181–191

Gerlanc D, Kirby K (2021) _bootES: bootstrap confidence intervals on effect sizes_. R Package Version 1(2):1

Giralt-Rueda JM, Santamaria L (2021) Complementary differences in primary production and phenology among vegetation types increase ecosystem resilience to climate change and grazing pressure in an iconic Mediterranean ecosystem. Remote Sens 13(19):3920

Gómez-Mercado F (2011) Vegetación y flora de la Sierra de Cazorla. Guineana 17:1–481

Gómez-Zotano J, Alcántara-Manzanares J, Olmedo-Cobo JA, Martínez-Ibarra E (2015) La sistematización del clima mediterráneo: identificación, clasificación y caracterización climática de Andalucía (España). Revista De Geografía Norte Grande 61:161–180

Gorné LD, Díaz S (2022) Herbivory, intraspecific trait variability and back to herbivory. Oikos 2022(6):e09054

Grant K, Kreyling J, Beierkuhnlein C, Jentsch A (2017) Importance of seasonality for the response of a mesic temperate grassland to increased precipitation variability and warming. Ecosystems 20(8):1454–1467

Hamel S, Garel M, Festa-Bianchet M, Gaillard JM, Côté SD (2009) Spring Normalized Difference Vegetation Index (NDVI) predicts annual variation in timing of peak faecal crude protein in mountain ungulates. J Appl Ecol 46(3):582–589

Hesselbarth MHK, Sciaini M, With KA, Wiegand K, Nowosad J (2019) Landscapemetrics: an open-source R tool to calculate landscape metrics. Ecography 42:1648–1657

Hevia V, Azcárate FM, Oteros-Rozas E, González JA (2013) Exploring the role of transhumance drove roads on the conservation of ant diversity in Mediterranean agroecosystems. Biodivers Conserv 22:2567–2581

Hijmans R (2022a) _raster: geographic data analysis and modeling_. R package version 3.5-29

Hijmans R (2022b) _terra: spatial data analysis_. R package version 1.6-7

Hughey LF, Shoemaker KT, Stewart KM, McCauley DJ, Cushman JH (2021) Effects of human-altered landscapes on a reintroduced ungulate: patterns of habitat selection at the rangeland-wildland interface. Biol Conserv 257:109086

Ibáñez-Alvarez M, Baraza E, Serrano E, Romero-Munar A, Cardona C, Bartolome J, Krumins JA (2022) Ungulates alter plant cover without consistent effect on soil ecosystem functioning. Agric Ecosyst Environ 326:107796

Jarque-Bascuñana L, Calleja JA, Ibañez M, Bartolomé J, Albanell E, Espunyes J et al (2022) Grazing influences biomass production and protein content of alpine meadows. Sci Total Environ 818:151771

Johnson HE, Gustine DD, Golden TS, Adams LG, Parrett LS, Lenart EA, Barboza PS (2018) NDVI exhibits mixed success in predicting spatiotemporal variation in caribou summer forage quality and quantity. Ecosphere 9(10):e02461

Kassambara A (2020) ggpubr: 'ggplot2' based publication ready plots. R package version 0.4.0

Kéfi S, Rietkerk M, Roy M, Franc A, De Ruiter PC, Pascual M (2011) Robust scaling in ecosystems and the meltdown of patch size distributions before extinction. Ecol Lett 14(1):29–35

Kerby JT, Krivak-Tetley FE, Shikesho SD, Bolger DT (2022) Livestock impacts on an iconic Namib Desert plant are mediated by abiotic conditions. Oecologia 199(1):229–242

Keyserlingk J, de Hoop M, Mayor AG, Dekker SC, Rietkerk M, Foerster S (2021) Resilience of vegetation to drought: studying the effect of grazing in a Mediterranean rangeland using satellite time series. Remote Sens Environ 255:112270

Khorchani M, Nadal-Romero E, Lasanta T, Tague C (2021) Effects of vegetation succession and shrub clearing after land abandonment on the hydrological dynamics in the Central Spanish Pyrenees. CATENA 204:105374

Klosterman S, Melaas E, Wang J, Martinez A, Frederick S, O'Keefe J, Orwig DA, Wang Z, Sun Q, Schaaf C, Friedl M, Richardson AD (2018) Fine-scale perspectives on landscape phenology from unmanned aerial vehicle (UAV) photography. Agric for Meteorol 248:397–407

Kolstad AL, Snøan IB, Austrheim G, Bollandsås OM, Solberg EJ, Speed JDM (2022) Airborne laser scanning reveals increased growth and complexity of boreal forest canopies across a network of ungulate exclosures in Norway. Remote Sens Ecol Conserv 8(1):5–17

