Journal of Environmental Management 391 (2025) 126378

Contents lists available at ScienceDirect

Journal of Environmental Management

journal homepage: www.elsevier.com/locate/jenvman

Research article

Plant trait responses to herbivore type managed as domestic or as wild

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ARTICLE INFO

Keywords:
grazing
herbaceous plant community
intraspecific variability
Przewalski horses
sheep
domestic horses

ABSTRACT

The urgency of restoring ecosystems over vast areas has placed rewilding using wild herbivores at the forefront. However, few scientific studies address its effects on biodiversity and ecosystem functioning compared to more traditional conservation interventions with domestic herbivores. *Equus ferus przewalskii* horses introduced 30 years ago in the National Park of Cévennes, France - as a step of a conservation program of the species for its reintroduction in Mongolia - now occur as a semi-wild horse population, socially natural (i.e., management is based on natural selection). This introduction allowed us to compare this management system ('as wild') with other breeding systems: domestic sheep or domestic horses. Rewilding projects especially focus on the restoration of ecological functions, we therefore sought to find out if there are differences in the functional traits of the vegetation depending on the grazer and its management (domestic *vs* 'as wild') with the aim to generalize our results to other rewilding projects. Two levels of organization were tested (1) plant communities – using the TRY database and botanical surveys and (2) plant populations – by selecting four indicator species with traits measured *in situ*. Our results show that at equivalent grazing pressure, domestic horses or 'as wild' horses preserve the same plant functional types as in the traditional reference ecosystem grazed by sheep. Whatever the grazer and its management, grassland plant communities are characterized and dominated by perennial polycarpic plants, with oligotrophic to mesotrophic nutrient requirement, hemicryptophytes, graminoids, plants with entire leaf blades, not spiny, erect and mainly forming tussock. Nevertheless, some interesting significant differences were measured between the plant communities growing under the three types of grazing (e.g., lower functional richness and more plants with entire leaf blade under sheep grazing). Even between horse sub-species, differences were significant for some traits (e.g., more chamaephyte species growing under 'as wild' horses), which could be linked to physiological and morphological differences between the two horses sub-species (e.g., nutritional requirements, herbivore size) and by herd management. However, the intraspecific variability on the four quantitative traits measured on four indicator species do not show a general pattern. Although these results are valid at a given time and in a particular ecosystem, the vegetation functional traits approach can help in decision-making regarding ecosystem management choices and highlight the fact that the 'as wild' management adds an interesting alternative to conservation.

1. Introduction

The current alarming decline of biodiversity (Ceballos et al., 2010; IUCN, 2021; Cowie et al., 2022) and the urgent need to restore ecosystems and their ecological functions has brought rewilding at the forefront of conservation or restoration strategies in the last two decades (Ceauşu et al., 2015; Jepson, 2016; Svenning, 2020; Svenning et al., 2024). Trophic rewilding, which aims at (re)introducing ecosystem engineers, is gaining interest and large herbivores are among them because (i) they have strong effects on ecosystems by their plant consumption, defecation, urination, and trampling (Forbes et al., 2019; Pringle et al., 2023), and (ii) they suffered major extinction especially due to ancient climate change and human hunting resulting in cascading effects along ecosystems (Gill, 2014; Malhi et al., 2016; Galetti et al.,

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https://doi.org/10.1016/j.jenvman.2025.126378
Received 18 March 2025; Received in revised form 1 May 2025; Accepted 25 June 2025

2018; Pringle et al., 2023). Overall, large herbivores play a critical role in plant community assemblage (Matches, 1992; Pringle et al., 2023; Török et al., 2024) by modifying diversity, coexistence and spatial heterogeneity (Olff and Ritchie, 1998; Adler et al., 2001; Louthan et al., 2014; Jia et al., 2018). However, these effects are context-dependent and can vary widely depending on habitat productivity (Bakker et al., 2006; Lezama et al., 2014), grazing pressure (Herrero-Jáuregui and Oesterheld, 2018) and the types of herbivore involved (Young et al., 2013; van der Plas et al., 2016).

Although there is growing empirical evidence that trophic rewilding has some positive effects on herbaceous species richness, primary productivity (Torres et al., 2018; Hart et al., 2023; Mutillod et al., 2024; Gottlieb et al., 2024), there is still a need for more scientific studies to reach a deeper understanding of large herbivore refaunation and its ecosystem functioning (Svenning et al., 2016, 2024; Hart et al., 2023; Atkinson et al., 2024).

Adopting a trait-based approach, rather than relying solely on taxonomy, offers a more mechanistic understanding of the effects of (re) introduced large herbivores, and may also help elucidate broader ecological patterns (McIntyre et al., 1999; Díaz et al., 2007; Atkinson et al., 2024). It also gives a possible way to evaluate and compare herbivore types and their related conservation management system effects between projects over the world. Likewise, it can help link responsive traits to trait effects to ecosystem functions (Lavorel and Garnier, 2002; Violle et al., 2007; de Bello et al., 2010; Lavorel, 2013) and enlighten answers to key hypothesized avenue by which large herbivores influence ecosystem processes (Pringle et al., 2023; Atkinson et al., 2024).

