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A B S T R A C T

Grazing is well-known to shape plant populations and plant communities and to affect several compartment characteristics of grazed ecosystems. Semi-natural grassland conservation depends on the maintenance of traditional extensive grazing systems which can exist for centuries, even millennia. However, very few studies have concomitantly investigated the effect of grazing management on plant, forage, litter and soil compartments and the implications of their potential interactions for conservation after recent changes in grazing practices.

This study thus aimed to identify the concomitant effects of sheep grazing on the latter compartments of Mediterranean grasslands. We further investigated the effects of a recent change from millenia-old traditional herding to contemporary fenced free grazing. We also sought to determine how this change may impact the agronomic and ecological value of these grasslands.

Surveys were carried out at 6 different study sites paired by the two different grazing practices in a French Mediterranean sub-steppic vegetation ("Crau" plain in Southeastern France).

Using linear models and distance-based redundancy analysis, effects of grazing intensity, grazing practices and their interactions were tested on plant community, forage, litter and soil physicochemical properties. Our results show that, there was a significant effect of grazing intensity on the four studied compartments, with significantly higher species richness and evenness at moderate grazing intensity. Biomass was also significantly higher at moderate grazing intensity. Digestibility of forage, litter quality and soil fertility decreased significantly under less intensive grazing. Significant differences were also found in the relative size of the areas covered by each plant communities. Recent fenced free grazing led to significantly more intensively grazed zones, with more mesophilous/nitrophilous vegetation. Conversely, in zones traditionally less intensively grazed, the contemporary free grazing led to higher plant species-richness but again with more mesophilous species. Implications for conservation management are that the legacy of millennia-old traditional herding still compensates partly for the effects of changing practice to contemporary fenced free grazing on plant community composition but not on their relative sizes. This indicates an increase in grazing intensity in the remotest zone which could lead to grassland plant community homogenization.

1. Introduction

Grasslands represent 27% of the terrestrial global ecosystems (Henwood, 1998). In the Mediterranean basin, grasslands are chiefly influenced by four environmental factors: climate, edaphic conditions, fire and human management, in particular livestock grazing (Blondel et al., 2010; Buisson et al., 2020; Vidaller et al., 2019). Although their total area has considerably declined in recent decades, Mediterranean grasslands still cover 424,371 km^2 worldwide (Dixon et al., 2014).

Traditional extensive grazing management, defined as using relatively large land areas per animal (Allen et al., 2011), is recognized as crucial for the conservation of semi-natural grassland ecosystems worldwide (Allen et al., 2011; Metera et al., 2010; Poschlod and WallisDeVries, 2002). Grazing creates a common recurrent disturbance in grassland ecosystems, mainly through plant defoliation, plant and soil trampling, urine, faeces and saliva deposits and also zoochory (Matches, 1992). These shape plant populations and communities (Naveh, 1975) and also affect soil parameters (Lin et al., 2010; Smith et al., 2016).

Extensive grazing is known to create spatial heterogeneity, thereby enhancing plant diversity (Adler et al., 2001; Dengler et al., 2014;

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McNaughton, 1984). According to the “intermediate disturbance” hypothesis, local biodiversity peaks at intermediate levels of disturbance (Connell, 1978; Grime, 1973). Absence of grazing or low grazing intensity can lead to a decline in plant species richness through release of competitive exclusion (Connell, 1978; Grime, 1979; Milchunas et al., 1988; Valkó et al., 2018). In contrast, overgrazing can result in irreversible vegetation changes due to the dominance of nitrophilous species highly tolerant to grazing or of unpalatable species (van de Koppel and Rietkerk, 2000).

In addition to its established effects on plant community, grazing can be expected to affect forage and litter quality through changes in species composition and plant abundance (Berauer et al., 2020; Khalsa et al., 2012). For example, it has been demonstrated that biomass production decreases with high grazing pressure, due to both plant consumption and a greater abundance of grazing-tolerant species with traits like short stature and prostrate growth, and thus lower biomass (Rupprecht et al., 2016). Another example is the compensatory growth under moderate grazing that may lead to higher biomass than when grazing intensity is high (Corcket and Moulinier, 2012; McNaughton, 1983, 1984). In general, forage and litter quality improve with high grazing intensity. Protein content and digestibility were found to be significantly higher with intensive grazing (Berauer et al., 2020; Pavlů et al., 2006). Litter quality (i.e., more easily digestible for sheep and degradable for most soil microorganisms) is enhanced by certain species promoted by grazing (Olofsson and Oksanen, 2002; Wang et al., 2018).

Lastly, grazing also affects soil parameters through soil compaction and bare ground exposure due to trampling. It potentially increases rates of soil erosion and soil moisture evaporation, as well as mineralization through deposits of urine and faeces, thus altering nutrient cycling (Hanke et al., 2014; Proulx and Mazumder, 1998) which may subsequently result in an increased productivity and forage quality (Augustine and McNaughton, 2006).

Undoubtedly, these four compartments of the grassland ecosystem interact through plant-soil feedbacks. Plant communities alter soil parameters, which in turn influence plant community composition (Pugnaire et al., 2019). For example, there is a positive relationship between vegetation cover and reduction of soil erosion and run-off (Elwell and Stocking, 1976). In contrast, several studies showed a negative relationship between plant species richness and high forage quality(Mitchley, 2001; White et al., 2004). This suggests that the grazing management strategy needs to be appropriate to the goal: agricultural production or nature conservation (Watkinson and Ormerod, 2001). However, while numerous studies have investigated the effect of grazing on plant communities and its role in conservation (Allen et al., 2011; Metera et al., 2010; Poschlod and WallisDeVries, 2002), few have addressed the concomitant effects of grazing on plants, soil, forage and litter in the same time. Yet understanding long-term patterns of spatial variation in grazing and the factors behind them is crucial in ecology, to enhance our ability to predict the concomitant response of these compartments to both natural and anthropogenic environmental change. Meeting different management objectives and reconciling their varying implications will require an understanding of these compartments’ responses to grazing (Watkinson and Ormerod, 2001).

This study examined the effect of two sheep grazing practices, traditional herding (i.e. sheep herded by a shepherd with herding dogs within open delimited sites) and the more recent fenced free grazing implemented to reduce the cost of employing shepherds (Wolff et al., 2013). Surveys were carried out at 6 different study sites paired by the two different grazing practices. In each site, we assessed grazing impact on vegetation, plant biomass, forage, litter quality, soil granulometry and chemistry in species rich Mediterranean dry grasslands of the “Crau” plain in Southern France, along spatial grazing intensity gradients determined by distance from sheepfolds. These Mediterranean dry grassland communities are still widespread in the Western Mediterranean (Buisson et al., 2020), but under constant decline and threatened by overgrazing, conversion to arable land or, conversely, by land abandonment (San Miguel, 2008). Formed and persisting under the concomitant effects of a Mediterranean climate, a particular soil and thousands of years of traditional grazing (Buisson and Dutoit, 2006), they are also protected by the EU habitat directive (EUNIS habitat E1.311, Natura 2000 habitat type 6220; European Commission, 2007, San Miguel, 2008) which recommends a traditional extensive grazing management for its conservation.

