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Assessing the persistence of semi-natural species-rich grasslands under changes in grazing practices: Insights for grassland restoration

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ABSTRACT

Grazing practices are well-known to shape plant populations and communities in semi-natural grasslands and the conservation and restoration of these ecosystems relies heavily on maintaining traditional extensive grazing systems, which have persisted for centuries or even millennia. However the changes of grazing practices in relation to climate change and socio-economic factors can result in biodiversity loss, shifts in vegetation composition, soil degradation, and declines in ecosystem services and habitat quality. This study aimed to understand the medium-term (3–16 years) effects of changes in grazing practices by comparing two sheep grazing methods in semi-natural rangelands of Southern France: millennia-old traditional herding with shepherds and herding dogs, and the recent practice of fenced free grazing, which emerged at the beginning of the 21st century. Surveys were conducted at six paired study sites over three years, assessing vegetation, mesological data, and plant traits. While the five vegetation zones created by traditional herding remain identifiable, the transition to fenced grazing has induced, for the first time in these grasslands, a mid-term homogenization of plant communities, marked by the spread of xero-mesophilous species and the disappearance of the historical grazing-intensity gradient. These findings highlight the ecological implications of altered grazing regimes, such as fenced grazing, for biodiversity conservation of rangelands with millennia-long grazing history, ecosystem functionality, and long-term persistence of high heritage value grasslands. They provide critical insights into designing adaptive and sustainable restoration strategies for degraded grasslands under changing environmental and socio-economic conditions.

1. Introduction

Grazing, a long-established practice in land management, profoundly influences plant populations and community dynamics, particularly in semi-natural grasslands where traditional grazing practices have shaped landscapes for centuries (Belsky, 1992; Briske and Noy-Meir, 1998). Beyond their cultural significance, these extensive grazing systems, i.e. systems characterized by the use of large land areas per animal are critical for biodiversity conservation (Allen et al., 2011; Metera et al., 2010). Traditional grazing systems, often characterized by the mobility of herds in rangelands, have long been recognized for their role in maintaining diverse plant communities and supporting a wide range of ecosystem services (Bakker, 1998; Bullock et al., 2011). However, recent changes in grazing practices pose significant threats to semi-natural grasslands. Traditional mobile herding and newer fenced grazing systems differ notably in spatial mobility, grazing intensity control, and nutrient redistribution, all factors strongly influencing biodiversity and vegetation structure (Ingty, 2021; Koch et al., 2017; Vidaller et al., 2022). These shifts are primarily driven by climate changes and/or socio-economic factors. For instance, in the rangelands of Southern France, winter grazing within enclosures has increased (Vidaller et al., 2022). Additionally, shifts from employing shepherds to implementing fences, and increased demand for protection against wolves, have altered traditional grazing practices (Wolff et al., 2013). These modifications can negatively impact the biodiversity and ecosystem services provided by semi-natural grasslands This concern is particularly pressing given that grasslands cover approximately 27 % of terrestrial ecosystems (Henwood, 1998) and have experienced a significant decline in areas in recent decades (Dixon et al., 2014). The ongoing loss of grassland habitats raises critical questions about their restoration and the role of grazing management (Farmilo et al., 2023). Indeed, such shifts in grazing practices often leads to degradation and a decline in

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specialized annual xerophilous and stress tolerant dry grassland species, disrupting delicate ecological balances (Milchunas et al., 1988; San Miguel, 2008; Valkó et al., 2018) even when the changes are minor (Koch et al., 2017). The loss of these species can reduce the persistence, i.e. the capacity of a community to maintain its species composition and diversity over time (Huang et al., 2013), of semi-natural species-rich ecosystems and diminish their capacity to provide essential services such as soil stabilization, water regulation, and habitat for wildlife (Díaz-Pereira et al., 2020; Kim et al., 2023). Moreover, these grazing practice changes often lead to the intensification of grazing, characterized by increased stocking densities or alterations in grazing patterns and can have detrimental effects on biodiversity and ecosystem functioning especially in fenced grazing systems (Ingty, 2021; Koch et al., 2017; van de Koppel and Rietkerk, 2000). Intensified grazing often leads to overgrazing, which can result in soil compaction and erosion, and the loss of plant species that are sensitive to heavy grazing pressure, to the dominance of ruderal and nitrophilous species highly tolerant to grazing or of unpalatable species (Herrero-Jáuregui and Oesterheld, 2018; O'Connor et al., 2010). These grazing practice changes can have cascading effects on the entire ecosystem, such as an alteration of nutrient cycles (He et al., 2020), affecting not only plant communities but also the fauna and microorganisms that depend on them (Zhang et al., 2021). Nevertheless, it must be noted that not all modifications to grazing regimes necessarily produce similar ecological outcomes, because different types of grazing changes, such as variations in grazing intensity or transitions from seasonal to continuous grazing, may influence plant communities, nutrient cycling, and soil biota in distinct and sometimes contrasting ways (Herrero-Jáuregui and Oesterheld, 2018). In this study, we will particularly focus on changes in grazing practices from mobile to fenced grazing in semi-arid Mediterranean grasslands. The medium-term consequences of these changes on plant communities and ecosystem dynamics remain a critical area of inquiry, especially in the context of shifting land management practices and global environmental change (San Miguel, 2008; Valkó et al., 2018).

Indeed, it is already known that centuries-old grazing practices have long-term and persisting impacts on ecosystems, known as legacy effects, particularly on plant and soil characteristics of semi-natural dry grasslands (Cuddington, 2011; Saatkamp et al., 2017; Saatkamp et al., 2020). For example, historical grazing legacy effects are detected on plant community structure and the dominance of certain species and enhance carbon sequestration in desert steppes (Han et al., 2014). Grazing-induced legacy effects can include improved plant adaptation to drought through increased root biomass allocation, enhancing plant resilience to climate change (Guo et al., 2021). These legacy effects can also manifest in altered stomatal characteristics and reduced photosynthesis in progeny plants from overgrazed areas, demonstrating the profound and lasting influence of past grazing activities on current plant physiology and ecosystem processes (Yin et al., 2020).

However, little is known about the persistence of legacy effects of traditional grazing systems in the middle term after grazing practice changes at the plant community scale. Nevertheless, understanding how these legacies interact with contemporary restoration practices is crucial for developing strategies that maintain or enhance ecosystem persistence (Foster et al., 2003). The continuous pressure of newly intensified grazing systems may eventually overwhelm these legacy adaptations, potentially resulting in further degradation of ecosystem functions and the decline of socio-ecosystems shaped by century or even millennia of co-adaptation with climate and traditional human use (Blondel, 2006).

