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Managed as wild, horses influence grassland vegetation differently than domestic herds

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ABSTRACT

The urgent need to preserve ecosystems over vast areas has placed rewilding with wild herbivores to the forefront. However, there are still few scientific experimental field studies dealing with its effects on biodiversity and ecosystem services. Since 1993, in France, a socially natural population of wild horses (*Equus ferus przewalskii*) has been managed for its conservation. This introduction is an opportunity to compare this new management system with the multi-secular extensive sheep breeding and the more recent conventional domestic horse breeding. We sought to discover if plant communities show differences depending on the grazers and the managing system. We surveyed 208 plots divided into six grazed sites (two sites per type of grazer), where all plants species and their percent cover were listed within $1m^2$, and environmental variables – such as stones percent cover, slope - were measured within $100m^2$. To focus on the grazer effects, we used a subsample of plots with similar environmental variables. To study the grazing system - management choices - effects, we ran the analyses using all the plots. At both scales, our results show that species richness, evenness and heterogeneity are significantly higher with wild horses than with sheep grazing. Intermediate value is measured for evenness concerning domestic horses at the grazing system scale. Species richness is significantly higher for domestic horses than sheep focusing on the grazer; intermediate values are measured for evenness and heterogeneity. At both scales, wild horses also favour dicots rather than monocots. Our results indicate that grazing by horses maintains and promotes grassland diversity, especially when horses are managed 'as wild' - allowing them to express their natural behaviour. However, further studies are needed focusing on populations of patrimonial plant species over time, other taxonomical groups and/or on functional diversity and ecosystem services to compare and test more finely the effects of an animal bred extensively and 'as wild'.

1. Introduction

The urgent need to preserve and restore ecosystems over vast areas (UN, 2019) has placed rewilding to the forefront for the last decade (Pettorelli et al., 2019). Trophic rewilding (Svenning et al., 2016) is increasingly applied along with conservation and restoration efforts. It is seen as a promising opportunity to restore grasslands (Saavedra et al., 2023), which are important ecosystems worldwide (White et al., 2000) but one of the most threatened (Bond, 2021; Petermann and Buzhdygan, 2021). Natural and semi-natural grassland formation is due to the combination of environmental factors (such as regular fires, climate, altitude) including grazing whether by wild or domestic herbivores (Bond, 2021; Hejcman et al., 2013; Weigl and Knowles, 2014). In Europe, semi-natural grasslands – which are mostly managed semi-natural ecosystems dominated by grasses (Allen et al., 2011) - are an essential part of the cultural landscape, shaped by centuries or millennia of low-intensity land uses (Blondel, 2006; Dengler et al., 2014; Hejcman et al., 2013). Since the 1960s, conservation management of threatened semi-natural grasslands in Europe has mostly been done by reinstating, imitating or subsidizing practices, such as mowing, cutting sods, rotational grazing with domestic herds, coppicing and burning (Johansen et al., 2019; Van Wieren, 1995). For decades, grazing by livestock has

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been demonstrated to be an adequate management strategy for maintaining and promoting the biodiversity of semi-natural grasslands (Fraser et al., 2022; Isselstein et al., 2005; Olff and Ritchie, 1998; Rook et al., 2004; Tälle et al., 2016; Van Wieren, 1995; Wrage et al., 2011). However, it is not always possible to maintain such traditional practices because of socio-economical changes (e.g., different management and/or grazers (Schmitz and Isselstein, 2020)). In such cases, rewilding can be a complementary (Mutillod et al., *in press*) and conceivable (Ceaușu et al., 2015) strategy for conservation and restoration efforts in Europe. It aims to restore biodiversity and ecosystem processes notably using keystone species or ecosystem engineers - such as large herbivores - and reducing human control (Carver et al., 2021). The concept is based on the assumption that, before anthropogenic uses, landscapes were shaped by large-bodied fauna - also called megafauna - that disappeared because of human activities (hunting, habitat transformation) during the Pleistocene (Owen-Smith, 1989, 1987, 1988). Megaherbivores (auroch, bison, horses and megaceros) shaped vegetation assemblages and heterogeneity, opening the landscape (Bakker et al., 2016; Doughty et al., 2016; Smith et al., 2023) even in Europe (Vera, 2000; Vera et al., 2006). Grazing by large herbivorous mammals is a key process shaping plant communities and habitat conditions, which themselves have directly or indirectly affected other organisms for millennia (Bakker et al., 2016; Galetti et al., 2018; Malhi et al., 2016), through foraging, trampling, plant dispersal and effects on nutrient cycling (Forbes et al., 2019; Hobbs, 1996; van Klink et al., 2015).

General theories about grazing effects on plant communities involve the reduction of competitive dominant plants leading to an increase in the species richness of subordinate taxa, the selection of preferred species conducting to their own decrease, and is assumed to favour seed dispersal when grazing pressure is intermediate (Couvreur et al., 2004; Olff and Ritchie, 1998). Evaluating grazing effects on grassland plant biodiversity is important for biodiversity management (Van Wieren and Bakker, 1998). The effects of domestic herds on plant communities have been well documented, showing their conservation potential at medium stocking rates notably when compared to non-grazed areas or other practices (e.g., mowing) (Olff and Ritchie, 1998; Stahlheber and D'Antonio, 2013; Tälle et al., 2016). However, the consequences of grazing vary with soils, regions, grazing regimes and type of grazers (Matches, 1992; Stahlheber and D'Antonio, 2013). Divergent effects on plant communities according to the type of grazers have been measured for domestic (Catorci et al., 2012; Nugent et al., 2022) and wild animals (van der Plas et al., 2016), and can be linked to grazer feeding, foraging strategies and dietary preferences, body size, social system and grazing system management leading to a selective pressure on plant species (Arnold, 1984; Grant et al., 1985). However, there are still few scientific experimental field results about the effects of large wild herbivores (re) introduced into ecosystems for conservation or restoration purposes (Svenning, 2020; Svenning et al., 2016) and even fewer comparing the effects of domestic and wild grazers with only a few examples in the African savannah, American's great plains and European grasslands (Allred et al., 2011; Kohl et al., 2013; Rupprecht et al., 2022; Veblen et al., 2016; Veblen and Young, 2010).

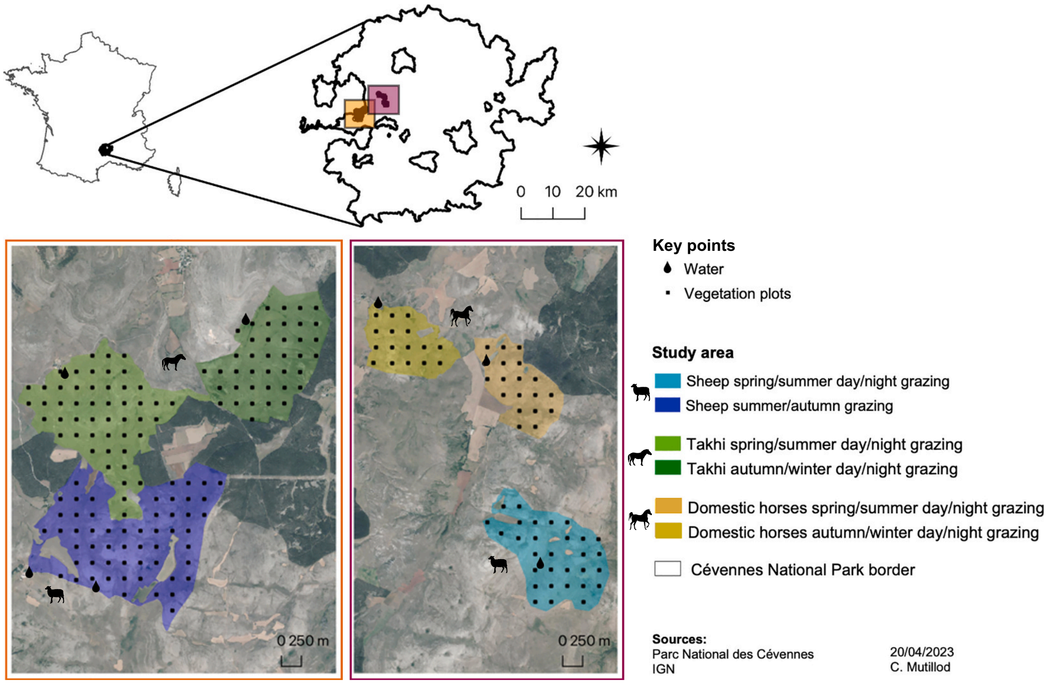
This study sought to assess how new management strategies involving domestic or wild horses are affecting plant communities in comparison with traditional management with sheep. In the southern plateaus of the *Massif Central* in France, sheep have been extensively bred for meat for centuries (Lepart et al., 2000; Marty et al., 2003). However, for a few decades, new grazers have appeared: i) domestic horses extensively bred for sport competitions (long distance races) and ii) horses managed as wild (*Equus ferus przewalskii*) (called takhi hereinafter, the Mongolian name for these horses (Van Dierendonck and Wallis de Vries, 1996)) for species and habitat conservation purposes – that could be referred to as rewilding. It seemed important to compare grasslands under the three types of grazing systems and better understand the possible differences induced by the use of wild animals versus domestic herds to conserve and/or restore semi-natural ecosystems. Since using different grazers also implies differences in the way farmlands are managed (e.g., when sheep or domestic horses are bred, farmers often cultivate cereals in small depressions, while this is not the case in rewilding projects), we studied the effects of i) grazers and ii) global grazing systems – comprising all choices made in the management strategy -, on the vegetation. The questions we investigated are: are there differences between plant community composition, plant diversity and spatial heterogeneity in areas (i) under these three types of grazing systems – i.e., taking management into consideration - and (ii) grazed by the three types of herbivores? (iii) Is the use of wild horses instead of domestic herds promoting grassland plant biodiversity (e.g., higher species richness, evenness and vegetation heterogeneity)? According to the literature, we expect differences in plant community composition, species-richness and evenness between the types of grazers and grazing systems because i) sheep and horses do not have the same diet nor the same foraging behaviour (Arnold, 1984; Duncan, 1991; Fleurance et al., 2011; Rutter, 2010, 2006) and ii) when horses are managed 'as wild' their impact on vegetation could be different to their domestic counterpart. They could use the space differently because of the social system (e.g., with several males, different reproductive status) leading to changes in activity budget (Boyd, 1988), and/or having different feeding strategies (e.g., eating other plant species for self-medication as has been shown for other wild animals (Krief, 2011)) which could lead to the creation of richer mosaics of micro habitats.

2. Material and methods

2.1. Study area

The study area is located in the mountainous southeast zone of the *Massif Central* (south of France, Fig. 1), specifically on the *Causse Méjean*. It is a calcareous plateau located between 800 and 1250 m in altitude and limited by two canyons, the *Tarn* and the *Jonte* rivers characterized by karst topography, poor, dry soils, and steppe-like grasslands with cultivated areas located in depressions (Marty et al., 2003). Seasons alternate between cold wet winters and hot dry summers, resulting from the influence of a mixed continental - Mediterranean climate (Caplat et al., 2006). The mean minimum temperature is 3 °C and occurs in January, the mean maximum is in July with 23 °C (Fonderflick et al., 2010b), annual temperatures can be very contrasted (with extremes: −17.5 °C recorded in January 1985, 38 °C recorded in August in 2003, (*Mairie de Hures-la-Parade: station Millau - Soulobres*)). Annual precipitations vary from 900 mm to 1200 mm (Fonderflick et al., 2010a). The *Causse Méjean* has a long history of human land use – based on livestock farming, fires, wood harvesting and cereal cropping (Robin et al., 2018). The combination of these uses and the specific climate and soil conditions have generated a steppe-like environment – except where forestry takes place - (Lepart et al., 2000) with a high biological diversity (O'Rourke, 1999). Indeed, the flora is marked by a high rate of endemism and by the presence of species with steppe origin (Tison et al., 2014). This grassland is part of the Mediterraneo-montane steppes EUNIS habitat type (code E1.51, European Environment Agency, 2019). Mediterraneo-montane steppes are formally described as « sparse or discontinuous xerophile grasslands of *Stipa pennata*, *Festuca auquieri* (*Festuca duriuscula*), *Festuca hervieri*, *Koeleria vallesiana* or *Sesleria albicans* var. *elegantissima* with *Helianthemum apenninum*, *Helianthemum canum*, *Genista* spp., *Globularia* spp., *Ononis striata*, *Euphorbia seguierana*, *Potentilla crantzii*, *Thymus dolomiticus*, *Plantago argentea*, *Rosa pimpinellifolia*, *Dianthus sylvestris*, *Lavandula angustifolia*, *Aster alpinus*, *Anthyllis* spp., *Carex humilis*, best developed in the Causses, but also present locally in Provence and Languedoc, from the Alps to Catalonia (European Environment Agency, 2019)».