Laguna E, Carpio AJ, Vicente J, Barasona JA, Triguero-Ocaña R, Jiménez-Ruiz S et al (2021) The spatial ecology of red deer under different land use and management scenarios: protected areas, mixed farms and fenced hunting estates. Sci Total Environ 786:147124

Li W, Buitenwerf R, Munk M, Bøcher PK, Svenning JC (2020) Deep-learning based high-resolution mapping shows woody vegetation densification in greater Maasai Mara ecosystem. Remote Sens Environ 247:111953

Linnell JDC, Cretois B, Nilsen EB, Rolandsen CM, Solberg EJ, Veiberg V, Kaczensky P, Van Moorter B, Panzacchi M, Rauset GR, Kaltenborn B (2020) The challenges and opportunities of coexisting with wild ungulates in the human-dominated landscapes of Europe's Anthropocene. Biol Conserv 244:108500

Lohmann D, Tietjen B, Blaum N, Joubert DF, Jeltsch F (2012) Shifting thresholds and changing degradation patterns: climate change effects on the simulated long-term response of a semi-arid savanna to grazing. J Appl Ecol 49(4):814–823

Magnusson A, Skaug H, Nielsen A, Berg C, Kristensen K, Maechler M et al (2017) Package 'glmmtmb'. R Package Version 0.2.0

Manier DJ, Hobbs NT (2007) Large herbivores in sagebrush steppe ecosystems: livestock and wild ungulates influence structure and function. Oecologia 152(4):739–750

Martínez TM (2002) Comparison and overlap of sympatric wild ungulate diet in Cazorla, Segura and Las Villas Natural Park. Pirineos 157:103–116

Mlambo R, Woodhouse IH, Gerard F, Anderson K (2017) Structure from motion (SfM) photogrammetry with drone data: a low cost method for monitoring greenhouse gas emissions from forests in developing countries. Forests 8(3):68

Moreno-De Las Heras M, Saco PM, Willgoose GR, Tongway DJ (2011) Assessing landscape structure and pattern fragmentation in semiarid ecosystems using patch-size distributions. Ecol Appl 21(7):2793–2805

Müllerová J, Gago X, Bučas M, Company J, Estrany J, Fortesa J, Kent R (2021) Characterizing vegetation complexity with unmanned aerial systems (UAS)–A framework and synthesis. Ecol Indic 131:108156

Muñoz Sabater J (2019) ERA5-land monthly averaged data from 1981 to present. Copernicus Climate Change Service (C3S) Climate Data Store (CDS). https://doi.org/10.24381/cds.68d2bb3. Accessed 19 Sep 2022

Murray BD, Webster CR, Bump JK (2013) Broadening the ecological context of ungulate–ecosystem interactions: the importance of space, seasonality, and nitrogen. Ecology 94(6):1317–1326

Newman M, Mitchell FJG, Kelly DL (2014) Exclusion of large herbivores: long-term changes within the plant community. For Ecol Manag 321:136–144

Nishizawa K, Tatsumi S, Kitagawa R, Mori AS (2016) Deer herbivory affects the functional diversity of forest floor plants via changes in competition-mediated assembly rules. Ecol Res 31(4):569–578

Odadi WO (2011) African wild ungulates compete with or facilitate cattle depending on season (Science (1753)). Science 334(6056):594

Oteros-Rozas E, Ontillera-Sánchez R, Sanosa P, Gómez-Baggethun E, Reyes-García V, González JA (2013) Traditional ecological knowledge among transhumant pastoralists in Mediterranean Spain. Ecol Soc 18(3)

Perea R, López-Sánchez A, Roig S (2016) The use of shrub cover to preserve Mediterranean oak dehesas: a comparison between sheep, cattle and wild ungulate management. Appl Veg Sci 19(2):244–253

Pringle RM, Young TP, Rubenstein DI, McCauley DJ (2007) Herbivore-initiated interaction cascades and their modulation by productivity in an African savanna. Proc Natl Acad Sci USA 104(1):193–197

Prošek J, Šímová P (2019) UAV for mapping shrubland vegetation: does fusion of spectral and vertical information derived from a single sensor increase the classification accuracy? Int J Appl Earth Observ Geoinf 75:151–162

QGIS DT (2022) QGIS geographic information system. Open Source Geospatial Foundation Project. http://qgis.osgeo.org

Ramirez JI, Jansen PA, den Ouden J, Goudzwaard L, Poorter L (2019) Long-term effects of wild ungulates on the structure, composition and succession of temperate forests. For Ecol Manag 432:478–488

