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RESEARCH ARTICLE

Impact of climate change on pasture quality in Mediterranean dehesas subjected to different grazing histories

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Abstract
Background and aims Forecasted climate change and overgrazing are threatening the sustainability of dehesas, human-managed ecosystems where pastures, livestock and scattered trees coexist. Pasture quality is particularly sensitive to these global-change drivers, but there are still many gaps to broaden knowledge about the interactive effects of both factors on it. In addition, scattered trees might play a relevant role in maintaining high levels of pasture quality under future scenarios of higher aridity, but its role remains largely unexplored.

Methods We designed a field manipulative experiment of rainfall exclusion and increased temperature aimed to evaluate the impact of forecasted climate on pasture quality under different historical grazing intensities. To test the potential buffering effect of trees, experimental plots were installed equally in two habitat types: under trees and open grassland.

Results Warming reduced the nutrient concentration of pasture, while drought increased it. Tree canopy improved soil fertility, which translated into an increase in pasture quality. Livestock exclusion and high grazing intensity caused a decrease in pasture quality, whereas moderate grazing intensity exerted positive effects on it. Finally, warming beneath tree canopy negatively affected the P concentration of pasture, specifically in the site subjected to moderate grazing intensity.

Conclusion Our findings suggest that communities subjected to moderate grazing are more sensitive to climate change from a nutritional standpoint, likely because this management type provides high levels of P to the soil. In addition, we highlight the essential role of trees in agroforestry ecosystems to maintain high values of nutritional quality of pasture.

Keywords Buffer effect · Grasslands · Nutrient concentration · Rainfall exclusion · Warming

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Introduction

Climate change models predict a temperature increase of 2–3 °C by the end of the XXI century for the Mediterranean area. Likewise, longer time periods of drought combined with more intense rainy events are forecasted for this region (IPCC 2021). In addition, overgrazing constitutes another major threat for the sustainability and functioning of terrestrial ecosystems (Fleischner 1994; Vázquez and Simberloff 2003), since herbivores reduce plant cover and may cause serious problems of soil degradation. Both stress sources could cause diverse effects on different ecosystem processes, including those that strongly depend on soil nutrients, such as net primary productivity, fiber content or carbon sequestration, among others (Hidalgo-Galvez et al. 2022; Sternberg and Yakir 2015; Yuan and Chen 2015).

Warming can induce contrasted effects on plant nutrient balance and their use efficiency depending on the region, the intensity and duration of temperature increase, the target species and the duration of the growing season (Polley et al. 2013; Thornton et al. 2009). In general, a temperature increase (within an optimal range) alters microbial activity and decomposition rates of organic matter, stimulates root growth and increases leaf transpiration rate, commonly leading to an increase in plant uptake of soil water and nutrients (Pregitzer and King 2005; Viciedo et al. 2021). However, in water-limited ecosystems, the effect of warming is commonly negative since high temperatures tend to increase water deficit that triggers stomatal closure, therefore reducing water diffusion pathway in leaves (Abbate et al. 2004) and the uptake of water-soluble nutrients (Brouder and Volenec 2008; Cramer et al. 2009). In addition, an increase in temperature enhances the use of photosynthetic nitrogen (Dwyer et al. 2007) and decreases the phosphorus content of pasture due to a dilution effect caused by a more accelerated plant growth (Martinez et al. 2014; Reich and Oleksyn 2004).

Plant acclimation to drought is complex and depends on different factors, such as the species characteristics or the duration of water restriction (Farooq et al. 2009). Drought alters plant associations with soil microorganisms, which are essential for nutrient uptake strategies (Pérez-Ramos et al. 2021; Schimel et al. 2007). Under moderate water stress, plant maturation can be delayed, thus nutrient values of pasture remain higher for a longer period (Coblentz et al. 2000). However, a more intense drought usually translates into reductions in plant cover, litter decomposition rates and nutrient mineralization (Homet et al. 2021; Jiao et al. 2016). This plant cover reduction increases the risk of soil nutrient loss due to leaching or erosion, which implies a depletion of nutrients in the medium to short term (Delgado-Baquerizo et al. 2013; Matías et al. 2011). However, most of previous studies have evaluated the independent effects of both sources of climate stress (temperature increase and drought) on pasture quality, while the impact of their interaction remains poorly known, particularly in semi-arid ecosystems.

The impact of climate change on nutrient cycling usually follows a strong spatial variation (Chang et al. 2021). An example of heterogeneous ecosystem is the Mediterranean dehesa, which is composed of a large layer of herbaceous species typical of grasslands that coexist with scattered trees (López-Díaz et al. 2015; Moreno 2008). Pasture growing beneath tree canopy usually has higher nutrient content than those located in open areas. This higher nutrient concentration is probably due to the higher soil fertility of this habitat coming from the nutrient transport from distant areas through tree lateral roots (Sileshi 2016; Tiedemann and Klemmedson 1973), tree litter decomposition (Aponte et al. 2012; Ludwig et al. 2008) and animal droppings coming from that graze and refuge under the tree cover (Serrano et al. 2018; Tucker et al. 2008). In addition, trees reduce solar radiation (Pezzopane et al. 2010; Siles et al. 2010) and air temperature (Rahman et al. 2017; Siles et al. 2010), leading to a stabilization of the microclimate, a decrease in the variability of CO_2 flux (De Carvalho Gomes et al. 2016) and a reduction of evapotranspiration (Lin 2007). All these evidences suggest that trees could mitigate the impact of climate change on pasture growth and quality (Bayala et al. 2014; Sida et al. 2018). Microclimate conditions beneath tree canopies directly affect plant physiological processes, which delays the vegetative development and maintains higher metabolic levels for a longer period, which could increase pasture quality in this habitat type (Jackson and Ash 1998; Sousa et al. 2010). However, to our knowledge, no experimental studies to date have assessed under field conditions the potential buffering role of scattered trees in attenuating the impact of on-going aridity increase on pasture quality.

Additionally to climate change, changes in land use such as those derived from different livestock management constitutes other of the main factors modifying soil properties (Medina-Roldán et al. 2012; Panayiotou et al. 2017) and, therefore, pasture production (Geng et al. 2012; He et al. 2010). The impact of grazing varies depending on its intensity (Piñeiro et al. 2010; Zhou et al. 2017). On the one hand, a moderate grazing pressure increases the amount of organic material through animal droppings (Sitters and Venterink 2018; Wang et al. 2018) and increases soil nutrient concentrations (Han et al. 2008; Tessema et al. 2011), which generally translates into an increase in the nutritional value of pasture (McCarthy et al. 2013; Miao et al. 2015). Moreover, livestock droppings accelerate litter mineralization rates and provide a source of readily available nutrients for plants and soil microorganisms (López-Mársico et al. 2015; Schrama et al. 2013). On the other hand, a higher grazing intensity might reduce drastically plant cover (Eldridge et al. 2016, 2017; Pulido et al. 2018), decrease plant growth rate (Bilotta et al. 2007; Smith 1979) and alter some physical soil properties (Bilotta et al. 2007; Carrero-González et al. 2012).