We specifically address the following research questions:

(1) How do changes in grazing intensity and grazing practice (from traditional herding to fenced free grazing) concomitantly affect plant community (composition, species-richness, evenness, dissimilarity), plant biomass, forage and litter quality and soil physicochemical properties of Mediterranean grasslands?
(2) Does the legacy of millennia-old traditional herding continue to impact these compartments several decades (30–10 years) after the grazing practice changes?
(3) What are the implications for agricultural and conservation/restoration management of these changes on species-rich Mediterranean grasslands?

2. Materials and methods

2.1. Study area

The study was conducted in the “Crau” Mediterranean sub-steppic grassland (EUNIS habitat E1.311, Natura 2000 habitat type 6220; European Commission, 2007, San Miguel, 2008) located in Southeastern France (Fig. 1).

The study region is characterized by hot/dry summers and mild/humid winters with an annual precipitation of 517 mm (1980–2010) and a mean temperature of 15.3 °C (Meteo-France, meteorological station of Saint-Martin-de-Crau – Fig. 1). The soils of the study area are Haplic Cambisol with a mean pH of 6.8. The vegetation is shaped by a long history of grazing going back to the Neolithic (Badan et al., 1995; Henry et al., 2010; Saatkamp et al., 2020). The typical grassland is still grazed by itinerant sheep every spring. Traditional grazing involves sheep herded by a shepherd with herding dogs and sometimes protection dogs, within open delimited sites. Within these sites, grazing is centred around a sheepfold, next to a shepherd’s shelter, where sheep are herded at night. Consequently, sheep spend more time near the sheepfold and less time at the edges of the site, creating a spatial grazing pressure gradient according to distance from the sheepfolds (Dureau and Bonnefon, 1998; Molinier and Tallon, 1950; Génin et al., 2021) The

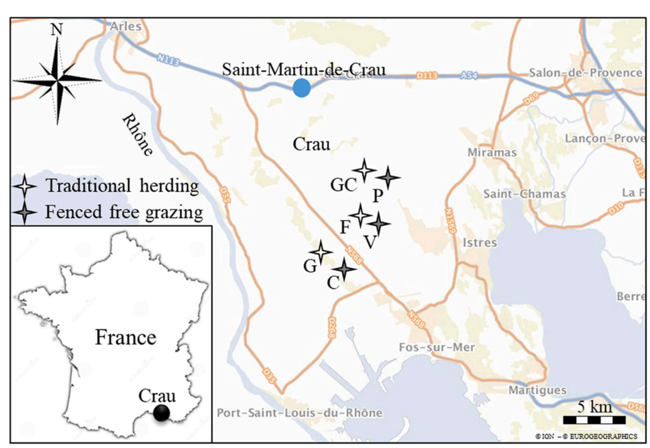

Fig. 1. Locations of the six study sites: Coucou (C), Généraux (G), Valigne (V), Figuières (F), Peyre Esteve (P) and Grand-Carton (GC) in the “Crau” plain in Southeastern France.

more recent fenced free grazing was implemented to reduce the cost of employing shepherds and in analogy to the use, as protection from wolves, of fenced pasture in the Alps mountain (Wolff et al., 2013).

The grassland is species-rich, dominated by annual plants, a perennial grass *Brachypodium retusum* and a small Mediterranean shrub *Thymus vulgaris* (Buisson and Dutoit, 2006). This unique dry grassland vegetation, also locally called "coussoul" (*Asphodelletum ayardii*, Molinier and Tallon, 1950), is threatened by anthropic activities and classified as a Nature Reserve (since 2001) and a Natura 2000 Habitat. 20% of the initial grassland area is still intact, 8600 ha, of which 5811 ha belong to the Nature Reserve (Wolff et al., 2013).

2.2. Site selection and experimental design

Pairs of sites (i.e. sheepfolds and associated rangeland) were chosen from traditional herding areas and from nearby fenced areas with free grazing set up over the past decades (30–10 years). In order to take into account the characteristic climatic and geopedological North-South gradient of the "Crau" plain (Devaux et al., 1983; Loisel et al., 1990), paired sites were selected in the North, Centre and South of the "Crau" plain (Fig. 1), resulting in a total of 6 study sites.

Grazing pressure from thousands of years of traditional herding practice has created five vegetation zones corresponding to different grassland types organized in more or less elliptic belts according to distance from the sheepfold (A, B, C, D and E; Fig. 2) (Devaux et al., 1983; Génin et al., 2021; Loisel et al., 1990; Molinier and Tallon, 1950; Tatin et al., 2013).

A. Around the sheepfold, an overgrazed zone (overtrampled and with substantial deposits of urine and faeces) characterized by hyper-nitrophilous vegetation, mainly dominated by a species of mallow (*Malva sylvestris*, Molinier and Tallon, 1950).
B. Slightly less overgrazed (*Hordeo leporini-Onopordetum illyrici*, Brullo and Marcenò, 1985) dominated by a thistle-like *Asteraceae* (*Onopordum illyricum*), still showing significant disturbance due to frequent passage of sheep but with less nitrogenous deposits (urine, faeces) than zone A because sheep are less stationary.

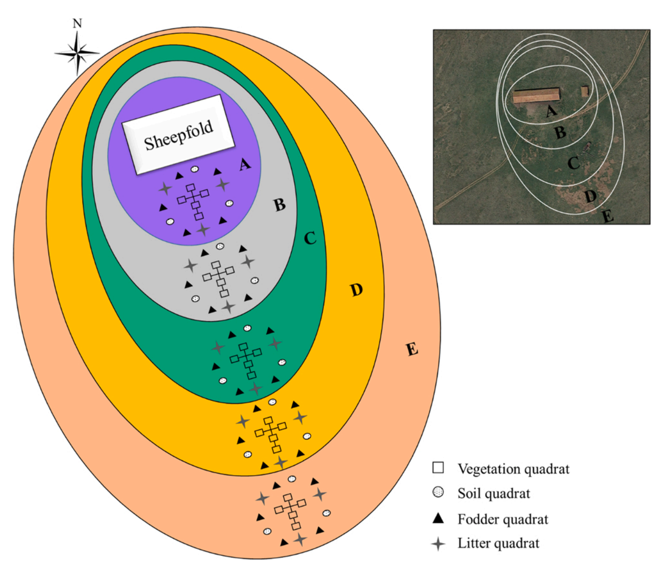

Fig. 2. Schematic drawing of the experimental design which shows the organization of the five vegetation zones (A, B, C, D and E) resulting from grazing pressure gradient according to distance from sheepfold and locations of vegetation, soil, fodder and litter quadrats (from Génin et al., 2021, modified). (Sizes and shapes of vegetation zones organized in schematic elliptic belts around the sheepfold are shown here and do not reflect variations among study sites). Example: "Grosse du Centre" site aerial photograph (
Source: GoogleEarth).

C. *Camphorosmo monspeliacae-Trifolietum subterranei* vegetation (Molinier and Tallon, 1950) dominated by a clover (*Trifolium subterraneum*), still showing nitrogenous deposits but less trampling just revealed by the presence of *Camphorosma monspeliaca.*
D. "Coussoul" sub-steppic Mediterranean grassland vegetation resulting from thousands of years of traditional itinerant sheep grazing (*Asphodelletum ayardii,* Molinier and Tallon, 1950).
E. "Hem" vegetation (Royer and Rameau, 1981) on the grazing site border, mainly dominated by the ramose False-Brome (*B. retusum*) due to low grazing intensity and situated between two different grazing sites belonging to two different farmers.