This territory is partially included in the *Parc National des Cévennes* (Cévennes National Park) and labelled as a UNESCO world heritage site, and contains NATURA 2000 habitats with continental biological value (European Environment Agency, 2002). The national park was created



Sources:
Parc National des Cévennes
IGN
20/04/2023
C. Mutillod

Fig. 1. Location of the studied sites in the *Parc National des Cévennes* (South of France) with the different seasonal pastures grazed by sheep (blue), takhi (*E. ferus przewalskii*; green) and domestic horses (yellow). Black squares show vegetation inventory plots. Drop-shapes show watering places. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

in 1970 in order to monitor this territory, support sustainable development, and welcome and educate the public.

2.2. Studied sites

The six sites selected for this study (Fig. 1) are located in the eastern part of the *Causse Méjean* plateau, with elevation ranging from 968 to 1196 m. They are located within the *Parc National des Cévennes* and have presented a similar grazing history for centuries: sheep breeding for meat (Osty et al., 1994). Grazing pressures in the studied sites have been similar over the past few years and are very similar between the three types of studied grazers, ranging from 0.048 to 0.062 LU/ha/year (Table 1).

Two sites grazed by domestic sheep (*Ovis aries* Linnaeus, 1758) were studied, characterising different breeding conditions on the *Causse Méjean* (Fig. 1). The first one has been grazed in summer and autumn for >50 years, as soon as the weather conditions are suitable - no extreme temperatures and no excessive snow cover; animals are driven to the grazing area by the sheep farmer with the help of dogs, and during the grazing time sheep are left alone, being driven back to shelter at night. The second site is grazed in spring and summer: since 2018 the animals do not return to the sheepfold during the grazing season (except for the first and last few days when nights are too cold) and are not herded by shepherds but guarded by dogs. Before 2018, animals were sheltered at night. We also chose these two sites because they were located close to horse-grazed areas - domestic and wild, and present similar environmental characteristics. In 1994, eleven takhi (*Equus ferus przewalskii* Poliakov 1881) - originating from eight European zoos (United Kingdom, Germany, France) were introduced into a 288 ha site (Saïdi and Mende, 1999; Tatin et al., 2009). The initial goal of the semi-free ranging management (i.e., animals roaming freely in a closed area without interference in their natural behaviour) of the takhi was to allow them (i) to rediscover and express their natural behaviour in a natural environment with similar climate conditions to their original distribution area (Asian steppes), and (ii) to recreate social groups before translocating them to Mongolia (King, 2005; Roche and Tatin, 2021; Tatin et al., 2009; Turghan et al., 2022; Zimmermann, 2005). The second goal was to maintain the steppe-like open habitat (Zimmermann, 2005) after a period of significant agricultural abandonment and modifications in land use practices, leading to natural shrub encroachment in several areas of the *Causse Méjean* (Caplat et al., 2006; Marty et al., 2003). At the time of the study, 35 takhi roamed semi-freely in two connected sites, one of 217 ha being grazed in spring and summer, the other (171 ha) grazed in autumn and winter. Movement from one enclosure to the other is a part of the land management strategy made mandatory by the municipality. Takhi are not led by humans here but rather their movement is induced by attracting them with salt licks and water point management (there is no direct human-horse interaction).

Table 1
Grazing pressure on the six studied enclosures and the number of vegetation plots surveyed in 2022.

Animal	Grazing season (from entry to exit)	Total area (ha)	Sampled area (ha)	Number of animals	Livestock Unit	Effective grazing (days)	LU/ha/year[a]	Number of plots
Sheep	May–December	412.8	136	386	57.9	165	0.061	30
	July–November (unless snow or excessive heat).	700	266.7	570	85.5	70	0.062	55
Domestic horses	November–March	77.7	77.7	15	11.7	150	0.062	16
	June–November	80.7	80.7	12	9.36	165	0.052	18
Takhi	November - Mid-May	170.7	170.7	35	19.25	167.5	0.052	40
	Mid-May - November	217.2	217.2	35	19.25	197.5	0.048	49

[a] Sheep = 0.15 Livestock Unit; Domestic horses = 0.78 LU; Takhi = 0.55 LU.

Due to the species conservation status, habitat management objectives and the way takhi are managed (see Roche and Tatin, 2021 for details), especially non-intervention on mate choice, we considered takhi here as being wild managed, which is a similar concept to rewilding.

Finally, domestic horses (*Equus ferus caballus* Linnaeus, 1758) have been extensively bred for endurance races on the selected farm on the *Causse Méjean* since 2008. From 2008 to 2018, sites were grazed by sheep and horses, and then, by horses only. Two enclosures were selected: one being used in spring and summer and the other used in autumn and winter (Table 1).

Domestic herds (sheep and horses) are managed animals: receiving sanitary treatments, such as deworming, with breeders forming batches according to age and often by sex, males and females being kept separate most of the time, and the animals have close contact with humans. This is not the case for takhi which follow their natural social system (Tatin et al., 2009) and human interactions are rare, occurring mostly when social groups are translocated (as was the case in 2004 and 2005 to Mongolia). Usually, in the case of domestic breeding, land depressions are cultivated with cereal crops or are grasslands reaped for hay production or intensively grazed.

2.3. Sampling design

Systematic random sampling was conducted in 2022 on the six sites (Fig. 1). It consisted of a set of plots located 200 m apart to avoid any spatial autocorrelation effect, totalling 208 plots. A grid was randomly arranged to place the plots on each site. The number of plots is proportional to the site size in order to encompass the studied area heterogeneity (see Table 1 for repartition in enclosure). A plot consisted of a 1m^2 quadrat in which we carried out a floristic inventory and a concentric 100m^2 (5.6 m radius) circle where we measured environmental parameters.

2.4. Floristic inventories and environmental parameters

Percent covers of each species were surveyed in the $208 \times 1\ \text{m}^2$ quadrats in spring (from the end of May until the end of June) at the peak of the flowering season. We used two flora for plant determination (Bernard, 2009; Tison et al., 2014) and we used the most recent taxonomy of Gargominy and collaborators (Gargominy et al., 2021). In the 1m^2 quadrat, we also measured soil depth at three randomly chosen points with a rebar. Around each quadrat, the 100m^2 circle was used to estimate the percent cover of: rocks, blocks i.e., $Ø > 25$ cm, stones i.e., $Ø < 25$ cm, the percent cover of bare ground and vegetation in the various layers (tree height (h) > 2 m; shrub $2\ \text{m} > \text{h} > 0.5$ m; herbaceous $\text{h} < 0.5$ m). We also estimated the percent cover of small walls and rock piles, remnants of the land use history on the *Causse Méjean*, as rocks and stones were piled to clear the ground to cultivate or improve pasture quality (Marty et al., 2003). We visually estimated the grazing pressure on each plot, attributing one of the five categories of the utilisation rate of the herbaceous stratum (0 being the lowest utilisation rate – i.e., no sign of grazing - and 5 the most grazed; Ruiz-Mirazo et al., 2011). For each 100 m^2 circle, we extracted the mean slope, exposure and altitude from a digital terrain model (1 m precision) available from the French National Geographical Institute (*Institut National de l'Information Géographique et Forestière*, 2022). The exposure values are subdivided into two between cos and sin, with sin = 1 indicating the north and cos = 1 indicating the east. We obtained information about lithology from the *Parc National des Cévennes* and assigned each plot to one of three categories: dolostone, limestone or alluvion/colluvium.

2.5. Statistical analysis

All the statistical analyses were run on R (R Core Team, 2022). In all the following analyses, except for the utilisation rate and the exposure, environmental data were log transformed ($y' = \log(y + 1)$) to avoid large differences in scale between the original data, similar to what was done in a previous study (Anderson and Willis, 2003).

2.5.1. Effect of grazing systems on plant communities

To explore the relationship between the composition of plant communities and the type of grazing systems, we studied the 208 sampled plots. First, we performed two Canonical Analyses of Principal coordinates (CAP) which are constrained analyses. We carried out these CAP based on Bray-Curtis dissimilarities calculated from square-rooted transformed species abundances. To evaluate the effect of the environmental parameters without the grazing systems effects, the first CAP (CAP-A) was run with environmental variables as the constraint and grazing systems as conditions. We then carried out a Principal Component Analysis (PCA) on the environmental parameters (see Supplementary material Fig. 1A & B). The three first axes of the PCA previously carried out, explaining respectively 17.6 %, 11 % and 10.3 % of the variability, were put as conditions in the second CAP (CAP—B) (with grazing systems as constraints) to explore the effects of the grazing system without the effects of environmental parameters. The constraints of the CAP were the values of the utilisation rate of the herbaceous stratum for each Grazing System (Sheep-GS, Domestic Horse-GS and Takhi-GS). We also categorised the grazing season (0 = Autumn/Winter, 1 = Summer/Autumn and 2 = Spring/Summer), and ran a CAP in order to verify its effect on plant communities. We consider the choice of the grazing season as being part of the grazing system. We performed Anova by terms with 999 permutations on the CAP model to obtain statistical information for each constraint variable.

We calculated diversity indices (*Vegan package*): species richness such as the average number of species per quadrat, the Pielou evenness index and heterogeneity using Bray-Curtis within each grazing system. To compare indices between grazing systems, we ran a Generalized Linear Model (GLM) followed by a Tukey post-hoc test five times with a random draw of sub-samples in order to obtain the same number of plots between groups ($n = 34$ plots). Random draws were done except for the heterogeneity, because we considered the size of the enclosure as being part of the management strategy. Poisson family was used for richness values, quasibinomial was used for both Pielou and Bray-Curtis values. Finally, we used the IndVal method (*Indicspecies package*) (Dufrêne and Legendre, 1997) to identify the most characteristic species depending on the grazing animal. Following Legendre & Legendre 1998 in (Sawchik et al., 2005), we removed rare species from the analysis (< 1 % of the total number recorded). We considered species having IndVal values >70 % as characteristic species of the assemblages because they showed strong habitat specificity and fidelity (McGeoch et al., 2002; Sawchik et al., 2005).

Using flora (Tison et al., 2014), we differentiated monocotyledons and dicotyledons species and calculated their mean cover percent using the total cover of dicotyledons or monocotyledons divided by the total vegetation cover multiplied by 100 for each plot. In order to know if grazing systems have an effect on these frequencies, we ran a GLM using the quasibinomial family with frequencies (monocots and dicotyledons) explained by the grazing systems and followed by a Tukey post-hoc test.

2.5.2. Effect of grazers on plant communities

To evaluate grazer effects on plant communities (without the effect of management, such as the choice whether to cultivate land depressions or not – i.e., the grazing system – and, without the natural environmental variations – e.g., soil), we studied the plots with similar environmental variables. To do so, we ran the following analyses. First, we ran a k-means cluster analysis using the environmental parameters, which resulted in a five-cluster solution. To decide the optimal number of clusters, we tested two-, three-, four-, five- and six-cluster models with *SAS FASTCLUS procedure* (SAS Institute Inc., 2014). We looked at the Pseudo F statistic, the approximate expected overall R-squared and the cubic clustering criterion – solutions with the highest pseudo F statistic and cubic clustering values are usually considered the best (Milligan and

Cooper, 1985). We choose the five-cluster solution, which was empirically and theoretically reasonable. Within this solution, we selected the third group (hereinafter called Cluster 3) because it was the most represented and homogeneous habitat among the grazed sites (sheep: n = 45; takhi: n = 34; domestic horses: n = 18; total n = 97). To compare plant communities between grazers, we ran a Non-metrical Multidimensional Scaling (NMDS) - based on the Bray–Curtis distances of vegetation composition - followed by an Adonis test and pairwise test, using the *Vegan package* and the *Adonis function*. We calculated species richness, the Pielou index and the Bray-Curtis heterogeneity using the same method as previously explained with grazers as an explanatory variable. We ran a GLM as explained in the previous part and a post-hoc Tukey tests 5 times with a random draw of 18 plots (n = 18). We finally calculated the IndVal for each group and the potential effects of the grazers on monocots and dicotyledons cover frequencies.