The main goal of this study is to elucidate the persistence of land use legacy associated with traditional grazing system by examining the medium-term effects (3–16 years) of recent grazing practice changes on inter-annual plant community dynamics (3 years) in semi-natural species-rich dry grasslands. This approach ensure that the medium-term responses of plant communities in this ecosystem where vegetation dynamics are particularly slow (Saatkamp et al., 2020, 2017). is adequately captured

To address this objective, we conducted a field study examining the impacts of two distinct sheep grazing practices: traditional herding and recent fenced free grazing. Traditional herding, characterized by the presence of shepherds and herding dogs within open delimited sites, represents a century-old approach to grazing management (Tatin et al., 2013). This practice typically involves guided grazing, where sheep are moved between different areas to prevent overgrazing and incursions into neighbouring grazing sites and allow vegetation recovery (Dureau and Bonnefon, 2010), creating a high plant diversity along a typical grazing gradient. In contrast, fenced free grazing, implemented to reduce the costs associated with employing shepherds, entails allowing sheep to roam freely within enclosed areas. Our hypothesis is that this new grazing practice can lead to changes in plant composition, species-richness and species-diversity inherited from traditional herding, as well as a homogenization of plant communities under newer fenced grazing systems.

Specifically, we aimed to determine whether historical management practices associated with traditional grazing could maintain plant composition, species-richness, diversity and ecosystem functions in the face of recent grazing practice changes. Our research focused on the following key questions:

(i) What are the effects of changes in grazing practices from traditional herding to fenced grazing systems on plant communities?
(ii) Which functional groups are most affected by changes in grazing practices?
(iii) What are the implications for grazing management and restoration efforts in preserving the ecological integrity of these species-rich semi-natural dry grasslands of high heritage value?

2. Materials and methods

2.1. Study area

The investigation took place within the "Crau" Mediterranean sub-steppic grassland (EUNIS habitat E1.311, Natura 2000 habitat type 6220; San Miguel, 2008) situated in Southeastern France (Fig. 1a).

This region experiences hot, arid summers and mild, wet winters, with an average 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. 1a). The soil composition in the study area consists predominantly of Haplic Cambisol, exhibiting a mean pH of 6.8 (Buisson and Dutoit, 2006). The landscape's vegetation bears the imprint of extensive sheep grazing practices dating back to the Roman era (Badan et al., 1995; Henry et al., 2010; Saatkamp et al., 2020). Even today, the traditional sight of itinerant sheep grazing on the grassland persists, particularly during the spring season. Traditional grazing involves shepherds and herding dogs, sometimes with protection dogs, guiding sheep within defined grazing areas. These zones are typically delineated, with grazing activity revolving around a central sheepfold, adjacent to a shepherd's shelter, where the flock rests at night (Molinier and Tallon, 1950). Consequently, there exists a discernible spatial gradient in grazing pressure, with sheep congregating more densely near the sheepfold and less so towards the peripheries of the grazing site (Dureau and Bonnefon, 2010). In more recent times, fenced free-range grazing has been introduced as a cost-effective alternative to employing shepherds, drawing inspiration from similar practices used in the Alps to protect against wolf predation (Wolff et al., 2013).

The grassland boasts a diverse array of species, with annual plants, the perennial grass *Brachypodium retusum*, and the Mediterranean shrub *Thymus vulgaris* dominating the landscape (Buisson and Dutoit, 2006). This distinctive dry grassland ecosystem (*Asphodelletum ayardii*, Molinier and Tallon, 1950), faces threats from human activities but despite conservation efforts, only 20 % of the original grassland area remains intact, comprising todays 8600 ha, of which 5811 ha are part of a Nature Reserve created in 2001 (Wolff et al., 2013).

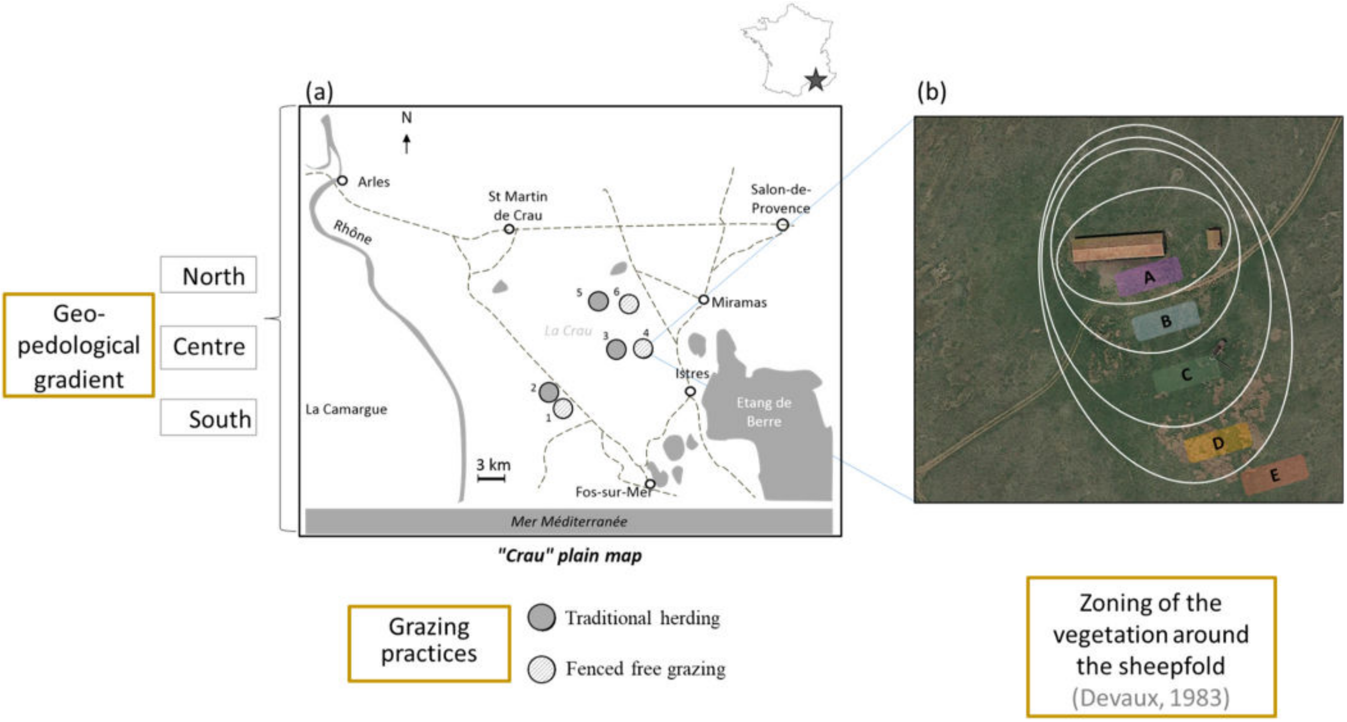

Fig. 1. (a) Sites location on Southern-French grassland. (b) Schematic organization of the five vegetation zones (A, B, C, D and E) resulting from grazing pressure gradient according to distance from sheepfold in traditional herding. (Sizes and shapes of vegetation zones organized in belts around the sheepfold are shown schematically here and do not reflect variations among study sites) (source: GoogleEarth).