Surveys were conducted along site transects passing through the five vegetation zones oriented towards the Southeast. This is the major axis of livestock movement, since the sheepfold protects the sheep from the cold northwesterly wind, the "Mistral".

2.3. Vegetation survey

Plant species composition was analysed in April 2020 during the peak of flowering, using the Pavon and Pires (2020) denomination. The percentage cover of all vascular plant species was estimated in 1 m^2 quadrats. For the 6 study sites, 5 quadrats spaced 5 m apart (Buisson et al., 2006) were recorded in each vegetation zone ($n = 150$).

The width of each vegetation zone and the total width of each site transect oriented Northwest-Southeast were measured. The relative proportion of each vegetation zone was then computed on this axis called relative width. Mesological data (i.e. environmental data of the quadrat) including bare ground percentage based on canopy cover, vegetation mean height, vegetation cover, pebble cover percentages were recorded for each quadrat. Vegetation vegetative height was measured at three points for each quadrat at random to estimate the height at which 90% of the quadrat biomass is represented (Dengler et al., 2016).

2.4. Biomass, forage and litter analysis

In February 2020, during the period of peak total biomass, after visual estimation of the proportions of green and dry biomass as a percentage of total plant cover, green biomass was harvested from each quadrat in each of the five zones on the six sites. Vegetation samples were collected 5 cm above soil surface, in 5 quadrats of 20 × 20 cm randomly arranged and separate from the vegetation monitoring and soil sampling quadrats. The 150 samples were then dried at 60 °C to constant weight and individually weighed to obtain plant dry matter content (DM). The five samples from each quadrat were then pooled for forage analysis which provides a measure of potential of the forage to supply nutrients to animals. Samples were ground to 1 mm (standards: INRA/GERM/BIPEA EC77-M-8506) and 20 fodder parameters were measured: cellulose content, nitrogen compounds content (NC, $g.kg^{-1}$), pepsin cellulase digestibility (PCD, %), phosphorus content (% P), calcium (% Ca), magnesium (% Mg), potassium (% K), sodium (% Na), copper (% Cu), zinc (% Zn), manganese (% Mn), iron (% Fe), available calcium for animals (Abs Ca, $g.kg^{-1}$), available phosphorus for animals (Abs P, $g.kg^{-1}$), meat forage unit (MFU) representing the amount of net energy absorbable during the fattening of a ruminant. The protein quality of fodder was then estimated by three intestinal digestible protein content measurements: intestinal digestible protein allowed by nitrogen (IDPN, $g.kg^{-1}$) needed by ruminal microorganisms; intestinal digestible protein allowed by energy (IDPE, $g.kg^{-1}$) and intestinal digestible protein of dietary origin (IDPD, $g.kg^{-1}$). The measurement methods are described in Supplementary materials (Supplementary material 1a).

In September 2020, litter was harvested from three 30 × 30 cm quadrats per vegetation zone and sent for analysis of lignin and nitrogen content (Supplementary material 1b).

2.5. Soil parameters

For each vegetation zone and close to each vegetation quadrat, three 100 g soil samples were collected from the top layer of soil (1–10 cm depth) in February 2020. The samples were then dried at 40 °C to constant weight and further sieved with a 2 mm mesh size to remove larger roots and coarse elements. The three samples from each quadrat were then pooled for soil analysis. Five parameters related to soil granulometry were measured: % clay, fine silt, coarse silt, fine sand, coarse sand, and 12 parameters related to soil chemistry: calcium oxide (CaO, $g.kg^{-1}$), potassium oxide (K_2O, $g.kg^{-1}$), magnesium oxide (MgO, $g.kg^{-1}$), sodium oxide (Na_2O, $g.kg^{-1}$), cation exchange capacity (CEC, mEq 0.100 g^{-1}), available phosphorus (P_2O_5, $g.kg^{-1}$ for a dry soil at 105 °C), total nitrogen (N, $g.kg^{-1}$), carbon to nitrogen ratio (C:N, $g.kg^{-1}$), organic carbon (organic C, $g.kg^{-1}$) and pH. Measurement methods are described in Supplementary materials (Supplementary material 1c).

2.6. Farmer interviews

Study sites and associated grazing practices were characterised through interviews conducted with the 6 farmers in April 2020. The interview included questions on type of farm, size of sites grazed, mean number of animals, dates of beginning and end of grazing, and date when grazing practice changed from traditional herding to fenced free grazing. These data enabled us to calculate the mean stocking rate for each grazing site (Supplementary Table 1).

2.7. Data analysis

Plant community data were analysed by calculating species richness (*S*), evenness (*J*′) and Bray–Curtis index (BC) using the R package Vegan. *J*′ evenness was calculated as $H'/\ln(S)$, H' being the Shannon diversity index (Pielou, 1969).

A split-plot ANOVA was performed to analyse effects of grazing practices and vegetation zones on individual response variables from the vegetation, forage, litter and soil compartments. Grazing practice (whole-plot factor) was tested against the geopedological gradient × grazing practice interaction. Vegetation zone (split-plot factor), vegetation zone × grazing practice interaction and geopedological gradient were tested against the model residuals.

All models complied with assumptions of linear models (normality and homoscedasticity). A Tukey HSD post-hoc test was calculated to analyse differences between factor levels if factor main effects or interactions were significant.

Additionally, partial distance-based redundancy analyses (dbRDA), a reliable method for analyzing species-environment relations (Jupke and Schäfer, 2020), were applied to evaluate the relationship between divergence in plant community and the environmental variables cited above (R package Vegan).

To avoid multicolinearity in environmental data, PCA and Pearson correlation tests between factors were performed on each compartment analysed (Supplementary Figure 1). Any factor with a correlation higher than 0.90 was removed from the analysis. Moreover, to avoid overfitting, we checked that selected variables did not explain more than the global model.

Partial dbRDAs were fitted separately for Bray Curtis distance between vegetation relevés using permutation testing (Legendre and Anderson, 1999). First, a marginal test was performed using only environmental variables as predictors. Second, a conditional test was run using geographical coordinates as covariate to take into account potential confounding effects of geographic distance between sites. The significance of environmental factors was evaluated using a dbRDA permutation test (9999 permutations).

All statistical analyses were run in R (R, v.4.0.2, R Development Core Team (2020)).

3. Results

3.1. Effect of grazing intensity and practice on plant communities and mesological data

A significant variation in plant species richness was found between vegetation zones, ranging from 12 to 39 species for 1 m^{-2} (Fig. 3a). Grazing practice (marginally), vegetation zone, geopedological gradient and their interactions (except grazing practice × geopedological gradient interaction) had a significant influence on plant species richness (Table 1a). Plant species richness was marginally higher with fenced free grazing than with traditional herding practices. Species richness significantly increased with distance from sheepfold and also increased from North to South along the gradient. Evenness was significantly influenced by vegetation zones, with lower evenness for zone A (closest to the sheepfold) than zones C, D and E. The significant effect of grazing practice × vegetation zone interaction was driven by significantly higher evenness for fenced free grazing in zone D.

Vegetation zones' relative widths differed, with a significantly higher relative width for zone E than for the others (Table 1b, Fig. 3b). Grazing practice interacted significantly with vegetation zone size. Fenced free grazing reduced the relative width of zone E, while it increased the relative width of zones B and D, explaining the significant effect of grazing practice × vegetation zone interaction (Table 1b, Fig. 3b).