3. Results

3.1. Plant community composition and bioindicator species

The first CAP (CAP-A), (Fig. 2A) gives a better understanding of the role of local ecological conditions, with some variables having significant effects on plant assemblages (Table 2), such as rock, stones, bare soil and shrub cover, altitude, slope, exposure and lithology. The second

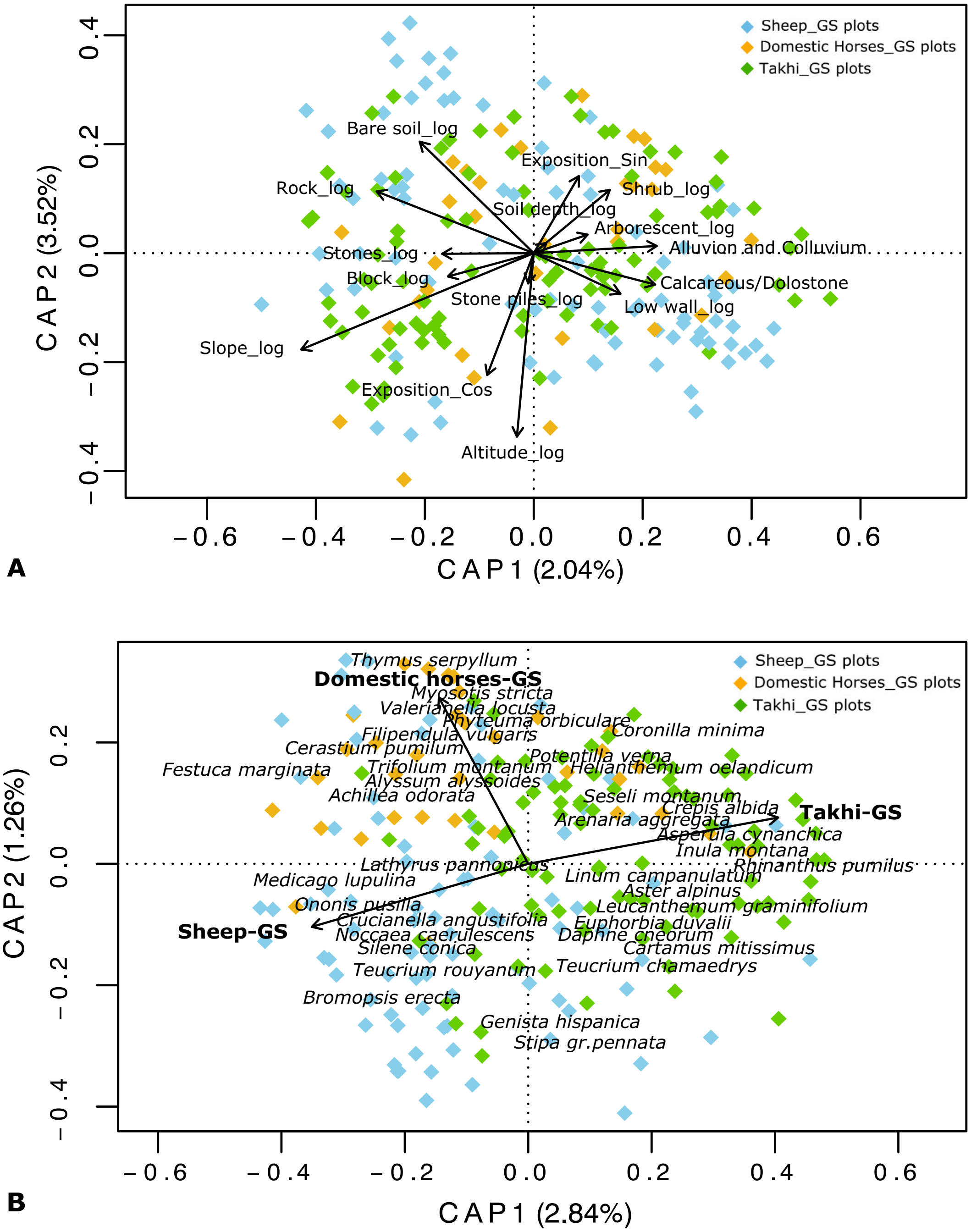


Fig. 2. A. Canonical Analysis of Principal coordinates (CAP) with environmental variables as constraint and grazers as conditions. B. CAP with grazing systems (-GS) as constraints and environmental variables (two firsts axis of the PCA) as conditions. The CAP displays the first three principal coordinate axes of a CAP analysis (model: Plant Species ~ Takhi + Horse + Sheep + Conditions (Axis1_PCA + Axis2_PCA + Axis3_PCA)).

Table 2
Summary of the results of Canonical Analysis of Principal coordinates (CAP).

CAP model	Proportion (constraint)	Proportion (condition)	Variables	Anova perm test $n = 999$	
				F	p-Value[a]
CAP-A Species ~ environmental variables + Conditions (Takhi-GS + Horse-GS + Sheep-GS)	0.11834	0.04844	Rock	2.5023	0.002**
			Block	1.0546	0.342
			Stones	2.2818	0.002**
			Bare soil	1.8800	0.010**
			Low wall	1.1444	0.234
			Stone piles	1.1694	0.197
			Soil depth	1.2916	0.104
			Altitude	3.1976	0.001***
			Slope	3.2439	0.001***
			Exposition-Cos	1.1276	0.024*
			Exposition-Sin	0.9469	0.497
			Shrub	2.0575	0.001***
			Arborescent	1.1309	0.229
			Calcareous/	1.8303	0.009**
			Dolostone	1.5267	0.027*
			Alluvion &		
			Colluvium		
CAP-B Species ~ Takhi-GS + Horse-GS + Sheep-GS + Conditions (Axis1_PCA + Axis2_PCA + Axis3_PCA)	0.04871	0.03450	Takhi-GS	5.2507	0.001***
			Horse-GS	2.9597	0.001***
			Sheep-GS	2.4679	0.001***

[a] p-Value (*: $p \leq 0.05$, **: $p \leq 0.01$, ***: $p \leq 0.001$)

CAP (CAP—B) evaluates the effect of the grazing system (Table 2) with 4.9 % of the total variation explained by the grazers (see Supplementary material Table S1 for the net effects of grazers and net effects of the ACP axis). On this analysis (CAP—B) (Fig. 2B), the first axis separates the plant assemblages into two groups, with plots from the Sheep-GS and the Domestic Horse-GS on one side, and the plots from the Takhi-GS on the

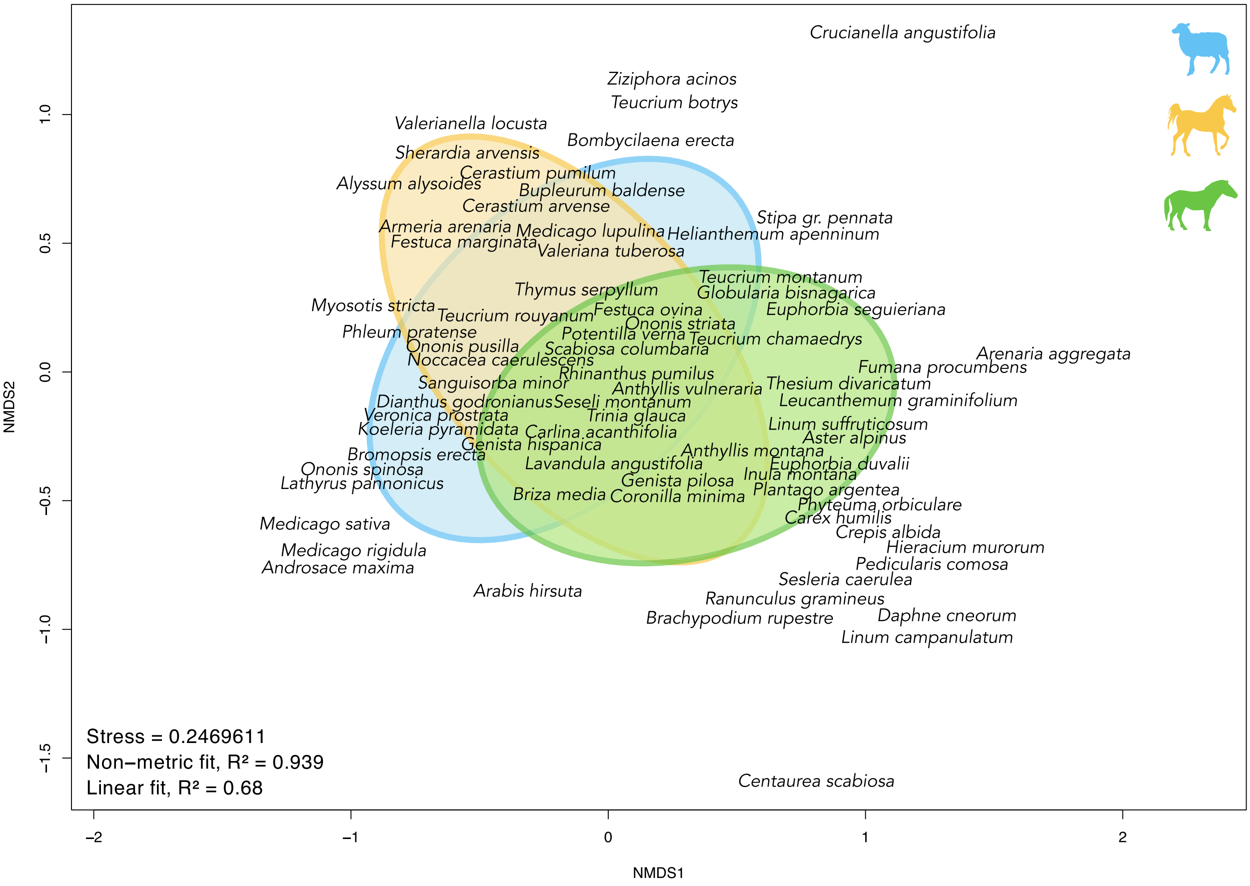


Fig. 3. Non-metrical multidimensional scaling (NMDS) of plant community composition of sites grazed by different animals from cluster 3 (Sheep in blue, $n = 45$; Domestic Horse in yellow, $n = 18$; Takhi in green, $n = 34$). Ellipse lines represent the standard deviation with 80 % confidence interval.
Stress = 0.247; Non-metric fit, $R^2 = 0.939$; Linear fit, $R^2 = 0.680$.
Associated Adonis pairwise test: Sheep vs Domestic Horse: F.model = 2.149, $R^2 = 0.034$, adjusted p-value = 0.090; Sheep vs Takhi: F.model = 6.550, $R^2 = 0.078$, adjusted p-value = 0.003*; Domestic Horse vs Takhi: F.model = 5.172, $R^2 = 0.094$, adjusted p-value = 0.003*. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

other. The second axis separates horse (domestic and wild) plots from sheep-grazed plots. The effect of the grazing season was measured at 1 %.

When we focus on the effects of the grazers on cluster 3, the ellipse comprising plant species growing in the site grazed by each type of grazers is partly superposed in the plane formed by axes 1 and 2 of the NMDS indicating that the three grazers share relatively similar plant community compositions (Fig. 3). Nevertheless, the community growing under takhi-grazing is significantly different from those grazed by sheep or by domestic horses (sheep vs takhi: F.Model = 6.550, *P* = 0.003*; domestic horses vs takhi: F.Model = 5.172, *P* = 0.003*). No significant differences were identified between domestic horses and sheep (F.Model = 2.149, *P* = 0.090). Species, such as *Aster alpinus, Euphorbia duvalii, Inula montana, Leucanthemum graminifolium, Phyteuma orbiculare, Thesium divaricatum,* characterize - by their higher frequency - the plant community of the takhi-grazed sites. *Bromopsis erecta, Bupleurum baldense, Cerastium pumilum, Festuca marginata, Sherardia arvensis, Teucrium rouyanum,* characterize more the plant communities in the sheep and domestic horse grazed sites.