2.2. Site selection and experimental design

Pairs of locations (comprising sheepfolds and associated rangeland) were carefully selected from traditional herding territories and neighboring fenced areas designated for free grazing, established over the past few decades (ranging from 3 to 16 years, Sup. Table 1). To address the distinct climatic and geopedological gradient running from North to South across the "Crau" plain (Devaux et al., 1983; Loisel et al., 1990), paired sites were identified in the Northern, Central, and Southern regions of the "Crau" plain (Fig. 1a), resulting in a total of six study sites.

The longstanding grazing practices, spanning thousands of years, have delineated five distinct vegetation zones, corresponding to various grassland types arranged in elliptical belts relative to the proximity to the sheepfold (labeled A, B, C, D, and E; Fig. 1b) (Molinier and Tallon, 1950, Devaux et al., 1983; Loisel et al., 1990, Vidaller et al., 2022).

A- Encircling the sheepfold, lies an overgrazed zone (marked by excessive trampling and notable deposits of urine and feces), characterized by hyper-nitrophilous vegetation, dominated by a species of mallow (*Malva sylvestris*, Molinier and Tallon, 1950).

B- Slightly less impacted by overgrazing (comprising *Hordeo leporini-Onopordetum illyrici*, (Brullo and Marcenò, 1985), dominated by a thistle-like Asteraceae (*Onopordum illyricum*), yet still showing considerable disturbance due to frequent sheep passage, albeit with fewer nitrogenous deposits (urine, feces) compared to zone A due to less prolonged sheep presence.

C- Encompassing *Camphorosmo monspeliacae-Trifolietum subterranei* vegetation (Molinier and Tallon, 1950), characterized by a clover (*Trifolium subterraneum*), with noticeable nitrogenous deposits but less trampling evident, indicated by the presence of *Camphorosma monspeliaca*.

D- Housing the typical sub-steppic Mediterranean grassland vegetation, a result of centuries of itinerant sheep grazing (*Asphodelletum ayardii*, Molinier and Tallon, 1950).

E- Marking the boundary of the grazing site, the "Hem" vegetation (Royer and Rameau, 1981) predominantly features the ramose False-Brome (*B. retusum*) due to reduced grazing intensity, situated between two distinct grazing areas managed by different farmers (Dureau and Bonnefon, 2010; Martin et al., 2022)

Surveys were conducted along transects within the sites, traversing the five vegetation zones, oriented towards the Southeast, which aligns with the primary axis of livestock movement, as the sheepfold provides shelter from the cold northwesterly winds (Molinier and Tallon, 1950).

2.3. Vegetation survey and mesological data

In April 2019, 2020 and 2021 at the peak of the flowering season, an analysis of plant species composition was conducted using the Pavon and Pires (2020) flora. The percentage cover of all vascular plant species was assessed within 1 m^2 quadrats. Across the 6 study sites, 5 quadrats, spaced 5 m apart were surveyed within each vegetation zone, resulting in a total of 150 quadrats sampled per year.

Measurements were taken, (in 2020), for the width of each vegetation zone and the overall width of each site transect, oriented from Northwest to Southeast. Subsequently, the relative width of each vegetation zone was calculated along this axis. Mesological data, encompassing environmental parameters of the quadrats, i.e. vegetation, bare soil and pebble cover percentages were estimated visually and mean vegetation height was measured for each quadrat in 2019, 2020 and 2021 to capture potential variations over time.

Furthermore, the vegetative height of the vegetation, further called vegetation height, was determined by measuring at three random points within each quadrat to estimate the height at which 90 % of the quadrat biomass is represented, following the approach outlined by Dengler et al., (2016).

2.4. Plant trait analysis

For each recorded species in the vegetation survey, we recorded detailed information on the life cycle (Annual, Annual-Perennial, Annual-Monocarpic Perennial, Perennial, and Monocarpic Perennial), life form (Chamephyte, Geophyte, Hemicryptophyte, Therophyte-Hemicryptophyte, and Therophyte) (Raunkiaer, 1934), and maximum and minimum plant height in the Flora of Mediterranean and Continental France (Tison et al., 2014). These traits were chosen because they are predictive traits of herbaceous plants' grazing response, and consistently documented in the flora and available literature, ensuring reliability and comparability across species (Díaz et al., 2001).

To provide a comprehensive understanding of the functional composition, we calculated the community weighted mean (CWM) of maximum plant height and the difference between maximum and minimum plant height, following the methodology described by (Garnier et al., 2004). CWM was chosen as it links species traits to ecosystem functions, highlights the role of dominant species, and allows for the comparison of functional composition across environmental gradients, providing insights into how trait composition mediates community responses and ecosystem processes.

2.5. Data analysis

Thanks to plant community data, we calculated species richness (S), evenness (J′), and the Bray–Curtis index (BC) using the R package Vegan. Evenness (J′) was determined by calculating H′/ln(S), with H′ representing the Shannon diversity index (Pielou, 1969).

A split-plot ANOVA, using stats R package, was conducted to assess the impacts of grazing practices, vegetation zones and year on various response variables within the vegetation, mesological and plant trait data. Grazing practice served as the whole-plot factor, with testing against the interaction of the geopedological gradient × grazing practice. Vegetation zone acted as the split-plot factor, with additional testing for the interaction of vegetation zone × grazing practice and the geopedological gradient against the model residuals.

All models adhered to the assumptions of parametric statistics, including normality and homoscedasticity. In cases where main effects or interactions were deemed significant, a Tukey HSD post-hoc test was employed to examine differences between factor levels.

Plant species composition was analyzed using Non-Metric Multidimensional Scaling (NMDS) via the metaMDS function, based on the Bray–Curtis similarity index (Borcard et al., 2011). This approach was used to visualize shifts in species composition. The NMDS was performed with 30 random initial configurations across 1–15 dimensions, and the solution with the lowest stress value was selected for interpretation. A permutational multivariate analysis of variance (PERMANOVA) using the R package adonis was then applied to test differences in community composition among grazing practices for all vegetation releves and across vegetation zones for traditional herding sites and then fenced free grazing sites. The analysis was computed on the Bray–Curtis dissimilarity matrix using 999 permutations.

Chord diagrams were created using the circlize package to visualize the variation in the number of species according to life cycle for each vegetation zone.

All statistical analyses were carried out in R (v.4.3.2, R Development Core Team, 2023).