Grazing practices did not significantly influence mesological data, except for mean height, which was greater in traditional herding sites than in fenced free grazing sites (Table 1b, Fig. 1c). Geopedological gradient was only a significant influence for pebble cover, which was greater in Northern sites. Vegetation zone was significant for all mesological data. There was significantly more bare ground in zone A, close to the sheepfold, than in the other zones. Vegetation cover was higher in zone E than in zones A and B. Pebble cover was significantly lower in zone A and significantly higher in zone D. Mean height was lowest in zone C and highest in zone E.

3.2. Effect of grazing on plant biomass, forage and litter

Above-ground green biomass was influenced significantly by vegetation zone, with lower biomass measured for D and E zones. A marginal effect of pedogeological gradient was found, with higher green biomass in the Northern part of the gradient than in the Centre. Finally, the grazing practice × vegetation zone interaction influenced green biomass: a lower percentage was measured in fenced free grazing sites of the E vegetation zones (Table 2a, Fig. 4a).

We found reverse effects on dry biomass, which was significantly higher in the North than in the Centre and South of the gradient. It was also significantly higher in the E zones than in the others. Dry biomass was also higher in zones D and B than C.

Forage quality (Table 3b,c) was not significantly influenced by grazing practice, except for Manganese (Fig. 4c) and Iron (marginally), which were higher in fenced free grazing sites. Geopedological gradient had no effect on any parameters of forage quality, while the effect of vegetation zone was significant for all parameters of forage quality. Cellulose (Fig. 4b) content increased with distance from the sheepfold, while nitrogen compounds, forage quality, digestibility and mineral content decreased (Fig. 4b,d). The grazing practice × geopedological gradient, grazing practice × vegetation zone, geopedological gradient × vegetation zone interactions had no significant effects on forage quality.

Litter analysis (Table 3d) also revealed a significant effect of vegetation zone on all measured parameters and a significant geopedological gradient effect on lignin and total Kjeldahl Nitrogen. Litter dry weight was significantly higher for zone E. Lignin was higher in zone B than A and higher in the Southern sites. Total Kjeldahl Nitrogen decreased with distance from the sheepfold and was lower in the Northern sites.

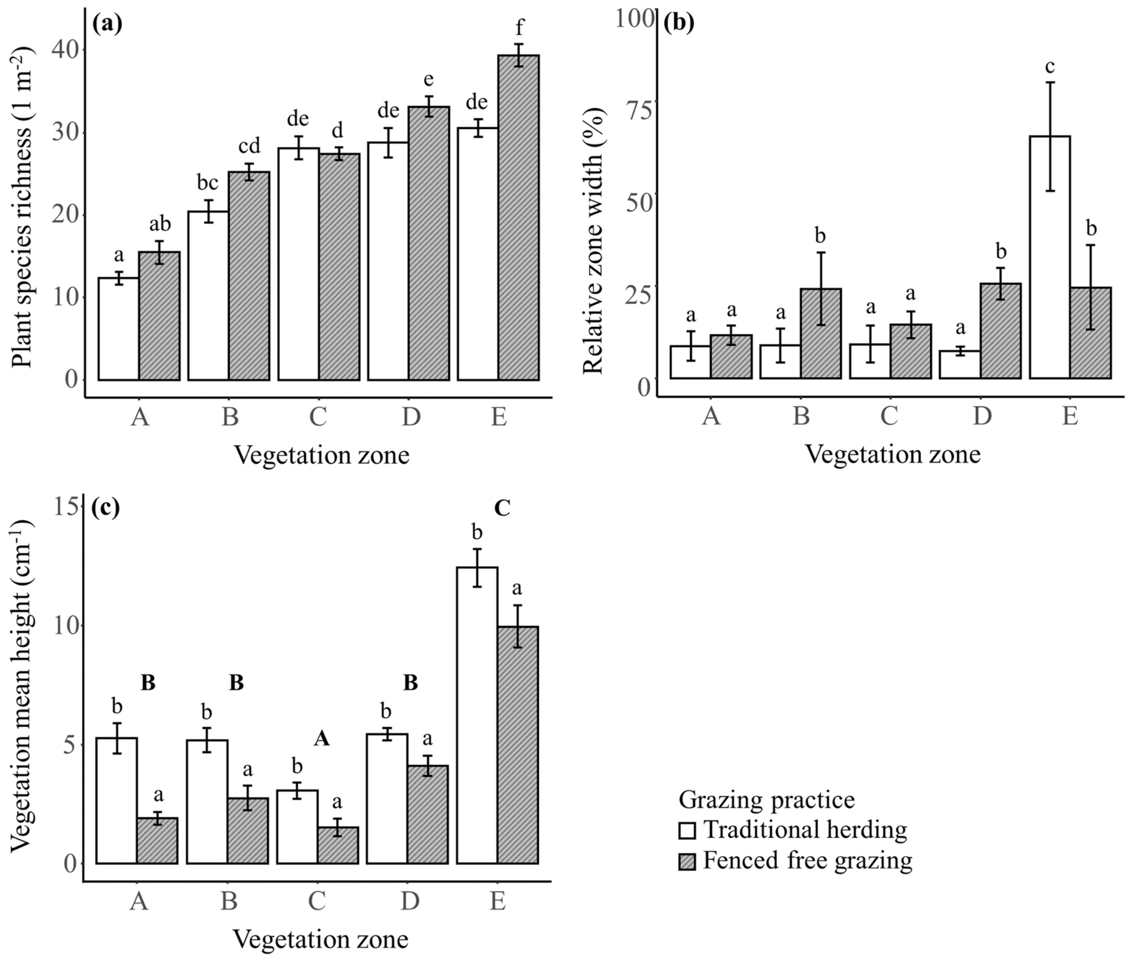

Fig. 3. Effect of grazing practice and vegetation zones on plant community and mesological data (mean ± SE). **(a)** Species richness (1 m^2), **(b)** Vegetation zone relative width, **(c)** Mean height. In **(a)** and **(b),** different lower case letters indicate significant differences in effect of grazing practice × vegetation zone interaction ($P < 0.05$). In **(c),** different lower case and upper case letters respectively indicate significant differences in grazing practice effect and in vegetation zone effect ($P < 0.05$). See Fig. 2 for vegetation zone code.

Table 1
ANOVA F-values, significance levels for effects of grazing practice, geopedological gradient, vegetation zone and their interactions on plant community and mesological data. . $p < 0.1$; * $p < 0.05$; * * $p < 0.01$; * ** $p < 0.001$, NS not significant.