Concerning the grazing systems, *Rhinanthus pumilus* (sqrtIV = 0.728) and *Potentilla verna* + *Rhinanthus pumilus* (sqrtIV = 0.704) are characteristic species for Takhi-GS. *Bromopsis erecta* (sqrtIV = 0.736) is the

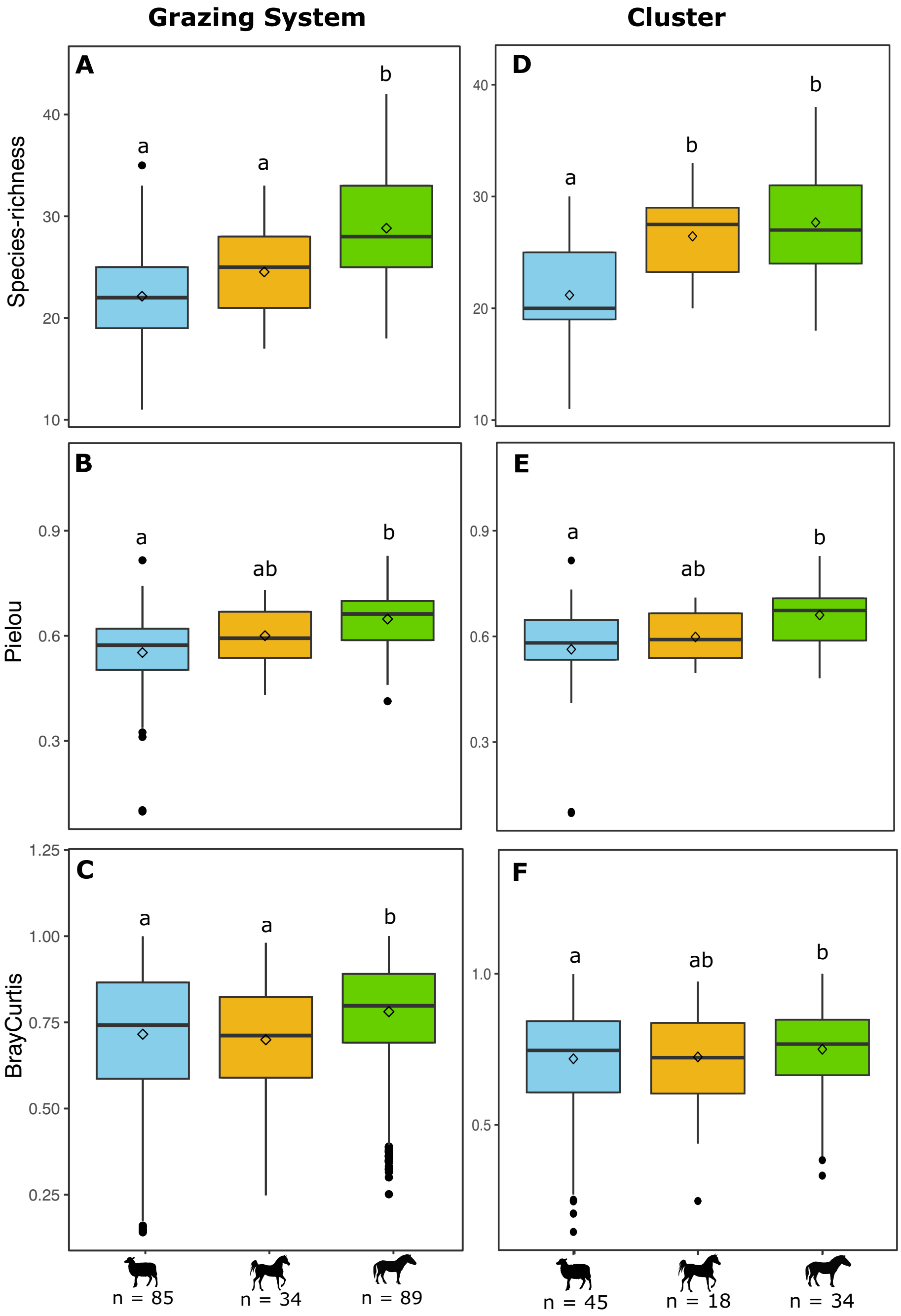


Fig. 4. Boxplots of species richness, the Pielou Index and the Bray-Curtis heterogeneity depending on the grazer respectively at the global scale (A, B and C: Domestic Horse n = 34, Sheep *n* = 85, Takhi *n* = 89) and on a cluster of plots (cluster 3) characterized by the stone cover (D, E and F: Domestic Horse n = 18, Sheep n = 45, Takhi n = 34). Letters (a,b,c) associated for species richness and the Pielou index are relative to statistical tests made on n = 34 plots at the system level and n = 18 plots at the cluster level randomly drawn for Sheep- and Takhi-grazed sites and run five times while Bray-Curtis, tests were run with all the plots for the system level and all the plots comprised in cluster 3. Black empty diamonds represent mean values per groups of plots. Black lines represent median values per groups of plots.

bioindicator of the Sheep-GS. *Teucrium rouyanum* is the second species in the list but with IndVal <70 % (sqrtIV = 0.609). No species with IndVal >70 % are given for Domestic Horse-GS. The first line result is *Bromopsis erecta* + *Bupleurum baldense* + *Festuca marginata* + *Helictochloa pratensis* (sqrtIV = 0.573).

Concerning the effect of grazers (cluster 3), species showing IndVal values >70 % are *Linum suffruticosum* (sqrtIV = 0.745), *Rhinanthus pumilus* (sqrtIV = 0.742) and *Rhinanthus pumilus* + *Seseli montanum* (sqrtIV = 0.707) for Takhi-grazed plots. *Bromopsis erecta* (sqrtIV = 0.750) and *Thymus serpyllum* (sqrtIV = 0.714) are the characteristic species for Sheep-grazed plots. We can also consider, *Festuca marginata* + *Koeleria valesiana* (sqrtIV = 0.692) which have values really close to 70. For Domestic Horse-grazed plots, no species with IndVal >70 % is given. The results of the two first lines are: *Bromopsis erecta* + *Bupleurum baldense* + *Potentilla verna* (sqrtIV = 0.642) and *Bromopsis erecta* + *Bupleurum baldense* + *Festuca marginata* + *Potentilla verna* (sqrtIV = 0.636).

3.2. Biodiversity indicators

A total of 171 species was recorded including all the plots and 147 within cluster 3. When analysing the effect of grazing systems, including all data (Fig. 4A), plant species richness per square-meter (mean ± SD) is significantly higher in the Takhi-GS (28.83 ± 5.36) than in the Sheep-GS plots (22.14 ± 4.42) (5 random draws of n = 34 each, estimate = 6.128, $p < 0.001$) or than in Domestic Horse-GS plots (24.53 ± 4.15) (estimate = 3.988, $p < 0.05$). No significant difference is identified between Domestic Horse-GS and Sheep-GS plots (estimate = −2.14, $p = 0.164$).

When analysing the effect of grazers in cluster 3 (Fig. 4D), plant species richness is still significantly lower in the Sheep-grazed plots (21.18 ± 4.33) (5 random draws of n = 18 each) than in the Takhi- (27.68 ± 4.76, estimate = 6.934, $p < 0.001$) or Domestic Horse-grazed (26.44 ± 3.90, estimate = 5.866, $p < 0.05$) plots. No significant difference is shown between Domestic Horse-grazed and Takhi-grazed plots (estimate = 1.065, $p = 0.681$).

Concerning the Pielou index, significant differences were only found between Sheep and Takhi both at the grazing system and at the cluster 3 level – i.e., grazers - (respectively n = 34 each, estimate = 0.096, $p < 0.05$; n = 18 each, estimate = 0.098, $p < 0.05$) (Fig. 4B & E). No significant difference was shown for Sheep-GS vs Domestic Horse-GS (estimate = 0.046, $p = 0.150$) neither for Domestic Horse-GS vs Takhi-GS (estimate = 0.050, $p = 0.093$). Average values at the management level are 0.55 ± 0.12 for Sheep-GS, 0.60 ± 0.08 for Domestic Horse-GS and 0.65 ± 0.09 for Takhi-GS (Fig. 4B). At the cluster 3 level, values are 0.56 ± 0.14 in Sheep-, 0.60 ± 0.072 in Domestic Horses- and 0.66 ± 0.09 in Takhi-grazed plots (Fig. 4E).

Finally, average values of the Bray-Curtis distances that explore vegetation heterogeneity between all plots grazed by animals are clearly different for Domestic Horse-GS vs Takhi-GS (estimate = 0.081, $p < 0.001$) and Sheep-GS vs Takhi-GS (estimate = 0.065, $p < 0.001$), and less obvious for Domestic Horse-GS vs Sheep-GS (estimate = 0.016, $p = 0.066$). Average values are 0.72 ± 0.18 in the Sheep-GS, 0.70 ± 0.16 in the Domestic Horse-GS and 0.78 ± 0.14 in the Takhi-GS (Fig. 4C). Clear differences are only shown between Sheep and Takhi grazed cluster 3 (estimate = 0.032, $p < 0.001$), but not between Domestic Horse and Takhi (estimate = 0.025, $p = 0.177$), nor between Sheep and Domestic Horse (estimate = −0.006, $p = 0.89$). Average values in cluster 3 are 0.72 ± 0.17 for Sheep, 0.72 ± 0.15 for Domestic Horse and 0.75 ± 0.13 for Takhi.

3.3. Percent covers of monocotyledons and dicotyledons

At the grazing system scale, 134 species recorded are dicotyledons and 37 are monocotyledons. Concerning cluster 3, 119 dicotyledons and 28 monocotyledons were recorded. Clear differences are shown for percent covers of dicotyledons between Takhi-GS and the domestic grazers-GS (Sheep vs Takhi: estimate = 0.160, $p < 0.001$) and Domestic horse-GS vs Takhi-GS: estimate = 0.128, $p < 0.001$) (Fig. 5). The same results were observed for grazer effects at the cluster 3 level (Sheep vs Takhi: estimate = 0.174, $p < 0.001$ and Domestic Horse vs Takhi: estimate = 0.126, $p < 0.05$).

No significant differences are shown concerning dicotyledons percent covers both at the grazing system level and the cluster level for Domestic Horse compared to Sheep (respectively at GS: estimate = 0.0319, $p = 0.622$ and Cluster 3: estimate = 0.0480, $p = 0.591$).

4. Discussion

Studying the effects of three different herbivores and their associated grazing systems on a grassland revealed differences on plant community composition, diversity and spatial heterogeneity between sheep and horses (domestic and wild) but also between management types i.e., domestic herds vs the wild herd. The management 'as wild' of takhi appears to promote biodiversity with higher species richness and spatial heterogeneity leading to the creation of the richest mosaic of microhabitats, and seems to generate new species frequencies in the plant community – with a similar pool species of the Mediterraneo-montane steppes EUNIS habitat type (code E1.51, European Environment Agency, 2019) - with more dicotyledons and the increased frequency of a hemiparasitic species (see below Section 4.3).

4.1. Effects of grazers on plant communities

Analysing plant communities grazed by sheep, domestic horses and takhi (at the level of cluster 3 to avoid environmental variations, both natural and chosen by managers), we measured differences in plant communities between domestic animals and takhi, for species richness (higher in plots grazed by the genus *Equus* than by sheep) and for evenness (higher for takhi than sheep). Differences measured between horses and sheep are probably linked to the morphology, the physiology and behaviour in terms of preferences, selectivity, foraging time and space used by these animals. Sheep are ruminant species and are qualified as intermediate feeders, but they are mainly grazers: they eat grasses, forbs and shrubs and they are effective in selecting the tender and palatable parts of plants (Dias-Silva and Abdalla Filho, 2020; Hofmann, 1989). Their circadian rhythm is characterized by long feeding periods, followed by long ruminating and resting periods (Hofmann, 1989). They adapt their feeding habits depending on resource availability, with higher selectivity when resources are high (Dias-Silva and Abdalla Filho, 2020). On the contrary, horses are monogastric and their digestive physiology is characterized by high food intake and digesta, with longer foraging times than sheep, facilitated by high chewing efficiency (Clauss, 2013; Duncan, 2012). Horses are considered as grazers, and their diets are dominated by grasses (Chodkiewicz, 2020; Cromsigt et al., 2018; Duncan, 2012), even if they also eat forbs and shrubs. As horses eat mostly grasses, and have a higher food intake than sheep or bovids - thus being more active – they have a greater trampling impact (Larson et al., 2015), creating ideal conditions for forb development, which explains differences with the lower species-richness measured in sheep-grazed plots. Moreover, we measure higher dicotyledons percent covers in takhi-grazed plots and with slightly more for domestic horses-grazed plots. This result is corroborated by the literature, as *Equus* are known to control dominant monocotyledons (Cosyns et al., 2001) and in a more effective way than small ruminants (Catorci et al., 2012), because their diet is mostly composed of *Poacea* (Duncan, 2012). Better control of the dominant species, such as *Bromopsis erecta* in our case, can leave more space for other species to develop and also explains the higher evenness in takhi-grazed plots than in sheep-grazed plots. Horses patch forage: they exploit the heterogeneity of resources taking a few bites of a plant before walking a few steps to choose a new feeding station (Prache et al., 1998). The feeding behaviour could also intensify the local heterogeneity and explain our results with higher

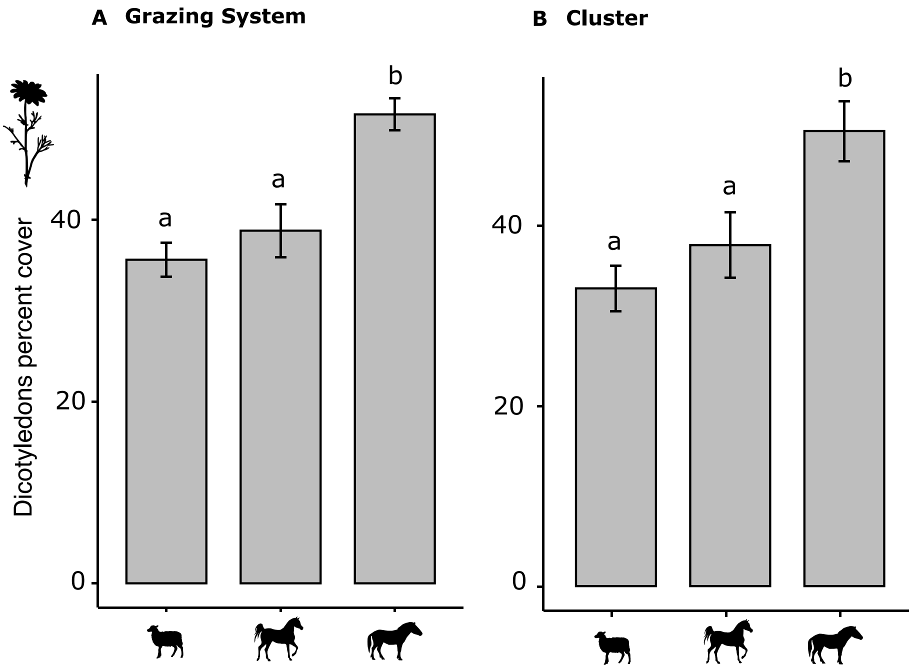


Fig. 5. Mean values ± SE of dicotyledons percent covers for each grazer at the grazing system level (A) and at the cluster level (B).