The majority of studies on large herbivore effects and plant functional traits have compared grazed *vs* ungrazed (Lebbink et al., 2023), while others focused on effects of various grazing intensities (e.g., Bullock et al., 2001; Borchardt et al., 2013; Chillo et al., 2017; Török et al., 2018). It has already been shown that grazing notably promotes plants with low stature (Díaz et al., 2007), and is mainly positively correlated with leaf nitrogen and Specific Leaf Area (SLA), and negatively with Leaf Dry Matter Content (LDMC) (Lebbink et al., 2023). The plant-herbivore relation is then a complex mechanism, including the plant's own biomass allocation strategy, plant physiology, and regulation of photosynthetic levels, all influenced by the reduction in soil nutrients. This means that plants invest more in growth to tolerate herbivory (Díaz et al., 2001). Herbivory promotes asexual reproduction (Wentao et al., 2023) in relation with grazing pressure. Loss of functional diversity with increasing grazing intensity has also been showed (Chillo et al., 2017).

Despite this knowledge, how different ungulate species may have contrasting effects on the functional diversity of grassland communities remains poorly understood. Very few studies have explored the effects of different herbivores on functional traits, and they lead to contrasted results, sometimes showing an effect of the herbivore type promoting specific traits (e.g., plant growth forms, life forms) (Catorci et al., 2012; van der Plas et al., 2016; Tóth et al., 2018; Rodríguez et al., 2023), and sometimes not (Kovacsics-Vári et al., 2023). Therefore, the aim of the present study is to compare how three herbivores (sheep, domestic horses and Przewalski horses – hereinafter called takhi their Mongolian name (Van Dierendonck and Wallis de Vries, 1996)) and their associated management (domestic, 'as wild') may modify plant trait responses on steppe-like grasslands under similar grazing pressure. A recent study has underlined taxonomic differences at the community level according to the type of herbivore and their management (Mutillod et al., 2024). i) The first objective of this work is thus to determine if these taxonomic differences are the reflection of differences in plant community functional trait structure.

Low-intensity drivers can affect the physiological performance at the individual scale without leaving detectable effects at the community level (De Bello et al., 2021). ii) The second objective was therefore to determine if the herbivore type and its management have an effect on the intraspecific variability (i.e., the variability of trait values expressed by individuals within a species (Albert et al., 2011)).

2. Material and methods

2.1. Study area and site description

The study takes place in the south east zone of the *Massif Central* (south of France, Fig. 1), on a calcareous plateau, the *Causse Méjean* (34,000 ha) at an altitude ranging between 800 and 1247m. The climate is mountainous continental-Mediterranean causing hot dry summer and cold wet winter (Caplat et al., 2006), annual precipitations is 1200 mm, the daily mean minimum temperature of −2 °C occurs in January and the daily mean maximum of 22 °C occurs in August (Meteoblue, 2025).

The *Causse Méjean* has a long history of breeding sheep (for milk, meat, wool) with the highest anthropic pressure between the 17th and the 19th centuries (Crosnier and Granger, 2004). The pastoral use has helped the formation of dry grasslands with great biodiversity, high rate of endemism and the presence of species of steppe origin (O'Rourke, 1999; Tison et al., 2014). The sampling took place in the eastern part of the plateau, where the steppe-like grassland is the most represented habitat (Fig. 1) classified as Mediterraneo-montane steppes (EUNIS classification code E1.51 (European Environment Agency, 2019),). Two sites grazed by sheep (*Ovis aries* Linnaeus, 1758) bred for meat were chosen which are considered as the reference ecosystem in this area. One is grazed mostly in summer and autumn (267ha) in a traditional way: sheep are taken out to graze as soon as weather conditions permit it. The second site (136ha) was traditional grazed until 2018, and since, is grazed in spring and summer: as soon as the weather is good, sheep are led and then left night and day under the guard of dogs, and do not return to the sheepfold at night.