(a) Plant community

	df	Species richness	Evenness
Grazing practice (GP)	1	18.41.	0.11 NS
Geopedological gradient (GG)	2	36.24 ***	0.60 NS
Vegetation zone (VZ)	4	133.41 ***	5.80 ***
GP × GG	2	2.27 NS	11.11 ***
GP × VZ	4	5.92 ***	4.82 **
GG × VZ	8	2.10 *	3.20 **

(b) Mesological data

	df	Relative zone width	Bare ground cover	Vegetation cover	Pebble cover	Vegetation mean height
Grazing practice (GP)	1	0.26 NS	0.05 NS	0.01 NS	3.06 NS	96.92 *
Geopedological gradient (GG)	2	0.04 NS	1.94 NS	4.02.	14.38 **	0.76 NS
Vegetation zone (VZ)	4	17.54 ***	4.74 *	4.72 *	21.11 ***	115.67 ***
GP × GG	2	0.04 NS	10.28 **	11.91 **	2.35 NS	0.61 NS
GP × VZ	4	12.29 **	1.43 NS	0.51 NS	2.23 NS	1.56 NS
GG × VZ	8	4.87 *	1.95 NS	1.62 NS	2.06 NS	7.66 ***

3.3. *Effect of grazing on soil parameters*

Grazing practice (Table 3a,b) had a significant effect on coarse silt and K_2O content, with higher coarse silt content and lower K_2O content (Fig. 5b) in fenced free grazing sites. The significance of geopedological gradient is explained by greater quantities of fine and coarse sands in Northern than in Southern sites. Vegetation zone was significant for several granulometry parameters (Table 3a) and almost all chemistry (Table 3b) parameters. Clay content (Fig. 5a) decreased with distance from the sheepfold, while coarse silt content increased. CaO, K_2O (Fig. 5b), MgO, CEC, Total N (marginally) and Organic Carbon (Fig. 5c) (D zone only) decreased with distance from the sheepfold, while the C:N

Table 2
ANOVA F-values, significance levels for effects of grazing practice, geopedological gradient, vegetation zone and their interactions on biomass and forage quality. . $p < 0.1$; * $p < 0.05$; * * $p < 0.01$; * ** $p < 0.001$, NS not significant.

(a) Biomass

	df	Green biomass cover	Dry biomass cover	Dry mass weight
Grazing practice (GP)	1	2.18 NS	2.18 NS	5.43 NS
Geopedological gradient (GG)	2	2.46.	2.46.	6.97 **
Vegetation zone (VZ)	4	117.88 * **	117.88 ***	131.51 ***
GP × GG	2	3.93 *	3.93 *	7.60 ***
GP × VZ	4	13.38 * **	13.38 ***	0.67 NS
GG × VZ	8	0.81 NS	0.81 NS	6.94 ***

(b) Forage quality

	df	Cellulose	NC	PCD	P	Ca	Mg	K	Na	Cu
Grazing practice (GP)	1	0.20 NS	1.97 NS	12.55 NS	9.20 NS	1.30 NS	16.40 NS	0.13 NS	0.09 NS	6.19 NS
Geopedological gradient (GG)	2	0.60 NS	1.85 NS	2.57 NS	0.26 NS	0.24 NS	2.23 NS	0.45 NS	1.67 NS	1.21 NS
Vegetation zone (VZ)	4	12.84 **	18.98 ***	86.29 ***	58.29 ***	22.73 ***	142.03 * **	54.01 ***	13.36 **	42.28 ***
GP × GG	2	0.19 NS	0.82 NS	1.18 NS	0.46 NS	0.50 NS	0.37 NS	4.56.	0.93 NS	1.44 NS
GP × VZ	4	0.79 NS	1.90 NS	1.37 NS	2.44 NS	0.28 NS	3.40.	0.57 NS	1.12 NS	1.20 NS
GG × VZ	8	0.35 NS	0.85 NS	1.39 NS	1.43 NS	0.25 NS	1.58 NS	1.72 NS	1.34 NS	0.54 NS

(c) Forage quality

	df	Zn	Mn	Fe	Abs Ca	Abs P	MFU	IDPN	PDIA	IDPD
Grazing practice (GP)	1	2.93 NS	35.33 **	87.15.	1.30 NS	9.20 NS	26.57 NS	1.98 NS	2.22 NS	0.07 NS
Geopedological gradient (GG)	2	0.17 NS	0.40 NS	1.78 NS	0.24 NS	0.26 NS	3.91.	1.83 NS	1.66 NS	3.27 NS
Vegetation zone (VZ)	4	8.28 * *	9.03 **	5.29 *	22.73 ***	58.29 ***	55.88 ***	18.51 ***	21.58 ***	36.34 ***
GP × GG	2	4.53.	1.31 NS	2.19 NS	0.50 NS	0.46 NS	1.85 NS	0.82 NS	0.57 NS	1.19 NS
GP × VZ	4	1.03 NS	1.64 NS	2.11 NS	0.28 NS	2.44 NS	2.30 NS	1.93 NS	1.69 NS	2.13 NS
GG × VZ	8	1.65 NS	0.69 NS	1.09 NS	0.25 NS	1.43 NS	1.62 NS	0.85 NS	0.79 NS	1.16 NS

(d) Litter

	df	Dry weight	Direct lignin	Total Kjeldahl N
Grazing practice (GP)	1	2.82 NS	4.95 NS	2.55 NS
Geopedological gradient (GG)	2	1.68 NS	11.36 **	5.35 *
Vegetation zone (VZ)	4	34.09 ***	4.82 *	6.76 *
P × GG	2	1.97 NS	0.25 NS	2.37 NS
P × VZ	4	2.29 NS	0.36 NS	0.74 NS
GG × VZ	8	1.09 NS	1.53 NS	0.67 NS

ratio increased.

The dbRDA results showed that floristic composition differed between vegetation zones (Fig. 6), and that there was a significant correlation between floristic composition and the environmental factors measured. Even when geographic distance was taken into account, these correlations remained significant, with only a moderate change in percentage of explained variation (Fig. 6, Supplementary Table 2).

4. Discussion

The spatial patterns of succession of these different vegetation zones according to distance from the sheepfold reflect a significant effect of grazing intensity, under both grazing practices. However, the four compartments studied, vegetation, fodder, litter and soil values, were impacted differently. This has implications for management policies with conservation vs agricultural objectives, whose practices will need to be reconciled. While there was little distinction between the effects of the two current grazing practices (traditional herding or fenced free grazing), likely due to the change being contemporary (10–30 years) and to the persisting legacy from thousands of years of traditional herding, a significant effect of grazing practice × vegetation zone interaction was measured on vegetation zone size and on several parameters. This points to an increase in grazing intensity in the remotest zone under fenced free grazing, which could lead to plant community homogenization and trivialization (e.g. extension of common ruderal and mesophilous species associated to a higher grazing intensity close to the sheepfold) in the long term.

4.1. *Effects of grazing intensity*

Overall, grazing intensity had a significant effect on all the compartments studied. Moderate grazing levels had a positive effect on plant richness and evenness, as already shown by numerous studies demonstrating a more positive effect of moderate grazing intensity than of higher grazing intensity (Alados et al., 2004; Connell, 1978; Grime, 1979; Milchunas et al., 1988). Our results also confirm again the presence of five vegetation zones organized in concentric belts according to distance from the sheepfold and explained by the natural gradient of grazing pressure from traditional herding (Devaux et al., 1983; Génin et al., 2021; Loisel et al., 1990; Molinier and Tallon, 1950; Tatin et al., 2013). In the zones nearest the sheepfold, where grazing is more intense, only a few species are able to persist (ruderal nitrophilous or unpalatable species), resulting in lower species richness and greater abundance of species whose traits promote avoidance or tolerance of herbivory (Carmona et al., 2012; De Bello et al., 2006; Souther et al., 2019). Thus, zone A is generally dominated by ruderal species such as the hemicryptophyte *Malva sylvestris* and the therophyte *Erodium cicutarium*. Sheep are selective (Dumont et al., 2012; Ren et al., 2015), as shown here by the dominance of *Onopordum illyricum* in zone B due to its unpalatability. Where grazing pressure is lower, in zones C, D and E, species richness is higher, species are more equally represented and typical perennial species from the sub-steppic grassland (e.g *Brachypodium retusum, Thymus vulgaris*) are present. In addition to selection by defoliation tolerance or avoidance traits, the changes in plant community composition and abundance may also reflect soil changes through increased nutrient supply in the more intensively grazed zones, due to the huge amount of urine and faeces deposits and soil trampling (Souther et al., 2019).