heterogeneity between takhi-grazed plots compared to sheep-grazed plots. The nuances with similar mean species richness but different plant communities between the two species of the genus *Equus*, could be explained by the following hypotheses (combined or not), needing further study to discriminate them. First, the time that domestic horses have been grazing these sites (14 years) and grazing them alone, without alternating with sheep (4 years) is shorter compared to takhi, which have been grazing their sites on their own since 1993 or 2001 depending on the enclosure. Second, takhi probably eat other species (or not) in the same proportions as domestic horses (e.g., *Lavandula angustifolia, Carlina acanthifolia* eaten by takhi, S. Carton de Grammont, conservation manager of takhi pers. comm.). These plant species contain high amounts of triterpenes also used in traditional medicine (Strzemski et al., 2016) and could be used by takhi to self-medicate (e.g., against worms). Miranda donkeys *Equus asinus,* (Couto et al., 2016)*,* goats (Amit et al., 2013) and sheep (Dias-Silva and Abdalla Filho, 2020), as well as wild animals, such as great apes (Dubost et al., 2019; Huffman, 1997; Krief, 2011) have already been observed feeding on specific plants for prophylactic or therapeutic purposes. Furthermore, here, takhi are a semi-free ranging population, thus both sexes and offspring maintain social interactions all year round, which is not the case for domestic animals. Typically foals and fillies disperse from the natal group between 1 and 2.5 years old (Monard et al., 1996) as observed in the studied population (Tatin and Carton de Grammont pers.com.). Learning and social transmission play a key role for herbivore diet selection (Bolzan et al., 2020; Provenza et al., 2003), in which individual and herd experiences combined with environmental conditions and social dynamics are important parameters (Bailey and Provenza, 2008; Duncan, 1983; King and Gurnell, 2005; Krüger and Flauger, 2008; Saïdi, 1998; Turner, 2015). Animals with experience are able to eat a large variety of forage even if they have other alternatives – with different nutrient and toxin levels – and are capable of self-regulating (Provenza, 2003), while naïve animals will only eat familiar forage. To explore these points further, it would be interesting in the future to analyse animal diets using metabarcoding (Cromsigt et al., 2018), and/or grazing behaviour (e.g., continuous bite monitoring) could be observed at different seasons because it will also vary over time following resource availability (Cosyns et al., 2001; Slivinska and Kopij, 2011).

4.2. *Effects of grazing systems on plant communities*

The constraint analysis displayed grazing system (i.e., management choices) effects on the variability of the plant communities. The value of 4.9 % of variability explained by grazers and 11.8 % by environmental variables approach values of a study looking at the influence of habitat conditions and management regimes on prealpine calcareous grasslands with 12 % explained by lithology, 5.2 % by soil moisture and 6 % explained by grazing intensity (Barbaro et al., 2004). A large part of the variability not explained by our variables (grazing systems nor environment) could be explained by other mesological variables, such as variations in microclimate, which could also explain the wide variation and heterogeneity measured between plots. A clear pattern is drawn by the constraint analysis, separating the genus *Equus* (domestic horses and takhi) from sheep on the second axis. The separation between *Equus* and sheep was expected, linked to their foraging behaviour, the grazers preferences and selectivity – as explained in 4.1. Interestingly, we also observe a separation between communities grazed by domestic animals (domestic horses and sheep) and takhi. This is confirmed by the species richness, which is higher in takhi- than in sheep- or domestic horse grazing systems. Heterogeneity in between the grazed sites is higher in takhi- than in sheep- and finally in domestic horse-grazed sites. The major differences between domestic animals and wild ones, are linked to the management system (no treatment, no induced mating choices) that allows socially natural behaviour. Free-roaming takhi, like other equids (feral horses, wild asses or zebras), form two main social groups, also called band types: i) a “family” (or harem) with usually one stallion (sometimes several (Feh, 1999)) and one to several mares with their foals up to the age of 1 to 2.5 years old (Monard et al., 1996), and ii) bachelor groups which are mostly composed of young males and old or fallen stallions (Bahloul et al., 2001; Klimov, 1988; Pereladova et al., 1999). This results in a different way of using the resources in space and in time (King and Gurnell, 2005; Linklater et al., 2000). In other studies regarding populations of Camargue horses roaming freely and takhi (on the *Causse Méjean*), feeding behaviour and feeding areas were different according to the social group, dominant ones (usually families) having preferential access to selected feeding areas (Duncan, 1983; Saïdi, 1998). On *the Causse Méjean* within the population of takhi and during spring, the stallion seems to drive its family out of areas close to bachelor groups (Saïdi, 1998; L. Tatin and S. Carton de Grammont pers. com.). When there are several families, some can cohabit in close proximity, and this behaviour can last for weeks, months or years (L. Tatin pers. Com.) inducing a local higher grazing pressure and so heterogeneity. Moreover, a diminution of the grazing activity was also measured during spring – with takhi mares' oestrus – permitting plant species to develop further and to finish their cycle (Saïdi, 1998). Another point that seems important is the choice made by domestic herd breeders to cultivate the land depressions of the plateau while they are all grazed in takhi enclosures. This choice adds small-scale heterogeneity, with more habitats and microhabitats, and induces another use of the total area because these places are usually more productive and do not have the same land-use history as the rest of the enclosures (Nicod and Salomon, 1999). A second choice is the surface available devoted to domestic horses: these enclosures are the smallest of the study - but the biggest we could find on the *Causse Méjean*. The surface could affect small-scale heterogeneity of the environmental variables and so the vegetation (Lundholm, 2009; Stein et al., 2014; Tamme et al., 2010). Furthermore, local biotic processes – such as soil micro-organism activity (Ettema and Wardle, 2002) - could also play an important role. The last point, even if stocking rates are very similar and very low – between 0.048 and 0.062 LU/ha/year – takhi have the lowest values. As has already been shown, higher grazing pressures can negatively impact species richness but it is affected differently depending on the environment (arid, humid) (Herrero-Jáuregui and Oesterheld, 2018). It is therefore difficult to directly compare stocking rates between studies but our values are in the low average stocking rate values of other farms within the *Causse Méjean* (Crosnier and Granger, 2004).

4.3. Bioindicator species

Three of the four bioindicator species of sheep-grazed sites clearly displayed by our analysis at the grazing system level and at the cluster level are *Poaceae* (*Bromopsis erecta, Festuca marginata, Koeleria valesiana*). This result underlines the tendency of *Poaceae* being more frequent in the sheep-grazed sites and is corroborated by literature, sheep showing diet preference for dicots (e.g., legumes) (Rutter, 2010). The fourth and fifth bioindicator species are: *Teucrium rouyanum* and *Thymus serpyllum*, two perennial chamaephytes belonging to genera containing secondary metabolites (Salehi et al., 2019; Stanković et al., 2012). Chamaephytes are less tolerant to trampling (contrary to annual species) (Catorci et al., 2012), and could indicate sheep grazing because this animal is less active than horses (Larson et al., 2015). *T. rouyanum* is an endemic species (autonomous amphidiploid probably between *T. aureum* and a diploid taxon close to *T. polium*) of the Causses, typical of the dry calcareous grasslands (Tison et al., 2014). Probably due to its chemical compounds, it is not appreciated by sheep, and forms ligneous vegetation islets (Puech, 1974).

A toxic (Novák, 2004) and facultative root-hemiparasitic plant (*Rhinanthus pumilus*) (Mudrák et al., 2014) is the bioindicator species found for takhi-grazed sites at both studied scales. Species from the genus *Rhinanthus* are facultative root-hemiparasitic plants occurring frequently in grassland communities (Mudrák et al., 2014). They generally prefer grasses and legumes as hosts (Cameron et al., 2006; Gibson and Watkinson, 1989). *Rhinanthus* spp. usually suppress grasses (Joshi et al., 2000) and promote forbs (Ameloot et al., 2008; Bardgett et al., 2006; Mudrák et al., 2014; Quested et al., 2005, 2003) and have a positive effect on plant biodiversity, they are thus considered as ecosystem engineers (Heer et al., 2018) and seem to be a practical tool in ecological restoration projects (Bullock and Pywell, 2005). The presence of *Rhinanthus* in takhi-grazed sites may generate a positive-feedback loop and additionally contribute to higher species richness, evenness and heterogeneity. A *Rosaceae* and perennial hemicryptophyte (*Potentilla verna*) (Tison et al., 2014) is also a bioindicator species at the grazing system scale. This species is frequently found in old grasslands, being a dominant or subdominant species (Karlík and Poschlod, 2019), it is also a calcareous grassland specialist (Harzé, 2017). The second bioindicator species highlighted by takhi grazing at the cluster scale, is a perennial hemicryptophyte and chamaephyte, typical of hill and dry grasslands (*Linum suffruticosum*) (Bernard, 2009). The third species is *Seseli montanum*, an *Apiaceae*, hemicryptophyte (Tison et al., 2014). *Apiaceae* species and some of the *Seseli* genius, are known for the chemical properties of their essential oil (Evergetis and Haroutounian, 2014; Gonçalves et al., 2012; Onder et al., 2023), and by eating it for self-medication takhi could play a role in the seeds' dispersal which could explain its presence and representativity in takhi-grazed plots.

No clear pattern is shown by our results concerning bioindicator species for sites grazed by domestic horses. However, it is interesting to see that there are three *Poaceae* again (*B. erecta, F. marginata, Helichtocloa pratensis*), and two dicotyledons, one annual species: *Bupleurum baldense* and one perennial specie *P. verna* as for takhi. The presence of *Poaceae* as a possible bioindicator species of grazing by domestic horses could be highlighting the transitional period between sheep and horse grazing. However, interestingly, in xeric habitats, annual species are considered as stress-tolerators (Madon and Médail, 1997). Its presence could be linked to the capability of annual species to colonise grassland gaps due to trampling by large herbivores.

5. Implications for conservation

The results of our study clearly show that extensive grazing (as are all three types of grazing studied here) of steppe-like grasslands is different depending on the grazer (sheep vs. horses) and the management choice (extensive grazing vs. 'as wild'). Domestic horse breeding can be a good substitute for traditional sheep breeding for plant community conservation as highlighted by our results – with only slight changes in the plant community compared to sheep. This is corroborated by scientific literature showing that horse grazing has contributed to protecting open habitats and specific plants (Bonavent et al., 2023; Fleurance et al., 2011; Köhler et al., 2016). Differences between domestic and wild horses mainly reside in the overall management and the possibility for animals to express all their natural social behaviours, a management type we named 'as wild'.

Where low intensity agricultural and breeding practices aimed at production (meat, dairy, wool, racehorses, etc.) are no longer possible or viable, or when alternative management is required, we have demonstrated that managing horse herds 'as wild' promotes biodiversity (species richness, evenness and heterogeneity) and therefore showed the benefits of (re)wilding. Here we have demonstrated that the site grazed 'as wild' are still Mediterraneo-montane steppes EUNIS habitat type (code E1.51, European Environment Agency, 2019). Rewilding with 'as wild' horses therefore contributes to the conservation of this open habitat. However, in terms of plant conservation, such management of horses changes plant communities and this should be taken into account if specific threatened species are the main focus. Further studies on plant species with high patrimonial value, other taxonomical groups and/or on functional diversity are needed to compare and test more finely the effects of horses managed 'as domestic' or 'as wild'.

Finally, socio-economic issues are of crucial concern and have not been investigated in this study. When considering managing domestic grazers 'as wild', it needs to be understood that this results in changing breeder/shepherd practices and raises the question of economic income. It could be considered as a new paradigm and might be another way to link pastoralism and biodiversity conservation but needs further studies and debate.