Although the impact of climate change and grazing intensity on pasture quality has been analyzed separately in previous studies, the interactive effects of both stress sources remain largely untested, particularly in Mediterranean ecosystems. Regarding this issue, Maestre et al. (2022) highlight the importance of taking into account the interactions between grazing and local abiotic and biotic factors when assessing ecosystem services in drylands. Here, we are interested in evaluating whether plant communities historically harboring high grazing pressure are more sensitive to climate change from a nutritional point of view or, conversely, these communities have developed efficient strategies that make them more resistant to those environmental changes forecasted by climate change models.

In the Iberian Peninsula, between 3.5 and 4 million hectares are dedicated to a type of ecosystem called *dehesa* in Spain or *montado* in Portugal (Olea and San Miguel-Ayanz 2006). Due to its economic importance and its potential susceptibility to changes in climate (Moreno and Pulido 2009), we carried out a field experiment for two years with different scenarios of temperature and rainfall. The aim of this study was to evaluate how pasture quality could be influenced by the temperature increase and reduced rainfall predicted by climate change models, as well as to analyze whether scattered trees could modulate these potential climate-induced changes in dehesas. In addition, we also tested if the impact of both climatic stressors could vary depending on the historical grazing pressure of the site. We raise several questions: (i) What are the effects of climate change (temperature increase and rainfall reduction) on pasture quality?; (ii) Can tree canopy alter pasture quality and buffer the impact of climate change on this ecosystem property? (iii) What is the influence of management history on pasture quality?; (iv) Is the impact of climate change more pronounced when plant communities have been historically subjected to higher grazing intensity? Results of this study will provide new insights into the interactive effects of two global change drivers threatening Mediterranean dehesas on pasture quality with the aim of designing action plans that mitigate the negative consequences of both stress sources on this ecosystem property.

Material and methods

Experimental design

This study was carried out in southwestern Spain (38°22′50.64”N, 4°45′27.69”W). The climate of the study area is continental-Mediterranean, with cold, wet winters and hot, dry summers. The annual precipitation is 416 mm/year and the mean annual temperature is 15.4 °C. January is the coldest and July the warmest month (5.9 °C and 26.9 °C on average, respectively; IFAPA weather station, Hinojosa del Duque; data from 2010 to 2020, https://www.juntadeandalucia.es/agriculturaypesca/ifapa/riaweb/web/estacion/14/102). The studied area is characterized by a dense herbaceous layer (≥ 80%), with a mean species richness of 9.6 ± 0.3 species/m^2 and it is dominated by native herbaceous species such as *Sinapis alba* L., *Avena sterilis* L., *Erodium moschatum* L. or *Hordeum murinum* L. subsp. *leporium* (Link) Acang. Scattered trees [*Quercus ilex* subsp. *ballota* (Desf.) Samp.] are frequent, with a mean density of 14.5 ± 1.3 trees/ha, by occupying approximately 20% of the total cover. Soils are usually shallow, reaching a maximum depth of 50 cm. Their pH is acid, varying between 6.2 and 6.4 and its texture is loamy-sandy. For this study, three neighboring dehesas with similar characteristics in terms of vegetation, tree density, slope, orientation, and soil texture and depth were selected (more details in Pérez-Ramos et al. 2021). Specifically, the distance across sites was 4.3 km. They were all located in the same valley in a very flat area (difference in elevation between highest and lowest site is 13 m, namely 685, 672 and 680 m.a.s.l.) with no hills or major elevations between them. Moreover, differences in rainfall across sites are minimal.

These dehesas were subjected to different grazing histories, from high livestock pressure (0.85 LU/ha), moderate grazing intensity (0.64 LU/ha), to livestock exclusion. Livestock was mainly composed of Iberian sheep and pigs; however, to avoid possible damages by them we fenced the experimental plots and we analyzed the legacy effects of the management history of each dehesa.

In September 2016, 36 sampling plots of 4 × 6 m were installed at a minimum distance of 20 m. They were equally and randomly distributed in the three study dehesas and in the two selected habitats (half of them under tree canopy and the other half in open grassland, more than 10 m from the edge of trees). In each plot, we simulated three climatic scenarios mimicking the predicted changes for the period 2040–2070 in the Mediterranean area (IPCC 2021). To reproduce the forecasted temperature increase (‘warming’ treatment), four open top chambers (OTCs, Marion et al. 1997) were placed per plot. They consist of hexagonal pyramids made up of 40 × 50 × 32 cm inclined panels of methacrylate without UV filter (Faberplast, Madrid) to avoid modifying the light spectrum and allow the transmission of wavelengths between 280 and 750 nm. They increase the interior temperature between 2 and 3 °C (more details in Pérez-Ramos et al. 2021). Following the design of Matías et al. (2012), we built rainfall exclusion shelters (2.5 × 2.5 × 1.5 m) using 6 methacrylate gutters (11 cm wide, at a distance from each other of 36 cm and inclined at an angle of 20°) in order to implement the ‘drought’ treatment. These rainfall exclusion structures do not modify the frequency of precipitation events, but reduce a third of the total precipitation (Yahdjian and Sala 2002). Two of the four OTCs installed in each plot were placed under these rainfall exclusion shelters with the aim of analyzing the impact of temperature increase and drought simultaneously (‘warming + drought’ treatment). Finally, an experimental unit called ‘control’ (2.5 × 2.5 m) was delimited and exposed to the current natural conditions of temperature and precipitation. Thus, the experimental design resulted in a total of 144 experimental units (3 dehesas × 2 habitats × 4 climatic treatments × 6 replicates).

Environmental characterization of the experimental plots

Chemical properties of the soil

Soil fertility was assessed in 2017 and 2019 by taking samples from the first 10 cm of the soil at four different locations within each of the 144 experimental units using a 3 cm diameter auger. In the laboratory, samples were air-dried and sieved. The fraction smaller than 2 mm was analyzed in order to evaluate nine chemical properties (Sparks 1996): pH (measured in a ratio 1:2.5 soil:water), total organic carbon (by oxidation of organic matter with H_2SO_4 and $K_2Cr_2O_7$ and determined by spectrophotemetry), organic matter [expressed as total organic carbon corrected with a coefficient assuming that the organic matter contains humic acids with 58% carbon (100/58 = 1.724, Van Bemmelen factor)], available phosphorus (by spectrophotometry), NH_4^+ and NO_3^- assimilable content (extracted with 1 KCl and determined by spectrophotemetry, and available Ca^{2+}, Mg^{2+} and K^+ (extracted with 1 N $NH_4CH_3CO_2$ and determined by atomic absorption spectroscopy).