3. Results

3.1. Effect of grazing practice changes on vegetation indices

A significant variation in plant species richness was measured among vegetation zones, ranging from 6 to 48 species per 1 m^2 (Fig. 2). Grazing practices, vegetation zone, geopedological gradient, year, and their interactions (except for grazing practice × geopedological gradient, grazing practice × year, and grazing practice × vegetation zone × year interactions) also significantly influenced plant species richness (Table 1). Species richness was generally significantly higher for fenced grazing. It increased significantly with distance from the sheepfold and from north to south along the geopedological gradient. Year also significantly impacted species richness, as it was higher in 2020 and 2021 compared to 2019, and these differences between years were significant for vegetation zones B, D, and E.

Evenness was also significantly influenced by vegetation zones (Table 1), being lower for zone A (closest to the sheepfold) than for zones B, C, D, and E. It was also significantly higher in 2020 and 2021 compared to 2019, similar to the effect on species richness, and the vegetation zone × year interaction was significant for vegetation zones

Table 1
F-values of the ANOVA, significance levels of the effects of grazing practices, geopedological gradient, vegetation zone, and their interactions on the plant community in 6 dry Mediterranean grasslands of the Crau area (Southern France) between 2019 and 2021. "× " symbol represents interaction between factors. $p < 0.1$; *$p < 0.05$; **$p < 0.01$; *** $p < 0.001$, MS marginally significant, NS not significant.

Plant community	*df*	Species richness	Evenness
Grazing practice (GP)	1	373.132 *	9.514 NS
Geopedological gradient (GG)	2	53.833 ***	8.497 ***
Vegetation zone (VZ)	4	271.375 ***	5.216 ***
Year (Y)	2	35.712 ***	81.810 ***
GP × GG	2	0.117 NS	2.872 MS
GP × VZ	4	11.866 ***	3.368 *
GG × VZ	8	7.811 ***	6.453 ***
VZ × Y	2	2.153 *	2.370 *
GP × Y	2	0.352 NS	0.846 NS
GP × VZ × Y	8	1.090 NS	3.334 **

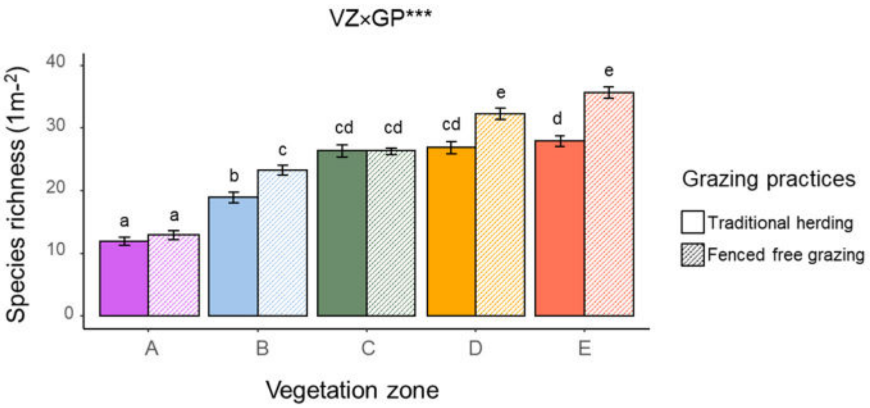

Fig. 2. Effect of grazing practice and vegetation zones on mean species richness (1 m^2) (mean ± SE) in 6 dry Mediterranean grasslands of the Crau area (Southern France) between 2019 and 2021. Different lower case letters respectively indicate significant differences in Tukey HSD post-hoc test ($P < 0.05$).

B, D, and E. The significant effect of grazing practices × vegetation zone interaction was due to significantly higher evenness for fenced free grazing in zone D. The significant triple interaction grazing practice × vegetation zone × year arose from lower evenness of species for fenced grazing in zone A, only in 2021, as well as higher evenness of zone E for fenced grazing in 2021.

3.2. Effect of grazing practice changes on vegetation composition and structure

In the NMDS plot for traditional herding (Fig. 3a), five distinct vegetation zones were identified. These zones exhibited clear separation, indicating distinct plant community compositions associated with traditional herding. Notable species included *Erodium cicutarium*, *Lepidium graminifolium*, and *Plantago coronopus* in zone A, which is closest to the sheepfold. As we moved to zones B, C, D, and E, there was a noticeable shift in species composition, with species like *Trifolium campestre*, *Catapodium rigidum*, and *Medicago truncatula* becoming more prevalent, particularly in zones further from the sheepfold (Sup. Mat. 1).

The NMDS plot for fenced free grazing (Fig. 3b) also identified five distinct vegetation zones, with some similarities to the traditional herding plot but notable differences as well. In fenced free grazing, the plant species composition within zones appeared more homogenized compared to traditional herding (Sup. Mat. 1). Pairwise PERMANOVA confirmed significant differences in plant community composition between grazing practices. Within traditional herding sites, vegetation zones were strongly differentiated, whereas under fenced free grazing sites, differences among zones were still significant but less pronounced (Sup. Table 2).

Species such as *Erodium cicutarium* and *Plantago coronopus* still dominated zone A, with an increase of *Trifolium* species cumulated cover (Sup. Mat. 1) but there was less distinction between zones B, C, and D compared to the traditional herding. Zone D exhibited a higher cumulative cover of *Medicago*, *Trifolium* species and *Hordeum murinum*, *Avena barbata*, *Lolium rigidum* and *Carduus tenuiflorus.* Zone E, showed a greater presence of species like *Bromus rubens, Bromus madritensis, Brachypodium distachyon, Verbascum sinuatum, Trifolium campestre, Conyza canadensis.* and *Thymus vulgaris* compared to the traditional herding plot (Sup. Mat. 1, 2).

3.3. Effect of grazing practice changes on plant functional traits

Grazing practices impacted life cycle across the five studied vegetation zones (Fig. 4). In all zones, annual species dominated under both grazing practices, with traditional herding supporting a higher number of these annual species.

Zone A showed that traditional herding maintained a higher species count in annual and perennial categories compared to fenced free grazing. Zone B followed an inverse trend, with fenced free grazing supporting more annual species. Zone C revealed a slight preference for traditional herding in annual and annual-monocarpic and perennial species, although traditional herding showed a higher count in annual-perennial species. Zone D, exhibited the most noticeable difference with traditional herding supported a higher number of both annual and perennial species. Finally, Zone E exhibited a higher number of annual species and lower number in perennial species in fenced free grazing.

Grazing practices also impacted life form across the five studied vegetation zones (Fig. 5).

In zone A, traditional herding supported more therophyte species, while fenced free grazing favored therophyte-hemicryptophyte species. Hemicryptophytes and geophytes showed a slight advantage with traditional herding. Zone B showed higher therophyte species with fenced free grazing, but traditional herding maintained more hemicryptophytes. Other categories showed similar species numbers between practices.