CRediT authorship contribution statement

Clémentine Mutillod: Conceptualization, Data curation, Formal analysis, Investigation, Methodology, Visualization, Writing – original draft, Writing – review & editing. **Elise Buisson:** Conceptualization, Formal analysis, Funding acquisition, Investigation, Methodology, Supervision, Writing – original draft, Writing – review & editing. **Laurent Tatin:** Conceptualization, Funding acquisition, Investigation, Methodology, Supervision, Writing – original draft, Writing – review & editing. **Gregory Mahy:** Conceptualization, Methodology, Writing – original draft, Writing – review & editing. **Marc Dufrêne:** Data curation, Formal analysis, Methodology, Writing – original draft. **François Mesléard:** Conceptualization, Methodology. **Thierry Dutoit:** Conceptualization, Investigation, Methodology, Project administration, Resources, Supervision, Writing – original draft, Writing – review & editing.

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.

Data availability

Data and R script supporting the findings will be available on request and in Zenodo following a 1 year embargo from the date of publication at https://zenodo.org/records/10548963, Data and R Script - Managed as wild, horses influence grassland vegetation differently than domestic herds, doi: 10.5281/zenodo.10548963.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.biocon.2024.110469.

References

Allen, V.G., Batello, C., Berretta, E.J., Hodgson, J., Kothmann, M., Li, X., McIvor, J., Milne, J., Morris, C., Peeters, A., Sanderson, M., The Forage and Grazing Terminology Committee, 2011. An international terminology for grazing lands and grazing animals. Grass and Forage Science 66, 2–28. https://doi.org/10.1111/j.1365-2494.2010.00780.x.

Allred, B.W., Fuhlendorf, S.D., Hamilton, R.G., 2011. The role of herbivores in Great Plains conservation: comparative ecology of bison and cattle. Ecosphere 2, art26. https://doi.org/10.1890/ES10-00152.1.

Ameloot, E., Verlinden, G., Boeckx, P., Verheyen, K., Hermy, M., 2008. Impact of hemiparasitic Rhinanthus angustifolius and R. Minor on nitrogen availability in grasslands. Plant and Soil 311, 255–268. https://doi.org/10.1007/s11104-008-9640-2.

Amit, M., Cohen, I., Marcovics, A., Muklada, H., Glasser, T.A., Ungar, E.D., Landau, S.Y., 2013. Self-medication with tannin-rich browse in goats infected with gastro-intestinal nematodes. Vet. Parasitol. 198, 305–311. https://doi.org/10.1016/j.vetpar.2013.09.019.

Anderson, M.J., Willis, T.J., 2003. Canonical analysis of principal coordinates: a useful method of constrained ordination for ecology. Ecology 84, 511–525. https://doi.org/10.1890/0012-9658(2003)084[0511:CAOPCA]2.0.CO;2.

Arnold, G.W., 1984. Comparison of the time budgets and circadian patterns of maintenance activities in sheep, cattle and horses grouped together. Applied Animal Behaviour Science 13, 19–30. https://doi.org/10.1016/0168-1591(84)90048-0.

Bahloul, K., Pereladova, O.B., Soldatova, N., Fisenko, G., Sidorenko, E., Sempéré, A.J., 2001. Social organization and dispersion of introduced kulans (Equus hemionus kulan) and Przewalski horses (Equus przewalski) in the Bukhara reserve, Uzbekistan. J. Arid Environ. 47, 309–323. https://doi.org/10.1006/jare.2000.0714.

Bailey, D.W., Provenza, F.D., 2008. Mechanisms determining large-herbivore distribution. In: Prins, H.H.T., Van Langevelde, F. (Eds.), Resource Ecology, Wageningen UR Frontis Series. Springer, Netherlands, Dordrecht, pp. 7–28. https://doi.org/10.1007/978-1-4020-6850-8_2.

Bakker, E.S., Gill, J.L., Johnson, C.N., Vera, F.W.M., Sandom, C.J., Asner, G.P., Svenning, J.-C., 2016. Combining paleo-data and modern exclosure experiments to assess the impact of megafauna extinctions on woody vegetation. Proc. Natl. Acad. Sci. 113, 847–855. https://doi.org/10.1073/pnas.1502545112.

Barbaro, L., Dutoit, T., Anthelme, F., Corcket, E., 2004. Respective influence of habitat conditions and management regimes on prealpine calcareous grasslands. J. Environ. Manage. 72, 261–275. https://doi.org/10.1016/j.jenvman.2004.05.006.

Bardgett, R.D., Smith, R.S., Shiel, R.S., Peacock, S., Simkin, J.M., Quirk, H., Hobbs, P.J., 2006. Parasitic plants indirectly regulate below-ground properties in grassland ecosystems. Nature 439, 969–972. https://doi.org/10.1038/nature04197.

Bernard, C., 2009. Petite Flore portative des Causses (Bulletin de la Société Botanique du Centre-Ouest. ed).

Blondel, J., 2006. The 'design' of Mediterranean landscapes: a millennial story of humans and ecological systems during the historic period. Hum. Ecol. 34, 713–729. https://doi.org/10.1007/s10745-006-9030-4.

Bolzan, A.M.S., Bonnet, O.J.F., Wallau, M.O., Basso, C., Neves, A.P., Carvalho, P.C. de F., 2020. Foraging behavior development of foals in natural grassland. Rangel. Ecol. Manage. 73, 243–251. https://doi.org/10.1016/j.rama.2019.10.011.

Bonavent, C., Olsen, K., Ejrnæs, R., Fløjgaard, C., Hansen, M.D.D., Normand, S., Svenning, J.-C., Bruun, H.H., 2023. Grazing by semi-feral cattle and horses supports plant species richness and uniqueness in grasslands. Applied Vegetation Science 26, e12718. https://doi.org/10.1111/avsc.12718.

Bond, W.J., 2021. Out of the shadows: ecology of open ecosystems. Plant Ecology & Diversity 14, 205–222. https://doi.org/10.1080/17550874.2022.2034065.

Boyd, L.E., 1988. Time budgets of adult Przewalski horses: effects of sex, reproductive status and enclosure. Applied Animal Behaviour Science, Behavior of Przewalski horses 21, 19–39. https://doi.org/10.1016/0168-1591(88)90099-8.

Bullock, J.M., Pywell, R.F., 2005. Rhinanthus: a tool for restoring diverse grassland? Folia Geobot. 40, 273–288. https://doi.org/10.1007/BF02803240.

Cameron, D.D., Coats, A.M., Seel, W.E., 2006. Differential resistance among host and non-host species underlies the variable success of the hemi-parasitic plant Rhinanthus minor. Ann. Bot. 98, 1289–1299. https://doi.org/10.1093/aob/mcl218.

Caplat, P., Lepart, J., Marty, P., 2006. Landscape patterns and agriculture: modelling the long-term effects of human practices on Pinus sylvestris spatial dynamics (Causse Mejean, France). Landsc. Ecol. 21, 657–670. https://doi.org/10.1007/s10980-005-4430-1.

Carver, S., Convery, I., Hawkins, S., Beyers, R., Eagle, A., Kun, Z., Van Maanen, E., Cao, Y., Fisher, M., Edwards, S.R., Nelson, C., Gann, G.D., Shurter, S., Aguilar, K., Andrade, A., Ripple, W.J., Davis, J., Sinclair, A., Bekoff, M., Noss, R., Foreman, D., Pettersson, H., Root-Bernstein, M., Svenning, J., Taylor, P., Wynne-Jones, S., Featherstone, A.W., Fløjgaard, C., Stanley-Price, M., Navarro, L.M., Aykroyd, T., Parfitt, A., Soulé, M., 2021. Guiding principles for rewilding. Conserv. Biol. cobi.13730 https://doi.org/10.1111/cobi.13730.

Catorci, A., Gatti, R., Cesaretti, S., 2012. Effect of sheep and horse grazing on species and functional composition of sub-Mediterranean grasslands. Applied Vegetation Science 15, 459–469. https://doi.org/10.1111/j.1654-109X.2012.01197.x.

Ceaușu, S., Hofmann, M., Navarro, L.M., Carver, S., Verburg, P.H., Pereira, H.M., 2015. Mapping opportunities and challenges for rewilding in Europe. Conserv. Biol. 29, 1017–1027. https://doi.org/10.1111/cobi.12533.

Chodkiewicz, A., 2020. Advantages and disadvantages of polish primitive horse grazing on valuable nature areas – a review. Global Ecology and Conservation 21, e00879. https://doi.org/10.1016/j.gecco.2019.e00879.

Clauss, M., 2013. Digestive physiology and feeding behaviour of equids – a comparative approach. Horse Health Nutrition-European Equine Health Nutrition Congress 25–33. https://doi.org/10.5167/UZH-76378.

Cosyns, E., Degezelle, T., Demeulenaere, E., Hoffmann, M., 2001. Feeding ecology of Konik horses and donkeys in Belgian coastal dunes and its implications for nature management. Belg. J. Zool. 121, 111–118.

Couto, M., Santos, A.S., Laborda, J., Nóvoa, M., Ferreira, L.M., Madeira de Carvalho, L. M., 2016. Grazing behaviour of Miranda donkeys in a natural mountain pasture and parasitic level changes. Livestock Science, The impact of nutrition on metabolism in equines 186, 16–21. https://doi.org/10.1016/j.livsci.2016.01.005.

Couvreur, M., Christiaen, B., Verheyen, K., Hermy, M., 2004. Large herbivores as mobile links between isolated nature reserves through adhesive seed dispersal. Applied Vegetation Science 7, 229–236. https://doi.org/10.1111/j.1654-109X.2004.tb00614.x.

Cromsigt, J.P.G.M., Kemp, Y.J.M., Rodriguez, E., Kivit, H., 2018. Rewilding Europe's large grazer community: how functionally diverse are the diets of European bison, cattle, and horses? Restor. Ecol. 26, 891–899. https://doi.org/10.1111/rec.12661.

Crosnier, C., Granger, C., 2004. Le parc national des Cévennes: la population rurale à l'épreuve de la gestion des milieux ouverts. Approches alternatives, Environnement et sociétés rurales en mutation.

Dengler, J., Janišová, M., Török, P., Wellstein, C., 2014. Biodiversity of Palaearctic grasslands: a synthesis. Agriculture, Ecosystems & Environment, Biodiversity of

Palaearctic grasslands: processes, patterns and conservation 182, 1–14. https://doi.org/10.1016/j.agee.2013.12.015.

Dias-Silva, T.P., Abdalla Filho, A.L., 2020. Sheep and goat feeding behavior profile in grazing systems. Acta Sci. Anim. Sci. 43 https://doi.org/10.4025/actascianimsci.v43i1.51265.

Doughty, C.E., Faurby, S., Svenning, J.-C., 2016. The impact of the megafauna extinctions on savanna woody cover in South America. Ecography 39, 213–222. https://doi.org/10.1111/ecog.01593.

Dubost, J.-M., Lamxay, V., Krief, S., Falshaw, M., Manithip, C., Deharo, E., 2019. From plant selection by elephants to human and veterinary pharmacopeia of mahouts in Laos. J. Ethnopharmacol. 244, 112157 https://doi.org/10.1016/j.jep.2019.112157.

Dufrêne, M., Legendre, P., 1997. Species assemblages and indicator species: the need for a flexible asymmetrical approach. Ecol. Monogr. 67, 345–366.

Duncan, P., 1983. Determinants of the use of habitat by horses in a Mediterranean wetland. J. Anim. Ecol. 52, 93–109. https://doi.org/10.2307/4590.

Duncan, P., 1991. Horses and Grasses: The Nutritional Ecology of Equids and their Impact on the Camargue., Ecological Studies. Springer Verlag.

Duncan, P., 2012. Horses and Grasses: The Nutritional Ecology of Equids and their Impact on the Camargue. Springer Science & Business Media.

Ettema, C.H., Wardle, D.A., 2002. Spatial soil ecology. Trends Ecol. Evol. 17, 177–183. https://doi.org/10.1016/S0169-5347(02)02496-5.

European Environment Agency, 2002. Natura 2000 site (code FR9101379) - accessed September 2023. https://eunis.eea.europa.eu/sites/FR9101379.

European Environment Agency, 2019. EUNIS habitat classification 2012 amended 2019 - accessed September 2023. https://eunis.eea.europa.eu/habitats/993.

Evergetis, E., Haroutounian, S.A., 2014. Exploitation of apiaceae family plants as valuable renewable source of essential oils containing crops for the production of fine chemicals. Industrial Crops and Products 54, 70–77. https://doi.org/10.1016/j.indcrop.2014.01.009.

Feh, C., 1999. Alliances and reproductive success in Camargue stallions. Anim. Behav. 57, 705–713. https://doi.org/10.1006/anbe.1998.1009.

Fleurance, G., Duncan, P., Farruggia, A., Dumont, B., Lecomte, T., 2011. Impact du pâturage équin sur la diversité floristique et faunistique des milieux pâturés 12.

Fonderflick, J., Caplat, P., Lovaty, F., Thévenot, M., Prodon, R., 2010a. Avifauna trends following changes in a Mediterranean upland pastoral system. Agr Ecosyst Environ 137, 337–347. https://doi.org/10.1016/j.agee.2010.03.004.