Microclimate

Tree cover Tree cover was estimated in each of the 144 experimental units by measuring plant area index (PAI), which includes both leaves and branches. Hemispherical photographs of the canopy were taken in spring 2018, before sunrise or after sunset using a horizontally leveled digital camera (Coolpix 4500; Nikon, Tokyo, Japan) positioned 0.5 m aboveground and using a ‘fisheye’ lens with a wide field (FCE8; Nikon). Images were analyzed using Hemiview Canopy Analysis software version 2.1 (1999; Delta-TDevices Ltd., Cambridge, UK).

Thermal stress index In 24 randomly chosen experimental units, air temperature was hourly registered at ground level with a resolution of 0.1 °C using HOBOMX2201 data loggers (Onset Computer, Bourne, MA, USA). Plants experience a reduction in biomass production caused by a rapid decline in photosynthesis when the temperature exceeds 30 °C (Benavides et al. 2009; Fahad et al. 2017; Saini and Aspinall 1982). Moreover, seed sterility appears and root development is prevented (Ferris et al. 1998; Huang et al. 2012; Saini and Aspinall 1982) if temperatures overpass this threshold. For these reasons, it is considered that plants suffer stress above 30 °C and cumulated thermal stress was calculated for mean temperature during January–July (that is, the duration of pasture growth in the study area) using the following equation (Eq. 1):

$$\text{Thermal stress} = \frac{\text{Accumulated temperature}\left(T_{\text{mean}} - 30\right)}{\text{Monitoring days}_{(\text{January–July})}} \tag{1}$$

where T_{mean} is the daily mean temperature, and monitoring days represent the number of days of the period sampled.

Water stress index In 72 randomly chosen experimental units, soil volumetric water content (% VWC) was periodically (i.e. weekly in spring and monthly in the rest of the year) measured up to 40 cm deep at intervals of 10 cm using a PR2 humidity probe (Delta-T Devices Ltd., Cambridge, UK). For the purpose of determining the amount of water available for plants, the total transpirable soil water (% TTSW) was calculated for the average of the four depths (Eq. 2):

$$\text{TTSW} = \text{VWC}_{\text{max}} - \text{VWC}_{\text{min}} \tag{2}$$

where VWC_{max} and VWC_{min} represent the maximum and minimum soil volumetric water content (%) for each experimental unit during January–July period, respectively. This parameter represents the ability of plant communities to uptake water under particular soil conditions. It is based on the observed SWC dynamics and assumes that the minimum SWC in summer reflects the limit of plant water uptake.

According to Barkaoui et al. (2017), plants suffer water stress when the TTSW is below 30% (that is, when their accessible soil water reserve is almost empty). Thus, water stress index was calculated during January–July using the following formula (Eq. 3):

$$\text{Water stress index} = \frac{\text{VWC}_{\text{stress threshold}} - \text{VWC}_{\text{i}}}{\text{TTSW x } 0,3} \tag{3}$$

where VWC_{i} is the soil volumetric water content in each monitoring data, and $\text{VWC}_{\text{stress threshold}}$ shows the result of the sum of 30% TTSW and VWC_{min}.

Pasture quality

At the end of the vegetative cycle of 2017 and 2019, aboveground biomass produced in each of the 144 experimental units was collected using 50×50 cm quadrats. The collected samples were cleaned of non-herbaceous material, oven-dried at 70 °C for 48 hours and finely ground (< 2 mm) in an IKA mill. Pasture quality was determined through chemical analyses of nutrient concentration using the plant biomass previously collected. Using an Inductively Coupled Plasma Optical Emission Spectroscopy (ICP-OES), a multi-elemental inorganic analysis (P, Ca^{2+}, Mg^{2+} and K^{+}) was carried out in the Analysis Service of the Institute of Natural Resources and Agrobiology of Seville (IRNAS-CSIC), thanks to an ICP-OES VARIAN 720-ES spectrophotometer with electronic nebulizer. C and N concentration was determined at the Zaidin Experimental Station (EEZ-CSIC, Granada) using a LecoTruSpec C N elemental analyzer.

Statistical analyses

A Principal Component Analysis (PCA, hereafter) was carried out with soil chemical variables (pH, organic matter, carbon, ammonium, nitrate, phosphorus, calcium, magnesium and potassium) to analyze the correlations between them and identify the main axes of edaphic variation among the 144 experimental units. Factor 1 resulting from PCA (which we call 'soil fertility'; more details in the Results section) was included as a fixed factor in the statistical analyses explained below. Using Linear Mixed Models (LMMs, hereafter) we tested the individual and combined effects of the main factors considered in this study (year, habitat type, climatic treatment, management history and soil fertility) on the main nutrients of pasture (carbon, nitrogen, phosphorus, calcium, magnesium and potassium). Response variables were transformed when necessary to fulfil the normality and homoscedasticity criteria. Experimental plots were included as a random factor in the model and coded to affect only intercepts (not slopes). A 'complete model' was built based on the combination of all factors. In the cases where we detected a significant effect of any factor or its interaction with other(s), Tukey's post-hoc test was performed to identify those homogeneous subsets of means that did not differ from each other. In addition, through bivariate linear regressions, we evaluated the relationship between stress indices (thermal and hydric) and the different pasture nutrients, as well as between pasture and soil nutrients. Statistical analyses were performed in R v.4.0.0 (R Development Core Team 2020) using the following packages: *tidyverse* (for data manipulation and visualization), *nortest* (for normality calculation), *car* and *pbkrtest* (for testing the estimated parameters, *p value*), *lmerTest*, *ModelMetrics*, and *mgcv* (for running linear mixed models), and *ggplot2* and *ggpubr* (for graphical representation).

Results

Descriptive analysis of soil nutrients and their spatial distribution in the experimental plots

Results of the Principal Component Analysis (PCA) for the nine soil variables analyzed are shown in Fig. 1a. Factor 1 represented most of the variability (36.41%) and was related to the concentration of P, OM, C, Ca^{2+} and K^+ in the soil. Factor 2, with a variability of 17.82%, was related to pH, Ca^{2+} and Mg^{2+} in the soil (Fig. 1a). Table S1 shows the details of these relationships. In a second PCA using the averaged values of both sampling years for the nine edaphic variables quantified in this study, we observed that throughout Factor 1 (with 56.53% of variability) experimental units were distributed according to the habitat type, with those plots beneath tree canopies being located at the positive side of the axis and those installed in open grasslands at the negative side. This result indicates that plots located beneath tree canopies showed higher values for most of the soil nutrients analyzed (i.e. higher fertility). Throughout Factor 2 (with 18.03% of variability), experimental units were differentiated according to the management history, with plots subjected to moderate grazing intensity being located at the negative side of the axis and the remaining plots (subjected to null or high grazing intensity) at the positive side (Fig. 1b). Specifically, this means that soils subjected to moderate grazing intensity were less acid and more fertile in terms of Ca^{2+} and Mg^{2+} concentration.