Mesological data also showed a significant impact of grazing intensity. We found increased bare ground and decreased pebble cover (due to manure accumulation), vegetation height and biomass under high grazing intensity relative to moderate grazing, consistent with

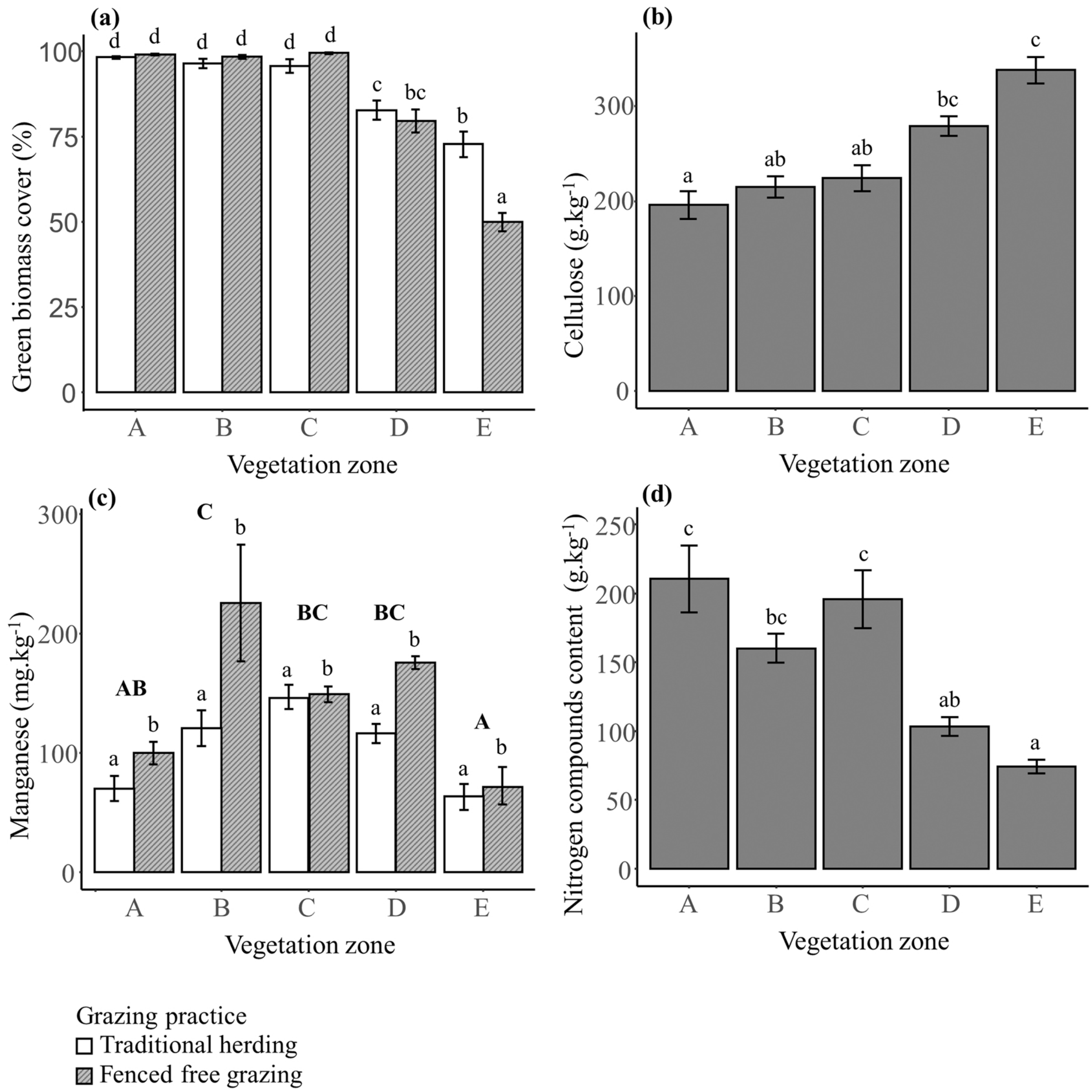

Fig. 4. Effect of grazing practice and vegetation zones on biomass and forage quality (mean ± SE). **(a)** Green biomass. Different lower case letters indicate significant differences in effect of grazing practice × vegetation zone interaction ($P < 0.05$). **(b)** Cellulose. Different lower case and upper case letters respectively indicate significant differences in the grazing practice effect and in the vegetation zone effect ($P < 0.05$). Effect of vegetation zones on biomass and forage quality (mean ± SE). **(c)** Manganese, (d) Nitrogen compounds content. Different lower case and upper case letters respectively indicate significant differences ($P < 0.05$). See Fig. 2 for vegetation zone code.

previous findings (Hanke et al., 2014; Jones, 2000; Proulx and Mazumder, 1998).

Higher forage and litter quality were measured under high grazing intensity. When grazing is intensive, forage is consumed less mature, leading to continuous regrowth during the growing season (Nelson, 2012; Waramit et al., 2011). For example, it was demonstrated that high cutting intensity increases nitrogen and protein content in forage (Pavlů et al., 2011; Walter et al., 2012), while fiber content decreases (Deak et al., 2007; Xu et al., 2018). In contrast, Lavorel et al. (2011) showed that low cutting intensity or no cutting increase leaf dry matter content and reduce forage quality. Moreover, several studies have demonstrated that the forage quality of species-rich communities is also strongly dependent on other compartments, such as plant species composition, abundance (Khalsa et al., 2012) and soil resource availability (Niu et al., 2016; White et al., 2004). These compartments are in turn affected by grazing intensity (Gilhaus and Hölzel, 2016; Rupprecht et al., 2016).

Soil granulometry changed with grazing intensity, showing a higher proportion of fine elements when grazing was intensive (due to manure accumulation). Soil fertility increased with grazing intensity, as noted in the review by Smith et al. (2016) for ecosystems with appropriate grazing management. Nevertheless, grazing intensity had no impact on several parameters of soil granulometry, likely because these variables do not respond to grazing intensities at a coarse scale (above 1 m) (Génin et al., 2021; Lin et al., 2010).

The discrepancy observed between soil functional parameters (i.e. mineral contents) and green biomass cover, that vary following a threshold between the first vegetation belt close to the sheepfold and the others, and on the other hand, the biodiversity parameters (i.e. plant species richness) that vary more gradually can be explain by nutrient transfers. Indeed, in extensive itinerant grazing systems, nutrients are transferred from the less fertile areas far to the sheepfold to the areas closed to the sheepfold because of higher artificial and longer concentration of sheep near the sheepfold due to flock management by the shepherds. Then, sheep disturbances (defoliation, trampling), feces and urine deposit are concentrated around the sheepfold that created positive feed-back processes in this area (i.e. herbivores increase soil fertility, plant productivity and palatability that in turn increase herbivory but decrease species-richness) (Augustine et al., 2003). The use of

Table 3
ANOVA F-values, significance levels for effects of grazing practice, geopedological gradient, vegetation zone and their interactions on soil granulometry (a) and chemistry (b).