Zone C indicated higher therophyte species numbers for traditional

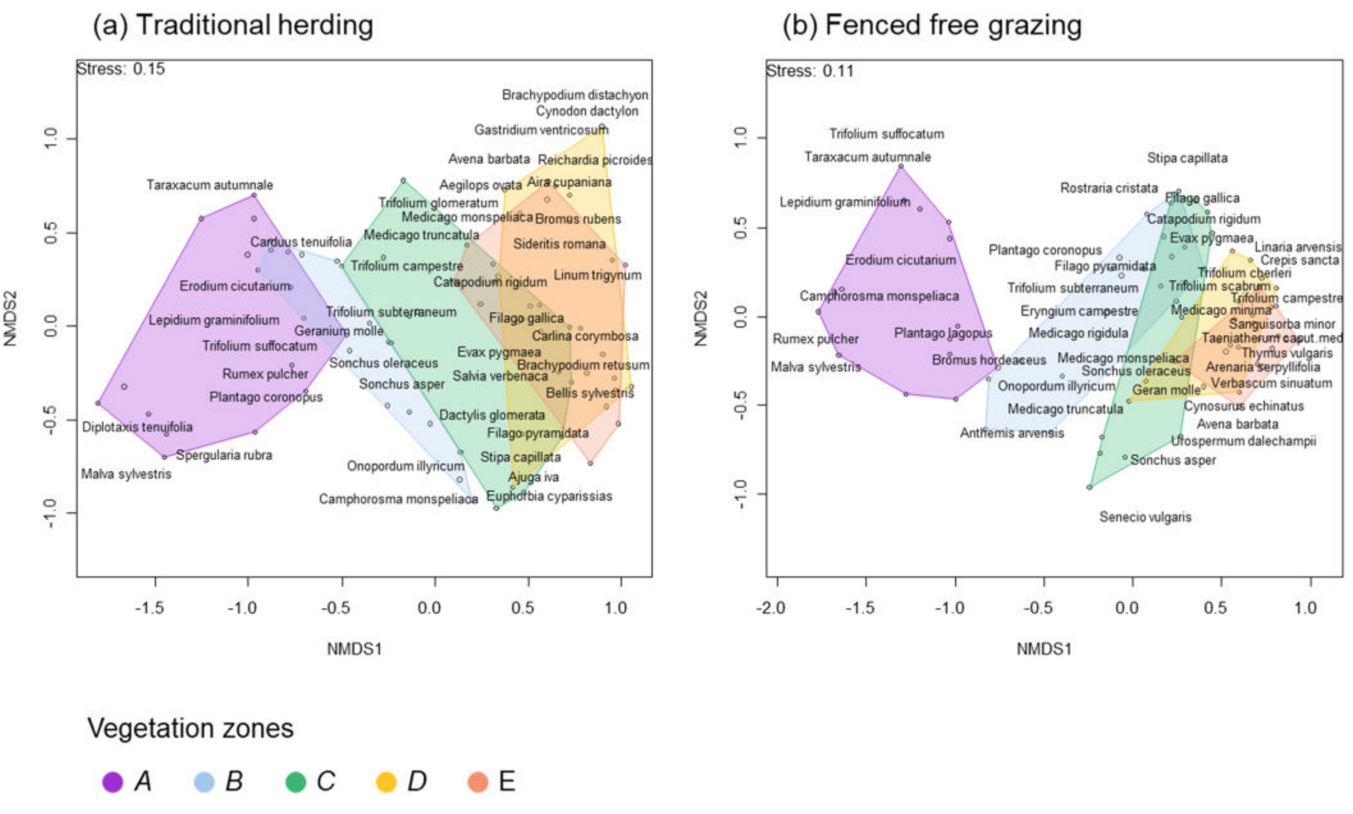

Fig. 3. Non-metric multidimensional scaling (NMDS) based on Bray-Curtis distances of vegetation releves on May 2019, 2021 and 2021 data from (a) Traditional herding and (b) Fenced free grazing sites in 6 dry Mediterranean grasslands of the Crau area (Southern France). The polygons illustrate the projection of vegetation zones on the NMDS. Only the first two axes (NMDS1 and NMDS2) are shown here. K= 3 (three dimensions).

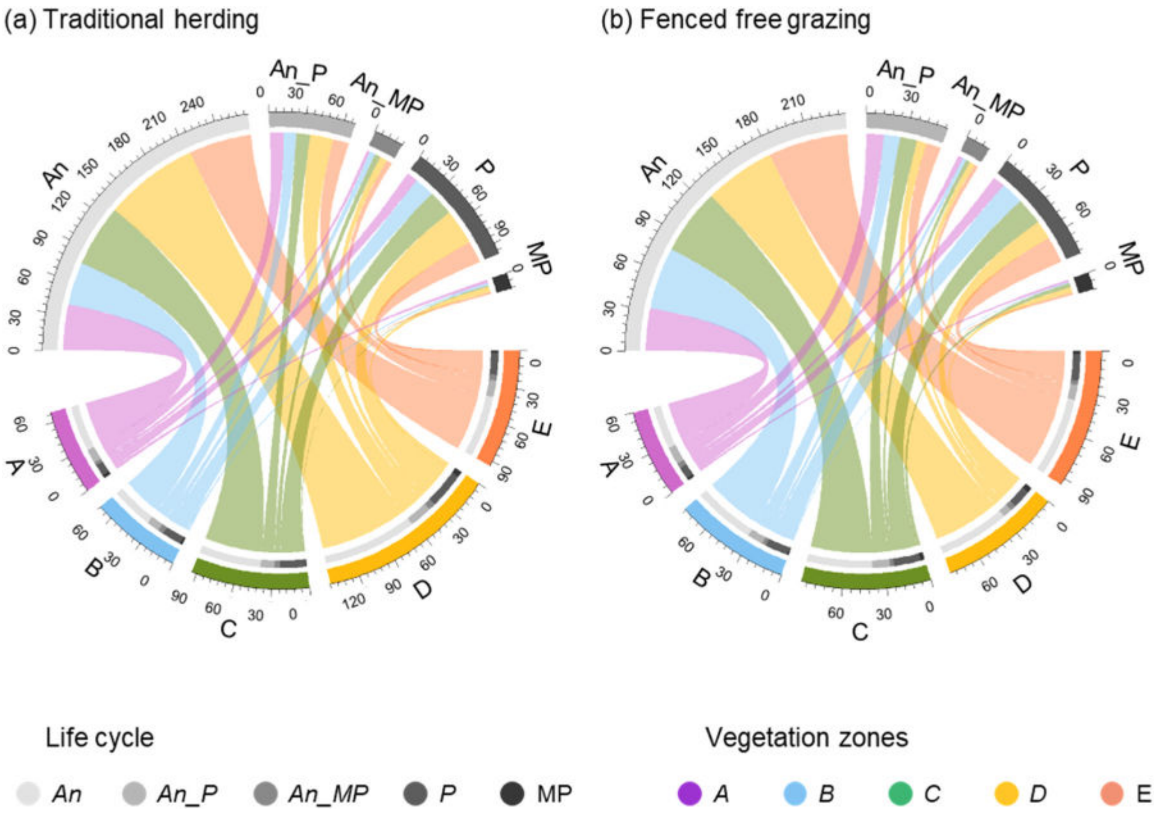

Fig. 4. Chord diagram showing the variation in number of species according to life cycle (top of the arc) for each vegetation zone (bottom of the arc). The width of the connecting bands is proportional to the number of species shared between categories. An: Annual, An_P: Annual – Perennial, An_MP: Annual – Monocarpic perennial, P: Perennial, MP: Monocarpic perennial.