Factors influencing pasture quality

Results from the linear mixed models showed that all the pasture nutrients considered in our study (excepting carbon) were significantly affected by management history and habitat type (Table 1). However, only plant P and Ca^{2+} were influenced by climatic treatments. It is worth noting the interaction between management history and climatic treatment, which affected plant N, P and K^+. Although the interaction of both stress sources had a significant effect on the concentration of these three pasture elements, only plant P showed significant differences between different climatic treatments when a Tukey's post-hoc test was applied (Fig. S1). Specifically, plant P was negatively affected by warming, but this effect was only evident beneath tree canopies in the site subjected to moderate grazing intensity.

Effects of climate change on pasture quality

Plant P and Ca^{2+} were the only pasture elements influenced by climatic treatments. Plant P was significantly lower in the treatments that simulated a temperature increase (i.e. warming and warming + drought) compared to those located outside the OTCs (i.e. control and drought). Compared to warming, drought treatment induced higher P concentration in the pasture (Fig. 2a). Plant Ca^{2+} was significantly lower in warming than in drought treatment (Fig. 2b). Intermediate values of this element were observed in the other two climatic treatments.

Effects of tree canopy on pasture quality

Overall, pasture quality was strongly influenced by habitat type (Table 1), appearing higher values of

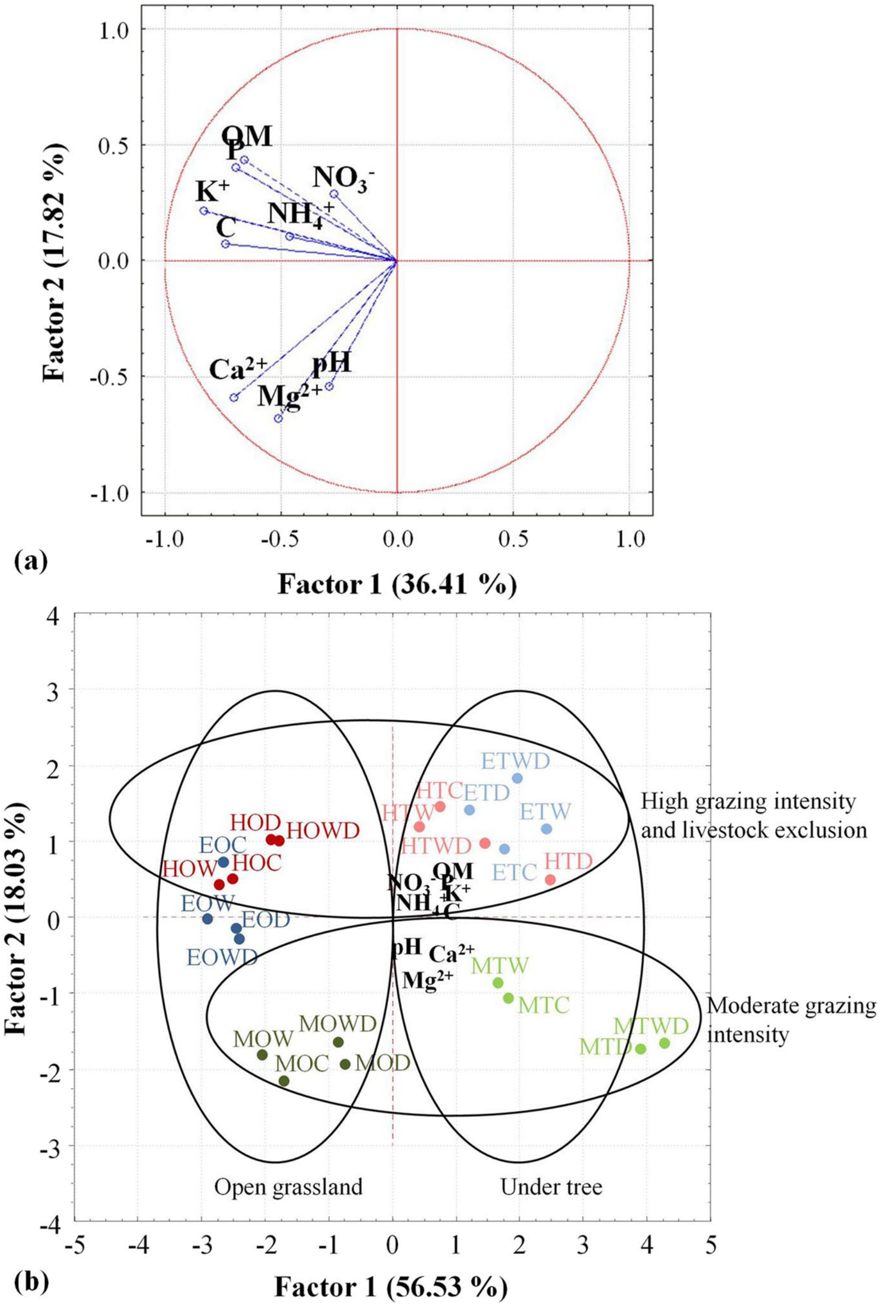


Fig. 1 Graphical representation of the first and second axis from the Principal Component Analysis (PCA). Soil nutrients (C, P, NO_3^-, NH_4^+, Ca^{2+}, Mg^{2+} and K^+), organic matter (OM) and soil pH for the 144 experimental units are represented over the two sampling years (2017 and 2019; panel **a**). Projection of the 24 combinations resulting from the three factors considered in this study (management history, habitat type and climatic treatment) along the plane defined by the two main PCA dimensions. Average values of the two sampling years (2017 and 2019) are represented. Abbreviations = H: high grazing intensity (in red); M: moderate grazing intensity (in green); E: livestock exclusion (in blue); T: under tree (with light colours); O: open grassland (with dark colours); C: control; D: drought; W: warming, WD: warming + drought (panel **b**)

plant nutrients beneath tree canopies (Table S2). The largest differences between habitats appeared for N, which increased 33.8% under tree canopy in comparison with open grasslands. In both habitat types, C was the most important element present in the pasture and P the scarcest (Table S2).

Effect of thermal and water stress on pasture quality

Results from our linear regressions showed that pasture quality responded significantly to both sources of stress, with slight differences depending on the habitat type. Specifically, plant N increased with

Table 1 Results from the linear mixed models to evaluate the influence of management history, habitat type, climatic treatment, year and soil fertility on plant C, N, P, Ca^{2+}, Mg^{2+} and K^{+}. Only those factors (and their interactions) that exerted a significant effect on the response variables are included in the table