(a) Soil granulometry

	df	Clay	Fine silt	Coarse silt	Fine sand	Coarse sand
Grazing practice (GP)	1	0.13 NS	0.02 NS	16.10 *	3.42 NS	0.74 NS
Geopedological gradient (GG)	2	1.88 NS	0.15 NS	1.20 NS	4.22.	3.74.
Vegetation zone (VZ)	4	6.52 *	1.27 NS	4.71 *	1.64 NS	1.33 NS
GP × GG	2	8.62 *	0.10 NS	0.12 NS	0.42 NS	2.23 NS
GP × VZ	4	0.82 NS	0.12 NS	1.41 NS	0.92 NS	0.07 NS
GG × VZ	8	0.77 NS	0.42 NS	2.28 NS	1.17 NS	0.48 NS

(b) Soil chemistry

	df	CaO	K_2O	MgO	Na_2O	CEC	P_2O_5	Total N	Organic C	C:N	pH
Grazing practice (GP)	1	0.12 NS	14.29 *	2.56 NS	1.91 NS	0.23 NS	1.77 NS	0.01 NS	0.01 NS	0.11 NS	0.05 NS
Geopedological gradient (GG)	2	0.01 NS	2.78 NS	0.52 NS	0.18 NS	0.85 NS	0.26 NS	1.19 NS	2.25 NS	1.47 NS	0.40 NS
Vegetation zone (VZ)	4	2.85.	60.12 ***	4.18 *	2.04 NS	13.81 **	1.98 NS	2.88.	3.69 *	3.23.	1.37 NS
GP × GG	2	0.06 NS	0.19 NS	0.42 NS	2.69 NS	5.01 *	0.16 NS	0.28 NS	0.54 NS	0.40 NS	1.30 NS
GP × VZ	4	0.32 NS	3.07.	1.03 NS	3.56 *	3.65 *	0.33 NS	0.83 NS	0.73 NS	0.90 NS	1.52 NS
GG × VZ	8	0.15 NS	0.44 NS	1.22 NS	2.69 NS	0.64 NS	0.48 NS	0.57 NS	0.88 NS	0.72 NS	0.75 NS

GP × GG = grazing practice × geopedological gradient interaction; GP × VZ = grazing practice × vegetation zone, GG × VZ = geopedological gradient × vegetation zone interaction. . $p < 0.1$; * $p < 0.05$; * * $p < 0.01$; * ** $p < 0.001$, NS not significant.

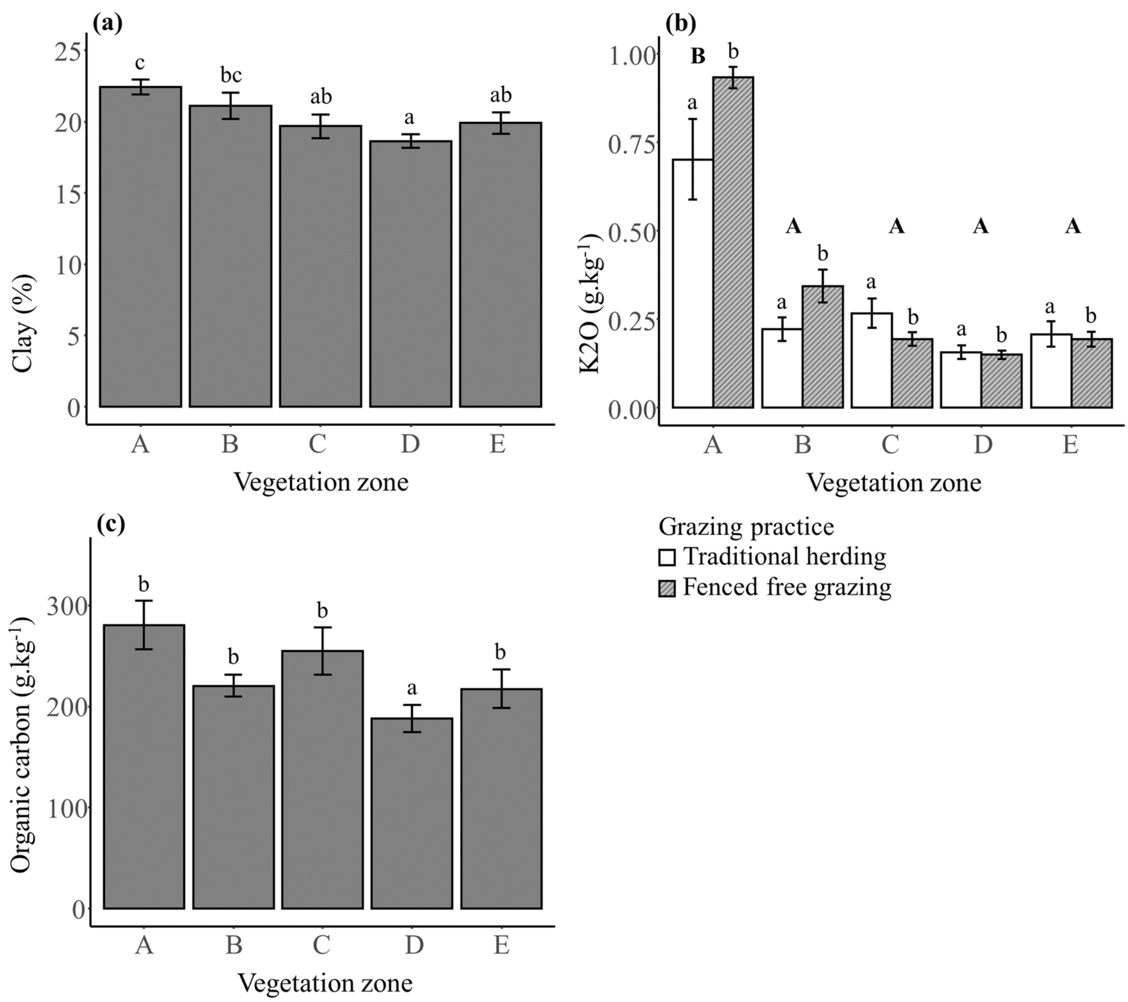

Fig. 5. Effect of grazing practice and vegetation zones on soil parameters (mean ± SE). **(a)** Clay content and **(c)** Organic Carbon content. Different lower case letters indicate significant differences in vegetation zone effect (P < 0.05). **(b)** K_2O content. Different lower case and upper case letters respectively indicate significant differences in grazing practice effect and in vegetation zone effect (P < 0.05). See Fig. 2 for vegetation zone code.

fenced free grazing for several decades tend to homogenize this gradient with the reduction of the relative width of the farthest undergrazed zone from the sheepfold (zone E), while it increased the relative width of intermediate mesophilous areas (zones B and D).