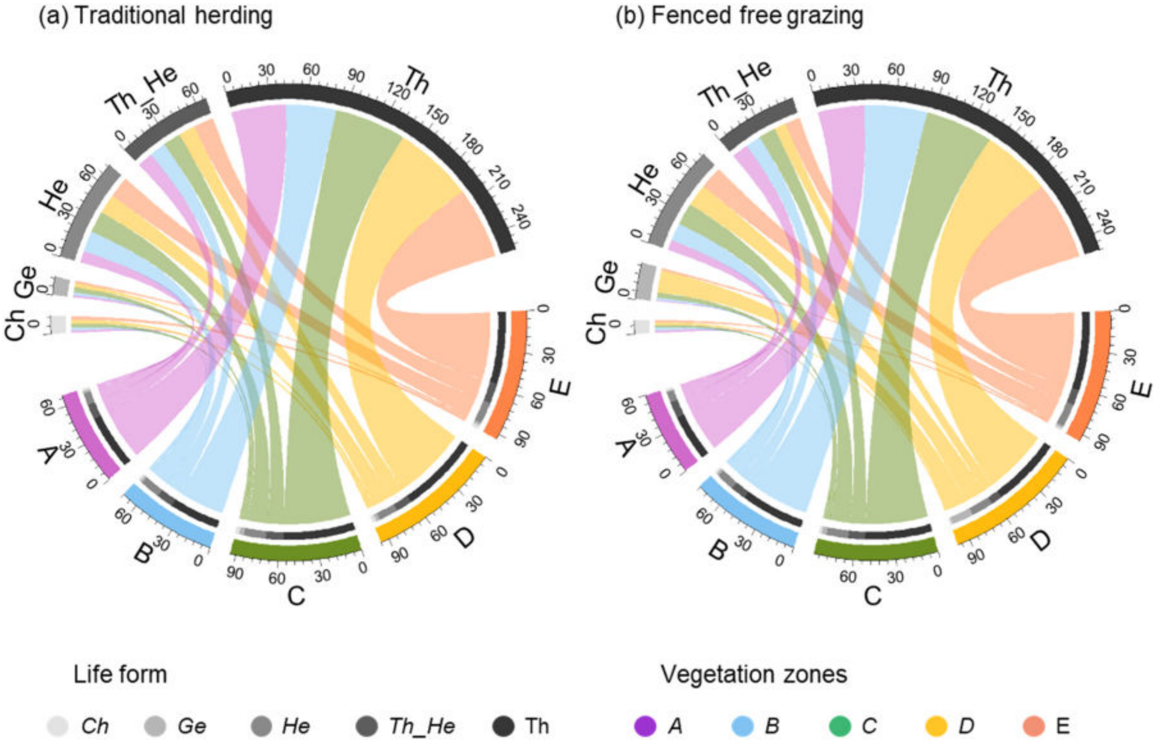

Fig. 5. Chord diagram showing the variation in number of species according to life form (top of the arc) for each vegetation zone (bottom of the arc). The width of the connecting bands is proportional to the number of species shared between categories. Ch: Chamephyte, Ge: Geophyte, He: Hemicryptophyte, Th_He: Therophyte – Hemicryptophyte, Th: Therophyte.

grazing. Zone D, as for life forms, exhibited the more noticeable results with higher therophyte, therophyte-hemicryptophyte and chamephyte species with traditional herding. Fenced with grazing favored a higher number of geophyte and hemicryptophyte species. Zone E showed higher therophyte and hemicryptophyte species for fenced free grazing and lower therophyte-hemicryptophyte.

Vegetation zone, geopedological gradient, year, and their interactions (except for grazing practice × vegetation zone × year interactions) also significantly influenced maximum plant height and the difference between maximum and minimum plant height (Table 2, Fig. 6).

Grazing practices in interaction with vegetation zone had a significant effect on the community-weighted mean (CWM) of the maximum plant height. In zone A, C and D traditional herding resulted in a significantly higher CWM maximum height and difference between maximum and minimum plant height compared to fenced free grazing. In zone E, CWM difference between maximum and minimum plant height was higher in fenced free grazing.

3.4. *Effect of grazing practice changes on mesological data*

In 2020, the relative widths of the vegetation zones differed, with a significantly higher relative width for zone E than for the others (Table 3). Grazing practices significantly interacted with the size of the vegetation zone. Fenced grazing reduced the relative width of zone E, while significantly increasing the relative widths of zones B and D, explaining the significant effect of grazing practices × vegetation zone interaction. Grazing practice significantly influenced two mesological variables: the average vegetation height, which was higher in traditional grazing sites than in fenced sites, and the percentage of pebble cover, which was marginally higher in traditional grazing sites (Table 3). The geopedological gradient had a significant influence on pebble cover, which is greater in sites north of the Crau plain compared to vegetation cover and height, which are higher in the south and center of the plain. The vegetation zones show significant differences for all mesological data. There is significantly more bare soil in zone A, close to the sheepfold, than in other zones where bare soil decreases significantly before becoming similar between zones D and E. Vegetation cover is higher in zone E than in zones A and B. Pebble cover is significantly lower in zones A and B and significantly higher in zone D. Average vegetation height is higher in zones D and E (Table 3, Sup. Mat. 3).