Response variable	Factors with significant effect	SS	DF	F	*p*
Plant carbon	Year	1.83	1	5.29	0.02
Plant nitrogen	Management history	0.40	2	4.61	0.02
	Habitat type	1.60	1	36.68	<0.001
	Year	6.31	1	144.22	<0.001
	Soil fertility	0.38	1	8.69	0.004
	Management history × Climatic treatment	0.60	6	2.28	0.04
	Management history × Year	0.75	2	8.56	<0.001
	Habitat type × Year	0.40	1	9.25	0.003
	Management history × Climatic treatment × Year	0.67	6	2.57	0.02
Plant phosphorus	Management history	0.25	2	3.35	0.05
	Climatic treatment	1.49	3	13.06	<0.001
	Soil fertility	0.37	1	9.65	0.002
	Management history × Climatic treatment	0.57	6	2.49	0.02
	Management history × Year	0.41	2	5.36	0.01
	Management history × Habitat type × Climatic treatment	0.88	6	3.88	0.001
	Management history × Climatic treatment × Year	0.86	6	3.78	0.002
Plant calcium	Management history	3.21	2	20.33	<0.001
	Habitat type	0.52	1	6.62	0.01
	Climatic treatment	0.94	3	3.96	0.01
	Management history × Habitat type	0.96	2	6.08	0.01
	Management history × Year	2.83	2	17.88	<0.001
	Habitat type × Year	0.82	1	10.39	0.001
Plant magnesium	Management history	0.01	2	3.76	0.03
	Habitat type	0.01	1	4.76	0.03
	Year	0.03	1	21.80	<0.001
	Management history × Year	0.03	2	9.96	<0.001
	Habitat type × Year	0.02	1	13.21	<0.001
Plant potassium	Management history	0.13	2	4.67	0.02
	Habitat type	0.18	1	12.98	0.001
	Year	0.55	1	38.79	<0.001
	Soil fertility	0.14	1	9.95	0.002
	Management history × Climatic treatment	0.24	6	2.82	0.01
	Management history × Year	0.50	2	17.75	<0.001

increasing thermal stress (marginally significant in open grassland) (Fig. 3a). However, plant K^{+} showed the opposite pattern in both habitat types (Fig. 3b). Regarding water stress, an increase on it caused an increase in plant C (significant in open grassland) and plant K^{+} (in both habitat types; Fig. 3c-e). However, water stress caused a decrease in plant N (Fig. 3d). Table S3 shows differences in plant nutrients according to the habitat types. Figure 3 show s that the two habitat types differed in thermal stress (lower under trees than in open grasslands) but not in water stress.

Effects of management history on pasture quality

Management history influenced all pasture nutrients except C concentration. On the one hand, livestock exclusion reduced the nutrient concentration of some

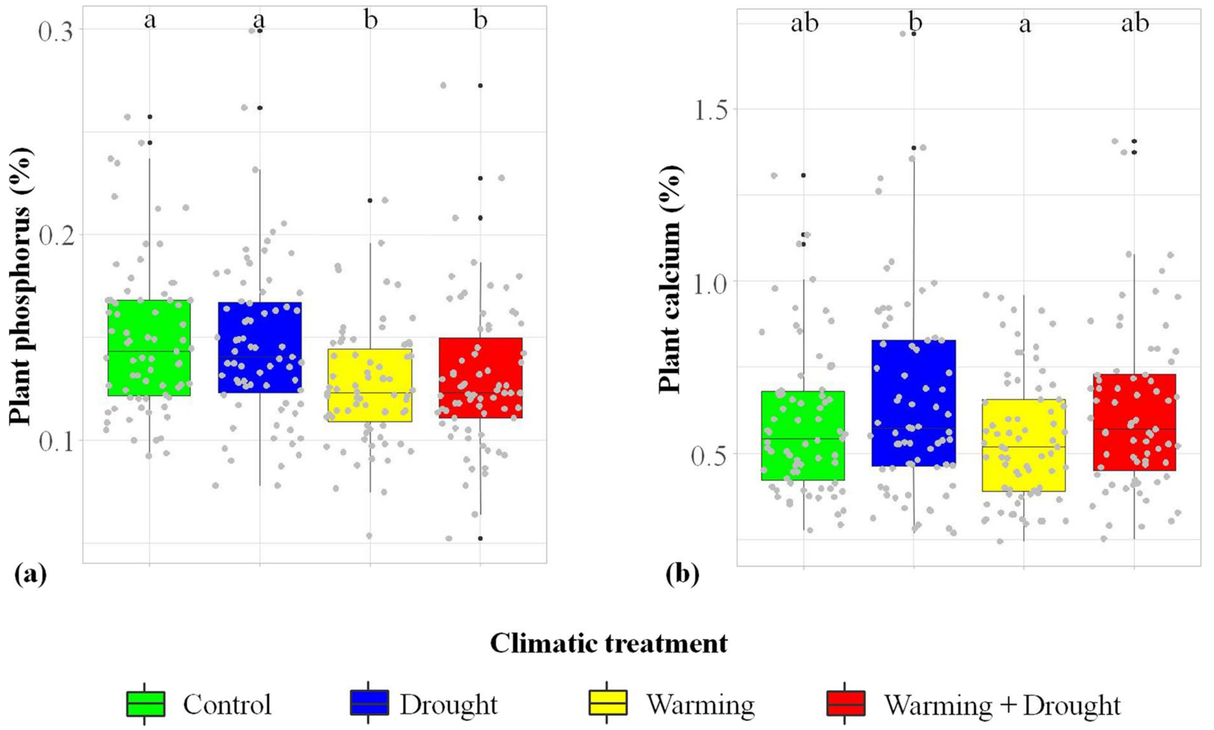


Fig. 2 Effects of the climatic treatments on plant P (panel **a**) and Ca^{2+} (panel **b**) (in %). Two sampling years (2017 and 2019) are represented. Different letters denote significant differences between climatic treatments after a Tukey post-hoc test

elements, appearing lower plant N (Fig. 4a) and Ca^{2+} (Fig. 4c) in those plots. Pastures subjected to moderate grazing intensity were significantly richer in P (Fig. 4b) and Mg^{2+} (Fig. 4d). Finally, plant K^+ differed when comparing the dehesas historically subjected to grazing, with higher values in those pastures subjected to high grazing intensity (Fig. 4e).

Effects of soil fertility on pasture quality

Soil N, P, Ca^{2+}, Mg^{2+} and K^+ influenced significantly and positively the concentration of them in the pasture (Fig. 5a-e). In addition, the same pattern was also observed between plant N and NO_3^- in the soil (Fig. 5f). Finally, a higher percentage of organic matter in the soil enhanced the concentration of plant C and N (Fig. 5g-h).

Effects of sampling year on pasture quality

Plant C, N, Mg^{2+} and K^+ differed strongly for the two sampling years. A significantly higher concentration of N was observed in the pasture collected in 2017 (1.31% in 2017 vs. 0.94% in 2019; $p < 0.001$; $R^2 = 0.18$). However, the pastures collected in 2019 presented a significantly higher concentration of Mg^{2+} (0.17% in 2019 vs. 0.16% in 2017; $p = 0.002$; $R^2 = 0.03$) and K^+ (1.26% in 2019 vs. 1.10% in 2017; $p < 0.001$; $R^2 = 0.04$).