Fonderflick, J., Lepart, J., Caplat, P., Debussche, M., Marty, P., 2010b. Managing agricultural change for biodiversity conservation in a Mediterranean upland. Biol. Conserv. 143, 737–746. https://doi.org/10.1016/j.biocon.2009.12.014.

Forbes, E.S., Cushman, J.H., Burkepile, D.E., Young, T.P., Klope, M., Young, H.S., 2019. Synthesizing the effects of large, wild herbivore exclusion on ecosystem function. Funct. Ecol. 33, 1597–1610. https://doi.org/10.1111/1365-2435.13376.

Fraser, M.D., Vallin, H.E., Roberts, B.P., 2022. Animal board invited review: grassland-based livestock farming and biodiversity. Animal 16, 100671. https://doi.org/10.1016/j.animal.2022.100671.

Galetti, M., Moleón, M., Jordano, P., Pires, M.M., Guimarães Jr., P.R., Pape, T., Nichols, E., Hansen, D., Olesen, J.M., Munk, M., de Mattos, J.S., Schweiger, A.H., Owen-Smith, N., Johnson, C.N., Marquis, R.J., Svenning, J.-C., 2018. Ecological and evolutionary legacy of megafauna extinctions. Biol. Rev. 93, 845–862. https://doi.org/10.1111/brv.12374.

Gargominy, O., Tercerie, S., Ramage, T., Dupont, P., Daskiewicz, P., Poncet, L., 2021. TAXREF v15, référentiel taxonomique pour la France: méthodologie, mise en œuvre et diffusion. In: (Rapport UMS PatriNat (OFB-CNRS-MNHN).). Muséum national d'Histoire naturelle, Paris.

Gibson, C.C., Watkinson, A.R., 1989. The host range and selectivity of a parasitic plant: Rhinanthus minor L. Oecologia 78, 401–406.

Gonçalves, M.J., Tavares, A.C., Cavaleiro, C., Cruz, M.T., Lopes, M.C., Canhoto, J., Salgueiro, L., 2012. Composition, antifungal activity and cytotoxicity of the essential oils of Seseli tortuosum L. and Seseli montanum subsp. peixotoanum (Samp.) M. Laínz from Portugal. Ind. Crop. Prod. 39, 204–209. https://doi.org/10.1016/j.indcrop.2012.02.025.

Grant, S.A., Suckling, D.E., Smith, H.K., Torvell, L., Forbes, T.D.A., Hodgson, J., 1985. Comparative studies of diet selection by sheep and cattle: the hill grasslands. J. Ecol. 73, 987–1004. https://doi.org/10.2307/2260163.

Harzé, M., 2017. Plant Traits Variability within and among Populations in the Context of Calcareous Grassland Restoration (Variabilité de traits au sein et entre populations de plantes dans un contexte de restauration de pelouses calcicoles).

Heer, N., Klimmek, F., Zwahlen, C., Fischer, M., Hölzel, N., Klaus, V.H., Kleinebecker, T., Prati, D., Boch, S., 2018. Hemiparasite-density effects on grassland plant diversity, composition and biomass. Perspectives in Plant Ecology, Evolution and Systematics 32, 22–29. https://doi.org/10.1016/j.ppees.2018.01.004.

Hejcman, M., Hejcmanová, P., Pavlů, V., Beneš, J., 2013. Origin and history of grasslands in Central Europe – a review. Grass Forage Sci. 68, 345–363. https://doi.org/10.1111/gfs.12066.

Herrero-Jáuregui, C., Oesterheld, M., 2018. Effects of grazing intensity on plant richness and diversity: a meta-analysis. Oikos 127, 757–766. https://doi.org/10.1111/oik.04893.

Hobbs, N.T., 1996. Modification of ecosystems by ungulates. J. Wildl. Manag. 60, 695–713. https://doi.org/10.2307/3802368.

Hofmann, R.R., 1989. Evolutionary steps of ecophysiological adaptation and diversification of ruminants: a comparative view of their digestive system. Oecologia 78, 443–457. https://doi.org/10.1007/BF00378733.

Huffman, M.A., 1997. Current evidence for self-medication in primates: a multidisciplinary perspective. Am. J. Phys. Anthropol. 104, 171–200. https://doi.org/10.1002/(SICI)1096-8644(1997)25+<171::AID-AJPA7>3.0.CO;2-7.

Institut National de l'Information Géographique et Forestière, 2022. RGE ALTI.

Isselstein, J., Jeangros, B., Pavlu, V., 2005. Agronomic aspects of biodiversity targeted management of temperate grasslands in Europe – a review. Agron. Res. 3, 139–151.

Johansen, L., Westin, A., Wehn, S., Iuga, A., Ivascu, C.M., Kallioniemi, E., Lennartsson, T., 2019. Traditional semi-natural grassland management with heterogeneous mowing times enhances flower resources for pollinators in agricultural landscapes. Global Ecology and Conservation 18, e00619. https://doi.org/10.1016/j.gecco.2019.e00619.

Joshi, J., Matthies, D., Schmid, B., 2000. Root hemiparasites and plant diversity in experimental grassland communities. J. Ecol. 88, 634–644. https://doi.org/10.1046/j.1365-2745.2000.00487.x.

Karlík, P., Poschlod, P., 2019. Identifying plant and environmental indicators of ancient and recent calcareous grasslands. Ecol. Indic. 104, 405–421. https://doi.org/10.1016/j.ecolind.2019.05.016.

King, S.R.B., 2005. Extinct in the wild to endangered: the history of Przewalski's horse (Equus ferus przewalskii) and its future conservation. Mong. J. Biol. Sci. 3 https://doi.org/10.22353/mjbs.2005.03.11.

King, S.R.B., Gurnell, J., 2005. Habitat use and spatial dynamics of takhi introduced to Hustai National Park, Mongolia. Biol. Conserv. 124, 277–290. https://doi.org/10.1016/j.biocon.2005.01.034.

Klimov, V.V., 1988. Spatial-ethological organization of the herd of Przewalski horses (Equus przewalskii) in Askania-Nova. Applied Animal Behaviour Science, Behavior of Przewalski horses 21, 99–115. https://doi.org/10.1016/0168-1591(88)90103-7.

Kohl, M.T., Krausman, P.R., Kunkel, K., Williams, D.M., 2013. Bison versus cattle: are they ecologically synonymous? Rangel. Ecol. Manage. 66, 721–731. https://doi.org/10.2111/REM-D-12-00113.1.

Köhler, M., Hiller, G., Tischew, S., 2016. Year-round horse grazing supports typical vascular plant species, orchids and rare bird communities in a dry calcareous grassland. Agr Ecosyst Environ 234, 48–57. https://doi.org/10.1016/j.agee.2016.03.020.

Krief, S., 2011. Do animals use natural properties of plants to self-medicate?. In: Applied Equine Nutrition and Training. Wageningen Academic Publishers, Wageningen, pp. 159–170. https://doi.org/10.3920/978-90-8686-740-0_10.

Krüger, K., Flauger, B., 2008. Social feeding decisions in horses (Equus caballus). Behav. Processes 78, 76–83. https://doi.org/10.1016/j.beproc.2008.01.009.

Larson, S., Barry, S., Bush, L., 2015. Cattle, Sheep, Goats, and Horses: What's the Difference for Working Rangelands? https://doi.org/10.3733/ucanr.8524.

Lepart, J., Marty, P., Rousset, O., 2000. Les conceptions normatives du paysage. Le cas des Grands Causses. Nature Sciences Sociétés 8, 15–25. https://doi.org/10.1016/S1240-1307(01)80003-0.

Linklater, W.L., Cameron, E.Z., Stafford, K.J., Veltman, C.J., 2000. Social and spatial structure and range use by Kaimanawa wild horses (Equus caballus: Equidae). N. Z. J. Ecol. 24, 139–152.

Lundholm, J.T., 2009. Plant species diversity and environmental heterogeneity: spatial scale and competing hypotheses. J. Veg. Sci. 20, 377–391. https://doi.org/10.1111/j.1654-1103.2009.05577.x.

Madon, O., Médail, F., 1997. The ecological significance of annuals on a Mediterranean grassland (Mt Ventoux, France). Plant Ecol. 129, 189–199. https://doi.org/10.1023/A:1009759730000.

Malhi, Y., Doughty, C.E., Galetti, M., Smith, F.A., Svenning, J.-C., Terborgh, J.W., 2016. Megafauna and ecosystem function from the Pleistocene to the Anthropocene. Proc. Natl. Acad. Sci. 113, 838–846. https://doi.org/10.1073/pnas.1502540113.

Marty, P., Pelaquier, E., Jaudon, B., Lepart, J., 2003. Spontaneous reforestation in a peri-Mediterranean landscape: history of agricultural systems and dynamics of woody species. Dynamiques des paysages végétaux et marqueurs écologiques/Vegetal Landscapes and Ecological Indicators 179–186.

Matches, A.G., 1992. Plant response to grazing: a review. J. Prod. Agric. 5, 1–7. https://doi.org/10.2134/jpa1992.0001.

McGeoch, M.A., Van Rensburg, B.J., Botes, A., 2002. The verification and application of bioindicators: a case study of dung beetles in a savanna ecosystem. J. Appl. Ecol. 39, 661–672. https://doi.org/10.1046/j.1365-2664.2002.00743.x.

Milligan, G.W., Cooper, M.C., 1985. An examination of procedures for determining the number of clusters in a data set. Psychometrika 50, 159–179. https://doi.org/10.1007/BF02294245.

Monard, A.-M., Duncan, P., Boy, V., 1996. The proximate mechanisms of Natal dispersal in female horses. Behaviour 133, 1095–1124. https://doi.org/10.1163/156853996X00611.

Mudrák, O., Mládek, J., Blažek, P., Lepš, J., Doležal, J., Nekvapilová, E., Těšitel, J., 2014. Establishment of hemiparasitic Rhinanthus spp. in grassland restoration: lessons learned from sowing experiments. Appl. Veg. Sci. 17, 274–287. https://doi.org/10.1111/avsc.12073.

Mutillod, C., Buisson, É., Mahy, G., Jaunatre, R., Bullock, J.M., Tatin, L., Dutoit, T.. Ecological restoration and rewilding: two approaches with complementary goals? Biol. Rev. doi:https://doi.org/10.1111/brv.13046, (in press).

Nicod, J., Salomon, J.-N., 1999. Impacts of agricultural transformation on the principal karstic regions of France. IJS 28, 15–31. https://doi.org/10.5038/1827-806X.28.1.2.

Novák, J., 2004. Evaluation of grassland quality. Ekologia(Bratislava)/Ecology (Bratislava) 23, 27–143.

Nugent, D.T., Baker-Gabb, D.J., Leonard, S.W.J., Morgan, J.W., 2022. Livestock grazing to maintain habitat of a critically endangered grassland bird: is grazer species important? Ecol. Appl. 32, e2587 https://doi.org/10.1002/eap.2587.

Olff, H., Ritchie, M.E., 1998. Effects of herbivores on grassland plant diversity. Trends Ecol. Evol. 13, 261–265. https://doi.org/10.1016/S0169-5347(98)01364-0.

Onder, A., Nahar, L., Cinar, A.S., Sarker, S.D., 2023. The genus Seseli L.: a comprehensive review on traditional uses, phytochemistry, and pharmacological properties. Journal of Herbal Medicine 38, 100625. https://doi.org/10.1016/j.hermed.2023.100625.

O'Rourke, E., 1999. The causse mejan: changing relationships between agriculture, environment and society within a French national park. Landsc. Res. 24, 141–165. https://doi.org/10.1080/01426399908706556.

Osty, P.-L., Lardon, S., Lhuillier, C., 1994. Systèmes techniques agricoles et qualité de l'organisation spatiale. Études et Recherches sur les Systèmes Agraires et le Développement 211–218.

Owen-Smith, N., 1987. Pleistocene extinctions: the pivotal role of megaherbivores. Paleobiology 13, 351–362. https://doi.org/10.1017/S0094837300008927.

Owen-Smith, N., 1989. Megafaunal extinctions: the conservation message from 11,000 years B.P. Conserv. Biol. 3, 405–412. https://doi.org/10.1111/j.1523-1739.1989.tb00246.x.

Owen-Smith, R.N., 1988. Megaherbivores: The Influence of Very Large Body Size on Ecology. Cambridge University Press.

Pereladova, O.B., Sempéeré, A.J., Soldatova, N.V., Dutov, V.U., Fisenko, G., Flint, V.E., 1999. Przewalski's horse—adaptation to semi-wild life in desert conditions. Oryx 33, 47–58. https://doi.org/10.1046/j.1365-3008.1999.00038.x.

Petermann, J.S., Buzhdygan, O.Y., 2021. Grassland biodiversity. Curr. Biol. 31, R1195–R1201. https://doi.org/10.1016/j.cub.2021.06.060.