The year effect is significant for bare soil cover, characterized by a higher percentage in 2019 compared to the other years, and for vegetation cover, showing the lowest cover in 2019, an increase in 2020 followed by a decrease in 2021, but with cover remaining higher than in 2019. The grazing practice × vegetation zone interaction is significant regardless of the measured mesological parameter. Bare soil and vegetation cover change over time according to vegetation zones, with a decrease in bare soil in 2020 and 2021 compared to 2019 for zones A and B, as well as higher vegetation cover for zones C, D, E in 2020. Finally, the grazing × year interaction is significant for 3 out of 4 mesological parameters. Bare soil cover was higher in fenced grazing than in traditional grazing in 2020, while vegetation cover was higher in traditional grazing than in fenced grazing for the same year. Pebble cover was also higher in traditional grazing than in fenced grazing for the years 2020 and 2021. The triple interaction is significant for bare soil, with a significant increase in bare soil for vegetation zone B, in traditional grazing compared to fenced grazing in 2019, as well as significantly higher cover for all 3 years in zone D in fenced grazing compared to traditional grazing. The marginally significant effect for average vegetation height results in higher height, always in traditional grazing - in zone A, in 2019; in zone B in 2020 and 2021; in zone C 2020 and in zone D regardless of the year.

Table 2

F-values of the ANOVA, significance levels of the effects of grazing practices, geopedological gradient, vegetation zone, and their interactions on the community weighted mean of maximum plant height in 6 dry Mediterranean grasslands of the Crau area (Southern France) between 2019 and 2021. "× " symbol represents interaction between factors. $p < 0.1$; *$p < 0.05$; **$p < 0.01$; *** $p < 0.001$, MS marginally significant, NS not significant.

Community weighted mean	*df*	Maximum height	Delta max-min height
Grazing practice (GP)	1	2.21 NS	0.438 NS
Geopedological gradient (GG)	2	22.143 ***	20.665 ***
Vegetation zone (VZ)	4	26.314 ***	47.374 ***
Year (Y)	2	0.373 NS	0.288 NS
GP × GG	2	16.174 **	13.572 ***
GP × VZ	4	4.150 **	3.298 *
GG × VZ	8	5.644 ***	5.007 ***
VZ × Y	2	2.354 *	1.695 MS
GP × Y	2	5.609 **	5.282 **
GP × VZ × Y	8	1.001 NS	1.372 NS

4. Discussion

The intricate relationship between grazing practices and vegetation dynamics has key implications for semi-natural grassland ecosystem functioning, biodiversity conservation and restoration (Koch et al., 2017). This study investigated the influence of grazing practice changes on various vegetation indices, specifically focusing on plant species richness, evenness, vegetation composition, and structure, as well as plant traits and mesological parameters across different vegetation zones resulting of the traditional herding in a dry Mediterranean grassland in Southern France. After three years of survey we measured now significant variations due to grazing practice changes leading mainly to plant community homogenization along the traditional grazing pressure gradient correlated to distance from sheepfolds. A greater plant cover was measured for more mesophilic, open habitat and unpalatable species which are not typical of the ecosystem in recent fenced grazing. These results provide insights into ecosystem responses to land management interventions for the conservation and restoration of the species-rich dry grasslands.

4.1. *Recent fenced grazing enhances plant species richness in areas distant from sheepfolds but homogenizes plant community composition and structure along the grazing gradient*

Our results demonstrated a significant variation in plant species richness. This variation was influenced by grazing practices, vegetation zones, geopedological gradients, and their interactions. The higher species richness found generally for fenced grazing sites and for B, D and E vegetation zones under fenced grazing conditions were unexpected as experimental studies showed that traditional grazing practices allowed conservation of high plant species richness and diversity of this semi natural dry grassland (Römermann et al., 2009; Wahlman and Milberg, 2002). However, we questioned above the identity of these gained species as it is crucial to focus on plant species that are typical of this Natura 2000 habitat type 6220; European Commission, 2007, San Miguel, (2008)).

The significant increase in species richness with distance from the sheepfold could be attributed to reduced grazing pressure further to the sheepfold (Adler et al., 2001; Alados et al., 2004; Grime, 1979; Milchunas et al., 1988). The higher species richness measured in 2020 and 2021 compared to 2019 suggests a temporal variation possibly due to delayed responses to grazing management changes from traditional herding to fenced grazing (James et al., 2001; Souther et al., 2019).

Evenness was also significantly affected by vegetation zones and thus by the traditional grazing gradient with the lowest evenness in zone A (closest to the sheepfold) where the species richness is the lower and where only some species dominated (Génin et al., 2021)). The increase in evenness over time further supports the notion that temporal effects of

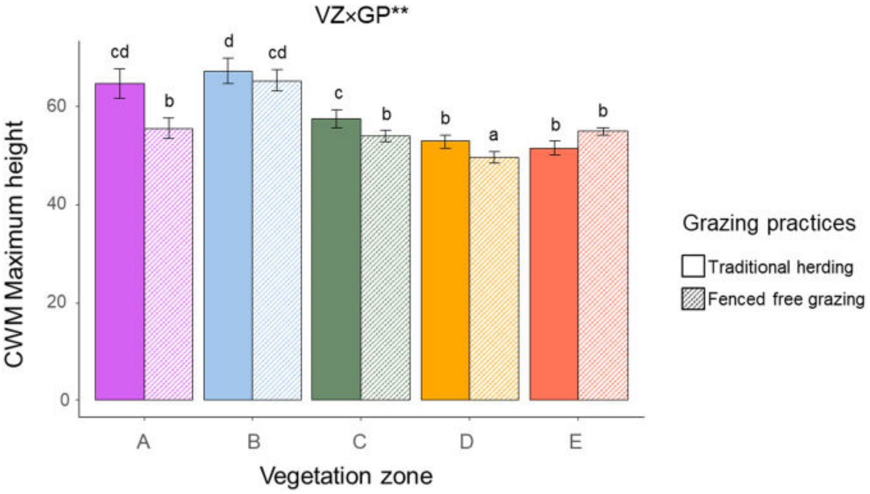

Fig. 6. Effect of grazing practice and vegetation zones on community weighted mean of the maximum plant height (mean ± SE). Different lower case letters respectively indicate significant differences a in Tukey HSD post-hoc test ($P < 0.05$).

Table 3

F-values of the ANOVA, significance levels of the effects of grazing practices, geopedological gradient, vegetation zone, and their interactions on the mesological data in 6 dry Mediterranean grasslands of the Crau area (Southern France) between 2019 and 2021. "× " symbol represents interaction between factors. $p < 0.1$; *$p < 0.05$; **$p < 0.01$; *** $p < 0.001$, MS marginally significant, NS not significant.