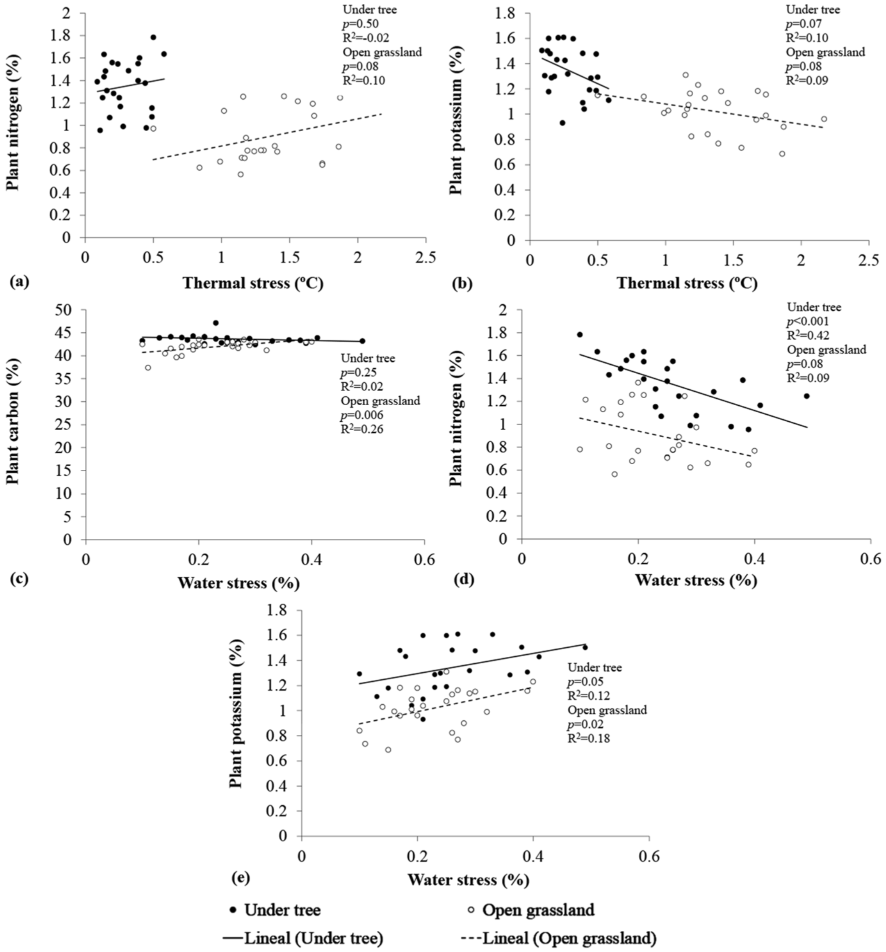
Discussion

Results from this study show how temperature increase, rainfall reduction and management history affect pasture quality, and highlight the important role that scattered trees could play in Mediterranean dehesas under future scenarios of higher aridity.

What are the effects of climate change on pasture quality?

This study shows that forecasted climate change could modify pasture quality in Mediterranean

Fig. 3 Effects of thermal stress on plant N (panel **a**), K^+ (panel **b**), and impact of water stress on plant C (panel **c**), N (panel **d**) and K^+ (panel **e**) (in %). Closed symbols represent the experimental plots located under tree and open symbols indicate those plots situated in open grasslands. Continuous lines are the result of the linear regressions for habitats located under trees and dashed lines for open grasslands (including the two sampling years)

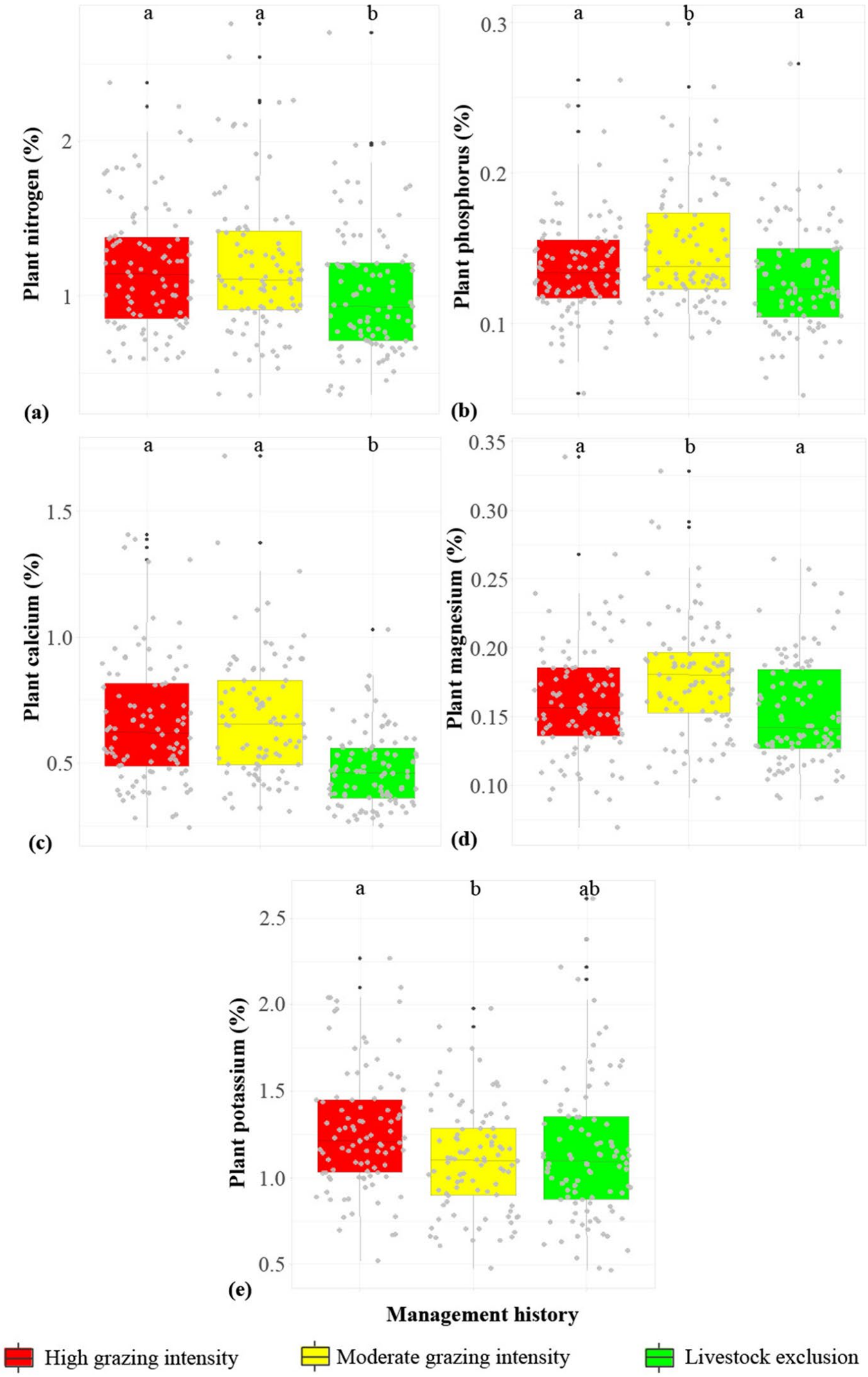


dehesa-type ecosystems, altering P and Ca^{2+} concentration. Specifically, we observed that temperature increase caused a significant decrease in the pasture concentration of both elements (Fig. 2). In the case of P, it could be caused by a dilution effect (Reich and Oleksyn 2004), which occurs when biomass growth is enhanced by an improved performance of photosystem II, as well as by different anatomical adjustments to temperature increase (Habermann et al. 2019; Martinez et al. 2014). The observed decrease in plant Ca^{2+} under warmer conditions could be a consequence of the extreme vapor pressure deficit potentially caused by the closure of the stomata, which reduces the flux of some water-soluble nutrients such as Ca^{2+} (Brouder and Volenec 2008; Cramer et al. 2009).