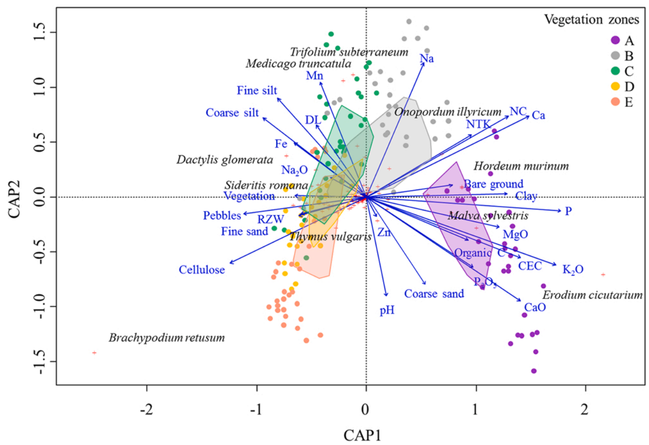

Fig. 6. Distance-based redundancy analysis (dbRDA) showing the influence of environmental variables on Bray Curtis distance among vegetation relevés. The polygons illustrate the projection of vegetation zones on the dbRDA. The vectors illustrate correlations between the original environmental variables and the dbRDA-axes. For environmental variable codes, see Tables 1, 2 and 3 and for vegetation zone code, see Fig. 2.

4.2. *Effects of the change in grazing practice*

Compared to the effect of distance from the sheepfold, type of grazing practice appeared to have only a limited effect on a few parameters. This could be because the change to fenced free grazing is recent (30–10 years) compared to millennia-old traditional herding (Molinier and Tallon, 1950; Tatin et al., 2013). It is well established that current ecological factors alone cannot explain current vegetation community composition and structure, and land-use legacies have already been found in several ecosystems (Cuddington, 2011; Karlík and Poschlod, 2014; Maezumi et al., 2018). Moreover, historical dynamics are also known to affect soil properties (Dambrine et al., 2007; Elgersma et al., 2011). Legacy effects can even outweigh a shift in ecosystem structure and functioning in the short term, such as plant invasion (Elgersma et al., 2011). For example, in our Mediterranean dry grassland sites, the effect of Roman grazing practices is still detectable (Saatkamp et al., 2020) even 1500 years after the abandonment of Roman sheepfolds. This suggests that a longer time would need to elapse before the effect of grazing practice change could reliably be measured.

However, we did find one significant effect on vegetation zone size, via a significant grazing practice × vegetation zone interaction. This is reflected in increased relative width for the zones at intermediate distance from the sheepfold (B and D) and decreased relative width for the zone farthest away (E). This change in vegetation zone relative width, together with the decrease in vegetation height and pebble cover, suggest a beginning of homogenization of the stocking rate (i.e. number of animals on a given amount of land over a certain period of time) along the grazing gradient in fenced free grazing sites. In traditional herding, shepherds said that they herd the sheep "*very tightly*" that is to say very constrained "*with the help of dogs and voice guidance*" to avoid "*tensions*" due to incursions into neighbouring grazing sites, creating a characteristic "Crau" plain "grazing bias" on the border zones between two grazing sites (Dureau and Bonnefon, 1998). The farmer in Figuières even told us that *"if the shepherds are beginners who have just come out of the Merle Noir School (the shepherd school of the region), they are stressed like anything, they don't know how to do it, so they prefer not to go near the neighbours!*". This "grazing bias" disappears under free grazing, with sheep guided only by their selectiveness (Dumont et al., 2012; Ren et al., 2015). Indeed, the farmer of Grand Carton (who is also shepherd) indicated that "*sheep like to go where there know that there is grass*".

Moreover, the grazing practice × vegetation zone interaction had a significant effect on several other parameters, mainly in the zones nearest and farthest from the sheepfold, suggesting that any practice change effect currently depends on grazing intensity. For example, fenced free grazing decreased green biomass and increased minerals near the sheepfold, as compared to traditional grazing. It also led to increased species richness in the remotest zone, mainly by promoting species typical of intensively grazed zones, but not the rare plants of the protected grassland vegetation, nor those of patrimonial value (e.g. Török et al., 2016).

In addition to the impact of sheep's behavioural change (i.e. from being herded by a shepherd to being free to graze at will), this is likely explained by another factor related to fenced free grazing. Sheep tend to graze earlier (in autumn) in fenced sites (Supplementary Table 1), whereas traditional herding only begins at the end of winter/beginning of spring. Along with grazing intensity, grazing season is also recognized to be of great importance, with effects differing by season (Zhai et al., 2018). Moreover, sheep also tend to graze longer in fenced sites, as the farmers indicated during our interviews.

4.3. *Effects of geopedological gradient*

The effects of the Northwest-Southeast geopedological gradient already identified in the "Crau" plain (Devaux et al., 1983; Loisel et al., 1990) are confirmed by our results. We found higher pebble cover in the North due to a previously stronger flow of the Durance River (Molliex et al., 2013), leading to lower plant species richness through lack of bare ground availability (Devaux et al., 1983). Thus, the effect of grazing practice and vegetation zone could be different depending of physical characteristics of the site and mainly of access to forage link with pebbles cover on the soil surface (e.g. Török et al., 2016).

4.4. *Implications for agricultural and conservation/restoration management*

Our findings confirm that extensive grazing is a crucial tool for dry grassland ecosystem conservation (Allen et al., 2011; Metera et al., 2010; Poschlod and WallisDeVries, 2002). However, the grazing regime needs to be appropriate to the target ecosystem. Overgrazing can lower productivity, lead to a critical loss of soil fertility and damage ecosystems, resulting for example in desertification in arid or semi-arid areas (Han et al., 2008; Rietkerk and van de Koppel, 1997). The effects of undergrazing can also lead to grassland ecosystem disruption. In long-term (since 2001) grazing exclosures, 40% of initially occurring grassland species were found to have disappeared, being replaced by high-growing herbaceous ruderal species (Saatkamp et al., 2018; Vidaller et al., 2019). Thus, an inappropriate land-use regime (e.g. intensive grazing) can threaten ecosystem stability (Blüthgen et al., 2016) through communities' homogenization (Gossner et al., 2016) and biodiversity loss (Allan et al., 2015; Newbold et al., 2015; San Miguel, 2008).

In our study, differences in grazing intensity with distance from the sheepfold had varying effects on vegetation, fodder, litter and soil. High grazing intensity near the sheepfold increased forage quality and soil fertility, while moderate grazing intensity maximised plant species richness and composition, as well as biomass. This raises a potential issue of conflicting conservation and agricultural objectives, which will need to be reconciled in conservation management planning (Watkinson and Ormerod, 2001).

Differences between traditional herding and fenced free grazing had so far limited effects, likely due to the change in grazing practice being relatively recent (30–10 years) and to a strong land-use legacy effect (several millennia) (Elgersma et al., 2011; Saatkamp et al., 2020). However, although a longer time span is needed to properly evaluate the effect of grazing practice change, the results even after one to three decades of fencing suggest a beginning of plant community homogenization. This can be attributed to disruption of the natural grazing gradient, due to sheep grazing longer in zones farther from the sheepfold. An interesting objective for future research would therefore be to assess the grazing pressure exerted on the different vegetation zones, using radio-tracking to monitor sheep movement and to characterize grazing gradient disruption (Turner et al., 2000; Schieltz et al., 2017).

Maintaining the millenia-old traditional herding system seems to be the best management strategy. Indeed, it supports plant species richness by providing niches for species with different requirements at a single site in different areas depending on the distance to the sheepfolds, both species more tolerant to high grazing intensity and those, typical of the grassland, which require moderate grazing intensity. These benefits have been demonstrated in other grassland ecosystems (Bonari et al., 2017; Török et al., 2016). Moreover, although forage quality here was improved by high grazing intensity, extensive grazing management generally provides sufficient forage quality for livestock (Berauer et al., 2020).

Declaration of Competing Interest

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

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Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.agee.2022.108085.

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