Pettorelli, N., Durant, S.M., du Toit, J.T., 2019. Rewilding: a captivating, controversial, twenty-first-century concept to address ecological degradation in a changing world. In: Rewilding, pp. 1–11.

Prache, S., Gordon, I.J., Rook, A.J., 1998. Foraging behaviour and diet selection in domestic herbivores. Ann. Zootech. 47, 335–345. https://doi.org/10.1051/animres:19980502.

Provenza, F.D., 2003. Twenty-five years of paradox in plant-herbivore interactions and" sustainable" grazing management. Rangelands Archives 25, 4–15.

Provenza, F.D., Villalba, J.J., Dziba, L.E., Atwood, S.B., Banner, R.E., 2003. Linking herbivore experience, varied diets, and plant biochemical diversity. Small Ruminant Research, Advanced research on nutrition of sheep and goats, with special reference to pasture and rangeland use 49, 257–274. https://doi.org/10.1016/S0921-4488(03)00143-3.

Puech, S., 1974. Polymorphisme, fertilité et ploïdie dans les populations caussenardes de Teucrium rouyanum Coste et Soulié. Bulletin de la Société Botanique de France 121, 23–34. https://doi.org/10.1080/00378941.1974.10839229.

Quested, H.M., Press, M.C., Callaghan, T.V., 2003. Litter of the hemiparasite Bartsia alpina enhances plant growth: evidence for a functional role in nutrient cycling. Oecologia 135, 606–614. https://doi.org/10.1007/s00442-003-1225-4.

Quested, H.M., Callaghan, T.V., Cornelissen, J.H.C., Press, M.C., 2005. The impact of Hemiparasitic plant litter on decomposition: direct, seasonal and litter mixing effects. J. Ecol. 93, 87–98.

R Core Team, 2022. A language and environment for statistical computing.

Robin, V., Nelle, O., Talon, B., Poschlod, P., Schwartz, D., Bal, M.-C., Allée, P., Vernet, J.-L., Dutoit, T., 2018. A comparative review of soil charcoal data: spatiotemporal patterns of origin and long-term dynamics of Western European nutrient-poor grasslands. The Holocene 28, 1313–1324. https://doi.org/10.1177/0959683618771496.

Roche, H., Tatin, L., 2021. Réintroduction du cheval de Przewalski: translocation d'une structure sociale. Faune Sauvage 30–31.

Rook, A.J., Dumont, B., Isselstein, J., Osoro, K., WallisDeVries, M.F., Parente, G., Mills, J., 2004. Matching type of livestock to desired biodiversity outcomes in pastures – a review. Biol. Conserv. 119, 137–150. https://doi.org/10.1016/j.biocon.2003.11.010.

Ruiz-Mirazo, J., Robles, A.B., González-Rebollar, J.L., 2011. Two-year evaluation of fuelbreaks grazed by livestock in the wildfire prevention program in Andalusia (Spain). Agr Ecosyst Environ 141, 13–22. https://doi.org/10.1016/j.agee.2011.02.002.

Rupprecht, D., Jedrzejek, B., Hölzel, N., 2022. Fallow deer foraging alone does not preserve the vegetation of traditionally sheep-grazed calcareous grasslands. J. Appl. Ecol. 59, 2520–2530. https://doi.org/10.1111/1365-2664.14253.

Rutter, S.M., 2006. Diet preference for grass and legumes in free-ranging domestic sheep and cattle: current theory and future application. Appl. Anim. Behav. Sci. 97, 17–35. https://doi.org/10.1016/j.applanim.2005.11.016.

Rutter, S.M., 2010. Review: grazing preferences in sheep and cattle: implications for production, the environment and animal welfare. Can. J. Anim. Sci. 90, 285–293. https://doi.org/10.4141/CJAS09119.

Saavedra, D., Fernández, N., Svenning, J.-C., 2023. Addressing challenges for large-scale trophic rewilding. J. Nat. Conserv. 73, 126382 https://doi.org/10.1016/j.jnc.2023.126382.

Saïdi, M.S., 1998. Evolution d'une pelouse post-ovine sous l'effet du pâturage du cheval de Przewalski (Causse Méjan-Lozère) (Doctoral Dissertation). Université de Montpellier 3.

Saïdi, S., Mende, C., 1999. L'utilisation des pelouses caussenardes par le cheval de Przewalski. Mappe Monde 53, 7.

Salehi, B., Abu-Darwish, M.S., Tarawneh, A.H., Cabral, C., Gadetskaya, A.V., Salgueiro, L., Hosseinabadi, T., Rajabi, S., Chanda, W., Sharifi-Rad, M., Mulaudzi, R. B., Ayatollahi, S.A., Kobarfard, F., Arserim-Uçar, D.K., Sharifi-Rad, J., Ata, A., Baghalpour, N., Contreras, M. del M., 2019. Thymus spp. plants - food applications and phytopharmacy properties. Trends Food Sci. Technol. 85, 287–306. https://doi.org/10.1016/j.tifs.2019.01.020.

SAS Institute Inc, 2014. SAS/STAT® 13.2 User's Guide. SAS Institute Inc., Cary, NC.

Sawchik, J., Dufrêne, M., Lebrun, P., 2005. Distribution patterns and indicator species of butterfly assemblages of wet meadows in southern Belgium. Belgium Journal of Zoology 1, 43–52.

Schmitz, A., Isselstein, J., 2020. Effect of grazing system on grassland plant species richness and vegetation characteristics: comparing horse and cattle grazing. Sustainability 12, 3300. https://doi.org/10.3390/su12083300.

Slivinska, K., Kopij, G., 2011. Diet of the Przewalski's horse Equus przewalskii in the Chernobyl exclusion zone. Pol. J. Ecol. 59, 841–847.

Smith, F.A., Elliott Smith, E.A., Hedberg, C.P., Lyons, S.K., Pardi, M.I., Tomé, C.P., 2023. After the mammoths: the ecological legacy of late Pleistocene megafauna extinctions. Camb. prisms Extinction 1–55. https://doi.org/10.1017/ext.2023.6.

Stahlheber, K.A., D'Antonio, C.M., 2013. Using livestock to manage plant composition: a meta-analysis of grazing in California Mediterranean grasslands. Biol. Conserv. 157, 300–308. https://doi.org/10.1016/j.biocon.2012.09.008.

Stanković, M., Stefanović, O., Čomić, L., Topuzović, M., Radojević, I., Solujić, S., 2012. Antimicrobial activity, total phenolic content and flavonoid concentrations of Teucrium species. Open Life Sciences 7, 664–671. https://doi.org/10.2478/s11535-012-0048-x.

Stein, A., Gerstner, K., Kreft, H., 2014. Environmental heterogeneity as a universal driver of species richness across taxa, biomes and spatial scales. Ecol. Lett. 17, 866–880. https://doi.org/10.1111/ele.12277.

Strzemski, M., Wójciak-Kosior, M., Sowa, I., Rutkowska, E., Szwerc, W., Kocjan, R., Latalski, M., 2016. Carlina species as a new source of bioactive pentacyclic triterpenes. Industrial Crops and Products 94, 498–504. https://doi.org/10.1016/j.indcrop.2016.09.025.

Svenning, J.-C., 2020. Rewilding should be central to global restoration efforts. One Earth 3, 657–660. https://doi.org/10.1016/j.oneear.2020.11.014.

Svenning, J.-C., Pedersen, P.B.M., Donlan, C.J., Ejrnæs, R., Faurby, S., Galetti, M., Hansen, D.M., Sandel, B., Sandom, C.J., Terborgh, J.W., Vera, F.W.M., 2016. Science for a wilder Anthropocene: synthesis and future directions for trophic rewilding research. Proc. Natl. Acad. Sci. U. S. A. 113, 898–906. https://doi.org/10.1073/pnas.1502556112.

Tälle, M., Deák, B., Poschlod, P., Valkó, O., Westerberg, L., Milberg, P., 2016. Grazing vs. mowing: a meta-analysis of biodiversity benefits for grassland management. Agr Ecosyst Environ 222, 200–212. https://doi.org/10.1016/j.agee.2016.02.008.

Tamme, R., Hiiesalu, I., Laanisto, L., Szava-Kovats, R., Pärtel, M., 2010. Environmental heterogeneity, species diversity and co-existence at different spatial scales. J. Veg. Sci. 21, 796–801. https://doi.org/10.1111/j.1654-1103.2010.01185.x.

Tatin, L., King, S.R.B., Munkhtuya, B., Hewison, A.J.M., Feh, C., 2009. Demography of a socially natural herd of Przewalski's horses: an example of a small, closed population. J. Zool. 277, 134–140. https://doi.org/10.1111/j.1469-7998.2008.00520.x.

Tison, J.M., Jauzein, P., Michaud, H., 2014. Flore de la France méditerranéenne continentale. Naturalia publications, Turriers.

Turghan, M.A., Jiang, Z., Niu, Z., 2022. An update on status and conservation of the Przewalski's horse (Equus ferus przewalskii): captive breeding and reintroduction projects. Animals 12, 3158. https://doi.org/10.3390/ani12223158.

Turner, J.W., 2015. Environmental influences on movements and distribution of a wild horse (Equus caballus) population in western Nevada, USA: a 25-year study. J. Nat. Hist. 49, 2437–2464. https://doi.org/10.1080/00222933.2015.1024778.

UN, 2019. Resolution adopted by the General Assembly on 1 March 2019.

van der Plas, F., Howison, R.A., Mpanza, N., Cromsigt, J.P.G.M., Olff, H., 2016. Different-sized grazers have distinctive effects on plant functional composition of an African savannah. J. Ecol. 104, 864–875. https://doi.org/10.1111/1365-2745.12549.

Van Dierendonck, M.C., Wallis de Vries, M.F., 1996. Ungulate reintroductions: experiences with the Takhi or Przewalski horse (Equus ferus przewalskii) in Mongolia. Conserv. Biol. 10, 728–740. https://doi.org/10.1046/j.1523-1739.1996.10030728.x.

van Klink, R., van der Plas, F., van Noordwijk, C.G.E. (Toos), WallisDeVries, M.F., Olff, H., 2015. Effects of large herbivores on grassland arthropod diversity. Biol. Rev. 90, 347–366. https://doi.org/10.1111/brv.12113.

Van Wieren, S.E., 1995. The potential role of large herbivores in nature conservation and extensive land use in Europe. Biol. J. Linn. Soc. 56, 11–23. https://doi.org/10.1111/j.1095-8312.1995.tb01114.x.

Van Wieren, S.E., Bakker, J.P., 1998. Grazing for conservation in the twenty-first century. In: WallisDeVries, M.F., Van Wieren, S.E., Bakker, J.P. (Eds.), Grazing and Conservation Management. Springer, Netherlands, Dordrecht, pp. 349–363. https://doi.org/10.1007/978-94-011-4391-2_11. Conservation Biology Series.

Veblen, K.E., Young, T.P., 2010. Contrasting effects of cattle and wildlife on the vegetation development of a savanna landscape mosaic. J. Ecol. 98, 993–1001. https://doi.org/10.1111/j.1365-2745.2010.01705.x.

Veblen, K.E., Porensky, L.M., Riginos, C., Young, T.P., 2016. Are cattle surrogate wildlife? Savanna plant community composition explained by total herbivory more than herbivore type. Ecol. Appl. 26, 1610–1623. https://doi.org/10.1890/15-1367.1.

Vera, F.W.M., 2000. Grazing Ecology and Forest History. New York, NY, CABI Pub, Wallingford, Oxon.

Vera, F.W.M., Bakker, E.S., Olff, H., 2006. Large herbivores: Missing partners of western European light-demanding tree and shrub species? In: Danell, K., Bergstrom, R., Duncan, P., Pastor, J. (Eds.), Large Herbivore Ecology, Ecosystem Dynamics and Conservation. Cambridge University Press, Cambridge, pp. 203–231. https://doi.org/10.1017/CBO9780511617461.009.

Weigl, P.D., Knowles, T.W., 2014. Temperate mountain grasslands: a climate-herbivore hypothesis for origins and persistence. Biol. Rev. 89, 466–476. https://doi.org/10.1111/brv.12063.

White, R.P., Murray, S., Rohweder, M., 2000. Pilot Analysis of Global Ecosystems Grassland Ecosystems.

Wrage, N., Strodthoff, J., Cuchillo, H.M., Isselstein, J., Kayser, M., 2011. Phytodiversity of temperate permanent grasslands: ecosystem services for agriculture and livestock management for diversity conservation. Biodivers. Conserv. 20, 3317–3339. https://doi.org/10.1007/s10531-011-0145-6.

Zimmermann, W., 2005. Przewalski's horses on the track to reintroduction-various projects compared. Zeitschrift des Kölner Zoo 183_209.