On the contrary, rainfall reduction induced an increase in plant P and Ca^{2+} in the pasture (Fig. 2). This result could be explained by the effects of a moderate water deficit, which usually induces a delay in plant maturation (Coblentz et al. 2000) and a reduction of leaf growth and development (caused by decreased stomatal conductance, leaf transpiration rate and photosynthesis), with a consequent plant nutrient enrichment (Guenni et al. 2002; Waraich et al. 2011). This finding might also be the consequence of reduced leaching of soil nutrients with precipitation, resulting in higher soil nutrient availability for plants (Matías et al. 2011; Munjonji et al. 2020). This is quite important in Mediterranean ecosystems, where high decomposition rates can occur in autumn when plants have a low demand for soil nutrients, and so, dissolved nutrients accumulate in the soil, with a high risk of leaching (Llorens et al. 2011).

The combination of both climatic treatments (warming + drought) did not cause significant changes on plant Ca^{2+} (Fig. 2), likely because the

Fig. 4 Effects of management history on plant N (panel **a**), P (panel **b**), Ca^{2+} (panel **c**), Mg^{2+} (panel **d**) and K^+ (panel **e**) (in %). Two sampling years (2017 and 2019) are represented. Different letters denote significant differences between management histories after a Tukey post-hoc test



negative effect of warming on this element was offset by the positive effect of water deficit. Similar results were found by Catunda et al. (2021) in a greenhouse experiment where two temperate pasture species from Australia (*Festuca arundinacea* and *Medicago sativa*) were subjected to warming (+ 4 °C) and drought (40% water holding capacity).

In addition to these direct effects on pasture quality, changes in climate can also indirectly alter plant nutrient concentration through changes in

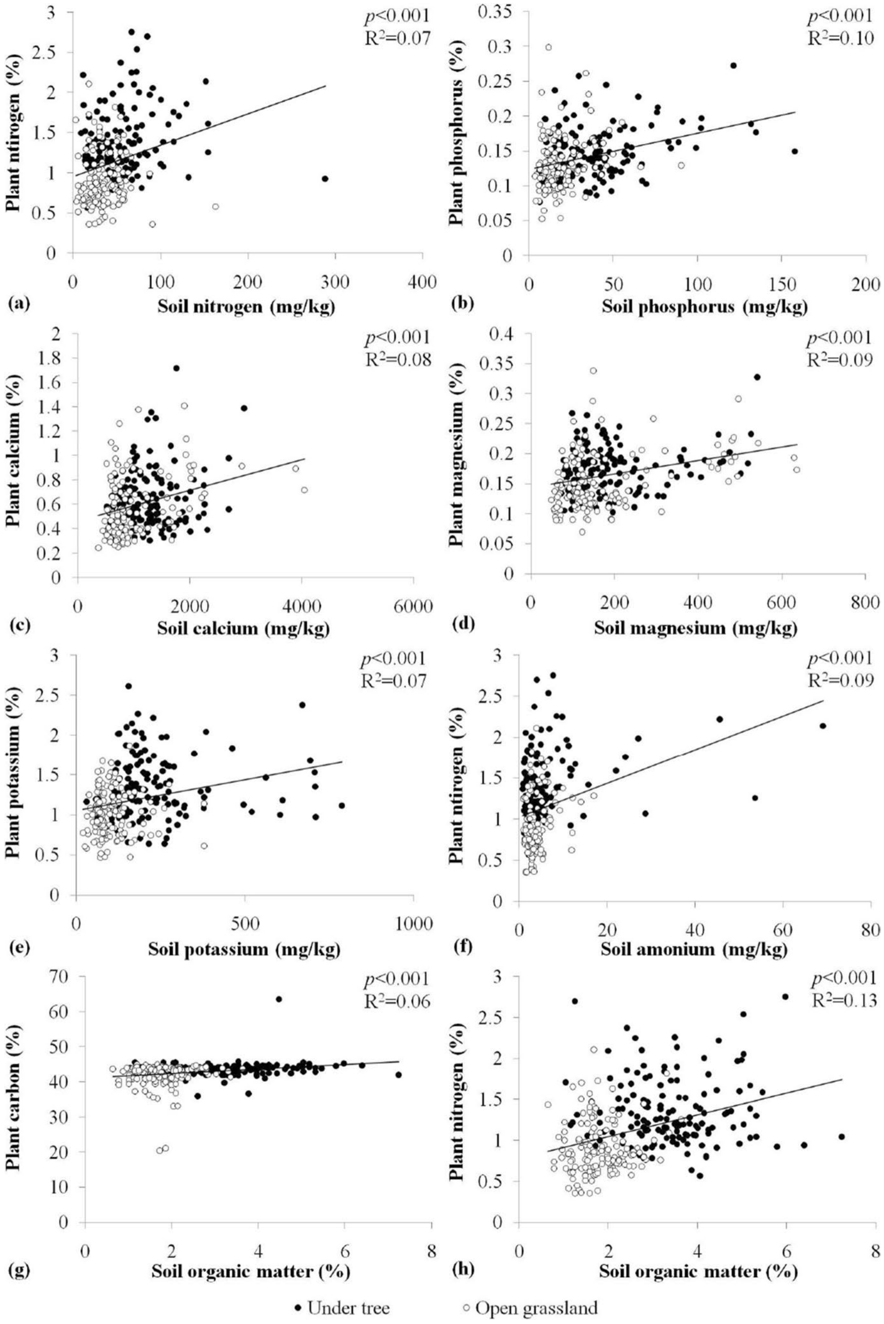


Fig. 5 Relationships among plant nutrient concentration and soil nutrient availability (panels **a**-**f**) or soil OM (panels **g** and **h**). Lines are the results of the linear regressions for the entire data set (including the two sampling years)

the amount of them in the soil. Our results indicated that all soil nutrients except C were positively related to them in plants; i.e., an increase of these elements in the soil generated an increase in the concentration of them in the pasture (Fig. 5). In semiarid ecosystems (as is the case of the study area), temperature and soil water availability are the main factors controlling nutrient uptake (Bassirirad 2000). Thus, a negative effect of climate change on soil nutrients will trigger indirect similar effects on plant nutrient concentration. Similar results were found in an evergreen Mediterranean shrubland (Sardans et al. 2008), where warming and drought altered nutrient concentration in both soil and several dominant plant species.