Mesological data	*df*	Relative zone width (2020)	Bare soil cover	Vegetation cover	Pebble cover	Vegetation mean height
Grazing practice (GP)	1	0.26 NS	0.005 NS	0.098 NS	12.645 MS	12.645 *
Geopedological gradient (GG)	2	0.04 NS	1.142 NS	11.741 ***	49.190 ***	4.940 **
Vegetation zone (VZ)	4	17.54 ***	50.432 ***	18.235 ***	75.777 ***	10.208 ***
Year (Y)	2		7.287 ***	36.677 ***	0.007 NS	1.162 NS
GP × GG	2	0.04 NS	38.014 ***	37.178 ***	5.559 **	8.250 ***
GP × VZ	4	12.29 **	7.271 ***	2.884 *	15.434 ***	2.004 MS
GG × VZ	8	4.87 *	3.531 ***	4.806 ***	9.704 ***	1.436 NS
VZ × Y	2		4.483 ***	1.725 MS	1.648 NS	1.416 NS
GP × Y	2		2.981 *	5.669 **	2.816 *	0.237 NS
GP × VZ × Y	8		2.992 *	0.869 NS	0.959 NS	2.230 MS

management practices influence very slowly plant community dynamics in the middle term (10–30 years) for dry grassland ecosystems as already shown by Peco et al., (2017).

The NMDS analysis revealed distinct vegetation zones for both traditional herding and fenced free grazing practices. The clear separation in plant community compositions associated with traditional herding suggests that this practice promotes distinct ecological plant communities. In contrast, the more homogenized plant species composition under fenced free grazing indicates a less heterogeneous environment, which may lead to reduced species richness over time as controlling grazing selectivity of animals is known to increase biodiversity outcomes (Bailey et al., 1998; Rook et al., 2004).

The species composition shift, due to grazing practice changes indicates a less intense grazing for recent fenced free grazing in zone A. Zone D for fenced free grazing exhibited a higher cover of more nitrophilous, ruderal and opportunistic species. Zone E, showed a greater presence of species indicating habitat openness and a higher *Thymus vulgaris* cover due to a decreased cover of *Brachypodium retusum* which is a more competitive species. This homogenization likely results from the loss of fine-scale grazing selectivity, which varies according to the species of grazing animal (Rook et al., 2004). Traditional herding systems promote diverse microhabitats and species coexistence through selective feeding patterns. By contrast, less selective grazing, due to for example fenced grazing, diminishes spatial heterogeneity and leads to more uniform plant communities (Ingty, 2021; Koch et al., 2017).

4.2. *Grazing practices significantly influence plant traits*

The effects of grazing on life cycle, life form traits were evident across the vegetation zones, as differences in species cycles and forms prevalence were found between traditional herding and fenced free grazing. Increased grazing intensity led to a rise in species richness with ruderal strategies, annual life histories, close to the sheepfolds and consistent with findings from previous studies (Briske and Noy-Meir, 1998; James et al., 2001; Noy-Meir and Oron, 2001; Pakeman, 2004).

The most pronounced effects were measured in Zone D, as for species richness, where there was a notable change in the plant traits of the typical grassland community with an increase in therophytes presence in fenced free grazing indicating an increase in grazing pressure comparing to traditional herding (Noy-Meir and Oron, 2001).

Plant height, widely considered as one of the most reliable indicators of species' responses to grazing (Díaz et al., 2001) also showed significant differences. Indeed, the significant effects of grazing practices on the community-weighted mean (CWM) of maximum plant height in zones A, C, and D, suggest that traditional herding may maintain taller vegetation structures due to selective grazing and trampling patterns (Díaz et al., 2001; Wild et al., 2023). Moreover, the differences between maximum and minimum plant heights revealed a similar trend, indicating that height variation is greater for traditional grazing in zones A, C, and D but lower in E zone. This suggest that traditional grazing practices create environmental heterogeneity that encourages species with adaptive growth strategies to thrive. This could be due to localized variations in grazing intensity and trampling, which create microhabitats with varying resource availability (Martin et al., 2022).

4.3. Traditional grazing enhances measured vegetation height and habitat heterogeneity

Mesological parameters were also significantly influenced by grazing practices and vegetation zones. Traditional grazing sites exhibited higher vegetation height and pebble cover, highlighting again an increase in grazing density, which lead to higher plant consumption and soil trampling for fenced free grazing sites (Hanke et al., 2014) and the role of grazing in shaping physical habitat characteristics (Molinier and Tallon, 1950; Martin et al., 2022).

The significant interaction between grazing practices and vegetation zones on several parameters indicates that grazing management can alter spatial vegetation patterns (Adler et al., 2001). At least, fenced grazing increased the relative widths of zones B and D while reducing the width of zone E, suggesting that fenced free grazing homogenize the spatial plant communities and micro-patterns distribution inherited from centuries of traditional herding practices (Molinier and Tallon, 1950).

4.4. Implications for grazing management and restoration practices

Understanding how different grazing practices shape plant communities and ecosystem functions is essential for developing sustainable land management strategies that balance agricultural productivity with biodiversity conservation and restoration (Duru et al., 2007; Fuhlendorf et al., 2012; Blaix et al., 2025). Our findings hold significant implications for grazing management and restoration practices, particularly in semi-natural grasslands, where strategies to mitigate biodiversity loss and ecosystem service decline are critical in the face of changes in grazing systems (Allan et al., 2015).

The increased species richness and evenness measured under fenced grazing could initially be interpreted as beneficial for grassland plant biodiversity restoration, similar to results reported for other ecosystems and herbivores (Moinardeau et al., 2021). However, our results indicate that traditional herding system better supports habitat-typical species assemblages, greater functional diversity and higher spatial heterogeneity in plant community distribution, which are crucial for maintaining key ecosystem processes and services (Dupré and Diekmann, 2001; Oñatibia and Aguiar, 2019; Zhang et al., 2021). Our results thus highlight the importance of considering not only species richness but also community structure, their spatial distribution and plant functional traits when evaluating grazing impacts. Indeed, while community changes may be subtle, particularly over short time periods, focusing on plant life cycles and forms allows for a more detailed understanding of these shifts (Díaz et al., 2001).

Overall, maintaining high species, trait diversity and plant communities spatial diversity requires varying grazing intensity (Török et al., 2016) and moderate grazing intensity led to the highest levels of typical species diversity.

Furthermore, incorporating traditional ecological knowledge, along with socio-economic factors, can offer new opportunities for restoring sustainable grazing management practices (Török et al., 2024). Future research should explore the underlying mechanisms driving these patterns and investigate how adaptive grazing strategies, specifically a return to traditional herding management and the abandonment of fenced grazing, can enhance ecosystem restoration. Future studies should also include analyses of soil physico-chemical characteristics, insects population and grassland bird communities to complement our results on plant communities, in order to better understand how changes in grazing practices influence below-ground processes and nutrient dynamics in the medium-term.

CRediT authorship contribution statement

Christel Vidaller: Writing – review & editing, Writing – original draft, Visualization, Validation, Supervision, Software, Resources, Project administration, Methodology, Investigation, Formal analysis, Data curation, Conceptualization. **Thierry Dutoit:** Writing – review & editing, Visualization, Validation, Supervision, Project administration, Methodology, Investigation, Funding acquisition, Conceptualization.

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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.2025.110169.

Data availability

Data will be made available on request.

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