Räsänen A, Aurela M, Juutinen S, Kumpula T, Lohila A, Penttilä T, Virtanen T (2020) Detecting northern peatland vegetation patterns at ultra-high spatial resolution. Remote Sens Ecol Conserv 6(4):457–471

REDIAM (2012a) WMS Mapa del Modelo de distribución de los Pisos bioclimáticos de Andalucía. http://www.ideandalucia.es/catalogo/inspire/srv/api/records/62bbaf30b135eb8554eca858db4049c802089634

REDIAM (2012b) WMS Mapa de Ombrotipos a escala de detalle (1:10.000). http://www.ideandalucia.es/catalogo/inspire/srv/api/records/add4aba68fc2dbe828622a50c9b0baeb4598f70e

Regos A, Arenas-Castro S, Tapia L, Domínguez J, Honrado JP (2021) Using remotely sensed indicators of primary productivity to improve prioritization of conservation areas for top predators. Ecol Indic 125:107503

Ren Y, Zhu Y, Baldan D, Fu M, Wang B, Li J, Chen A (2021) Optimizing livestock carrying capacity for wild ungulate-livestock coexistence in a Qinghai-Tibet Plateau grassland. Sci Rep 11(1):1–8

Riginos C, Grace JB, Augustine DJ, Young TP (2009) Local versus landscape-scale effects of savanna trees on grasses. J Ecol 97(6):1337–1345

Royo AA, Kramer DW, Miller KV, Nibbelink NP, Stout SL (2017) Spatio-temporal variation in foodscapes modifies deer browsing impact on vegetation. Landsc Ecol 32(12):2281–2295

Rueda M, Rebollo S (2013) Contrasting impacts of different-sized herbivores on species richness of Mediterranean annual pastures differing in primary productivity. Oecologia 172(2):449–459

San Miguel-Ayanz A, Perea García-Calvo A, Fernández-Olalla R (2010) Wild ungulates vs. extensive livestock. Looking back to face the future. Opt Meditérr 92:27–34

Sanaei A, Ali A, Chahouki MAZ, Jafari M (2018) Plant coverage is a potential ecological indicator for species diversity and aboveground biomass in semi-steppe rangelands. Ecol Indic 93:256–266

Sankey JB, Sankey TT, Li J, Ravi S, Wang G, Caster J, Kasprak A (2021) Quantifying plant-soil-nutrient dynamics in rangelands: fusion of UAV hyperspectral-LiDAR, UAV multispectral-photogrammetry, and ground-based LiDAR-digital photography in a shrub-encroached desert grassland. Remote Sens Environ 253:112223

Stavi I, Yizhaq H, Osem Y, Argaman E (2021) Positive impacts of livestock and wild ungulate routes on functioning of dryland ecosystems. Ecol Evol 11(20):13684–13691

Sun J, Du W (2017) Effects of precipitation and temperature on net primary productivity and precipitation use efficiency across China's grasslands. GIScience Remote Sens 54(6):881–897

Svenning JC, Pedersen PBM, Donlan CJ, Ejrnæs R, Faurby S, Galetti M, Hansen DM, Sandel B, Sandom CJ, Terborgh JW, Vera FWM (2016) Science for a wilder Anthropocene: synthesis and future directions for trophic rewilding research. Proc Natl Acad Sci USA 113(4):898–906

Valdés-Correcher E, Sitters J, Wassen M, Brion N, Olde Venterink H (2019) Herbivore dung quality affects plant community diversity. Sci Rep 9(1):5675

Velamazán M, San Miguel A, Escribano R, Perea R (2017) Threatened woody flora as an ecological indicator of large herbivore introductions. Biodivers Conserv 26(4):917–930

Velamazán M, San Miguel A, Escribano R, Perea R (2018) Use of firebreaks and artificial supply points by wild ungulates: effects on fuel load and woody vegetation along a distance gradient. For Ecol Manag 427:114–123

Vuorinen EM, Austrheim G, Mysterud A, Gya R, Vandvik V, Grytnes JA, Speed JDM (2021) Functional traits of alpine plant communities show long-term resistance to changing herbivore densities. Ecosphere 12(12):e03887

Wang H, Liu H, Cao G, Ma Z, Li Y, Zhang F et al (2020) Alpine grassland plants grow earlier and faster but biomass remains unchanged over 35 years of climate change. Ecol Lett 23(4):701–710

Wickham H (2016) ggplot2: elegant graphics for data analysis. Springer, New York

Zweifel-Schielly B, Kreuzer M, Ewald KC, Suter W (2009) Habitat selection by an Alpine ungulate: the significance of forage characteristics varies with scale and season. Ecography 32(1):103–113