Can tree canopy alter pasture quality and buffer the impact of climate change on this ecosystem property?

Our results revealed notable differences between habitat types on pasture quality. Thus, pastures growing in open grasslands showed lower values of nutrients compared to those located beneath tree canopies (Table S2). Different reasons might explain these differences, highlighting: 1) the lowest edaphic fertility in open areas, and/or 2) the highest thermal stress detected in this habitat. Our results showed that plant communities located under trees were subjected to lower thermal stress (Fig. 3), probably as a consequence of the microclimate generated by their canopies, which decreases solar radiation (Pezzopane et al. 2010; Siles et al. 2010), air temperature (Rahman et al. 2017; Siles et al. 2010) and evapotranspiration (Lin 2007). These microclimatic conditions usually result in less carbohydrate production and lower growth rates, which delay plant life cycle and give them a better physiological state as well as high metabolic levels for a longer period (Benavides et al. 2009; Hussain et al. 2009). The improvement in pasture quality detected under trees could be conditioned not only by microclimatic conditions, but also by an indirect effect through an increase in soil fertility. Soils under trees are richer in nutrients, since microclimatic conditions attract large herbivores, whose droppings increase soil nutrient content in this habitat type (Abdallah and Chaieb 2012; Tucker et al. 2008). Likewise, higher nutrient content in pasture of this habitat type may be caused by tree litter decomposition (Belsky et al. 1989; Serrano et al. 2018). Finally, through their lateral roots, trees bring on nutrients from distant areas to their canopies (Sileshi 2016; Tiedemann and Klemmedson 1973), increasing soil fertility and consequently that of pasture. This phenomenon is known as ‘fertile island’ effect in arid and semi-arid areas (Bardgett et al. 1998; Belsky 1994; Dijkstra et al. 2006).

The higher soil fertility beneath tree canopies might explain why the above-mentioned negative effect of warming on plant P was only significant under trees but not in open grasslands (despite following the same trend) (Fig. S1). In contrast, other studies carried out in the same field experiment but focused on other ecosystem processes, such as pasture digestibility (Hidalgo-Galvez et al. 2022) or soil respiration (Matías et al. 2021), did find that tree canopy attenuated the impact of climate change on these variables via changes in species composition (grasses dominance) and plant functional structure (favoring species with high competitive abilities for light uptake) and an improvement of microclimatic and edaphic conditions (lower temperature and higher soil fertility, among others). This fact could possibly be a consequence of the greater sensitivity to environmental changes exhibited by these variables, which are highly dependent on the activity of the microbial communities. Thus, trees could play a variable buffering effect on ecosystem functioning of Mediterranean dehesas depending on the sensitivity of the ecosystem properties to environmental changes.

What is the influence of management history on pasture quality?

Our results showed that management history could influence pasture quality, since all nutrients except C modified their concentration depending on historical grazing intensity (Fig. 4). Livestock-excluded site exhibited lower plant N and Ca^{2+} than the other two dehesas, probably due to the lack of animal excreta. It has been widely documented that livestock droppings accelerate litter mineralization rates and provide a source of readily available nutrients for plants and soil microorganisms (López-Társico et al. 2015; Schrama et al. 2013). Similarly, we observed that the site subjected to moderate grazing intensity showed higher plant P and Mg^{2+} when compared to the other two dehesas. These differences could be due to the high browsing rate in the site with high grazing intensity, which reduces plant cover and therefore decreases the biomass return to soil, thus modifying the nutrient cycle (Eldridge et al. 2016, 2017; Pulido et al. 2018) and increasing erosion chances and nutrient losses (Hao and He 2019). In addition, livestock alters soil physical properties through trampling, increasing its apparent density and reducing hydraulic conductivity, which results in a decrease of soluble nutrients (Krümmelbein et al. 2009; Zhao et al. 2007). Conversely, we detected that the site historically subjected to high grazing intensity showed higher plant K^+ when compared to the site with moderate grazing intensity. Feeding a large number of livestock leaves patches of bare soil, which could cause K^+ leached from the plant may to be largely adsorbed to the soil exchange complex (Kölbl et al. 2011; Kooijman and Smit 2001).

Is the impact of climate change more pronounced when plant communities are subjected to higher grazing intensity?

This study analyzed whether the combined effect of increased aridity and overgrazing could exacerbate the negative effects on pasture quality of both global-change drivers when acting individually. Our results suggest that historical grazing pressure conditions pasture responses (in nutritional terms) to climatic changes (Fig. S1). Thus, both drivers of global change interacted additively on the amount of plant P, one of the key elements for plant growth that is generally limiting in Mediterranean forests (Henkin et al. 1998; Sardans et al. 2004, 2005). Specifically, plant P was reduced under the experimental treatments of increased temperature, but only in the site historically subjected to moderate grazing intensity (Fig. S1). This finding could be explained because this site exhibited higher levels of P than the others, where the effect could be masked by the reduced amount of this element. Our results complement previous studies that also found a negative effect when they evaluated the combined effects of climate change and grazing on productivity and ecosystem performance (Belgacem and Louhaichi 2013; Freier et al. 2011).

Although our experimental study offers novel and relevant results about the influence of two main drivers of global change, it would be interesting to have a greater number of replicates in the future of each level of grazing intensity to draw more explicit conclusions on the interactive effects of both drivers on ecosystem functioning. Moreover, additional studies quantifying the impact of herbivores at real time under different climate change scenarios would be useful to better understand the interactive effects of these stress sources threatening the sustainability of dehesa ecosystems.

Conclusions

This study provides original findings on how different abiotic and biotic factors influence pasture quality in Mediterranean dehesa ecosystems. On the one hand, we detected that temperature increase reduced pasture quality, which could have negative repercussions for livestock feeding and, consequently, for the quality of their derived products. Our results could help to understand the reasons for a decrease in the quality of animal products due to the temperature increase forecasted for the Mediterranean area. On the other hand, our findings highlight the relevant role of scattered trees in Mediterranean dehesa ecosystems due to their potential effects to improve soil fertility and pasture quality. Trees amplify heterogeneity (both abiotic and biotic), provide food, shade and shelter for livestock, and add organic matter and nutrients to soil, which confers higher pasture quality for livestock. All these benefits indicate that maintaining an adequate tree density in dehesas is essential to preserve high levels of pasture quality for livestock breeding. However, despite the benefits provided by tree canopy, it did not play a mitigating role of climate change impact on pasture quality. Our results also suggest a strong influence of management history on pasture quality, which was maximized in the site subjected to moderate grazing pressure. Finally, we observed a significant interaction of the two studied drivers of global change on plant P, which suggests that some nutrients are more sensitive to climate change when they are also subjected to grazing. Our findings could be thus applied to develop more efficient management strategies of grazing control in order to reduce its impact not only on pasture quality but also on plant cover and soil characteristics, as well as its ability to interfere in plant community responses to forecasted global warming.

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Declarations

Competing interests 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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