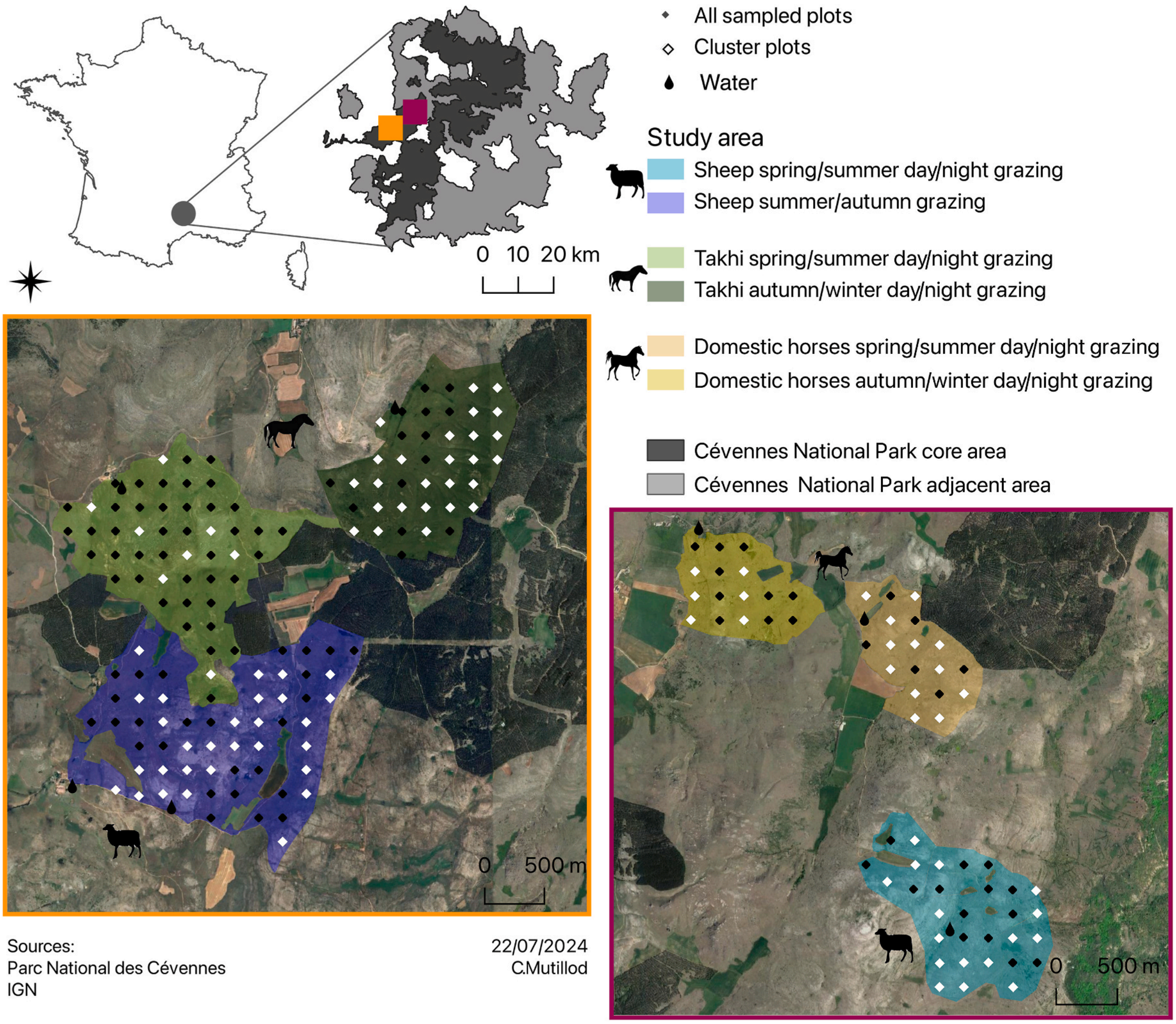
In 1993 and 1994, eleven takhi (*Equus ferus przewalskii* Poliakov, 1881) - three mares and five non-behavioral mature stallions followed by three more mares - from eight European zoos (United Kingdom, Germany and France) were introduced by the TAKH Association in 217ha closed area (Zimmermann, 2005; Roche and Tatin, 2021). A second site of 171ha was added in 2001. They were allowed to roam freely in this closed area without human interference (semi-free ranging management) in order (i) to rediscover and express their natural behaviors in a natural environment with similar climate conditions as their original distribution area (Asian steppes), (ii) to form social groups and reproduce before reintroducing some of them in Mongolia (Roche and Tatin, 2021), (iii) to maintain the steppe-like grasslands (Zimmermann, 2005). In 2022 (when the sampling was done) 35 takhi were present in two connected sites, one of 217ha mainly grazed in spring and summer, and the other of 171ha mainly grazed in autumn and winter.

Domestic horses (*Equus ferus caballus* Linnaeus, 1758) are breed for long distance race since 2008 within the selected farm. Before 2018, rangelands were grazed alternatively by sheep and horses, then by horses only. Two sites were chosen, one grazed in spring and summer (81ha), and the other grazed in autumn and winter (78ha).

While the three animals have different weights (domestic horses: ∼400 kg; takhi: ∼300 kg; sheep: ∼75 kg), all sites have had similar grazing pressure over the past few years (around 0.05–0.06 Livestock Units/ha/year) (Mutillod et al., 2024), and they were historically all grazed by sheep. Domestic herds (sheep and horses) are managed animals, they receive sanitary treatment (e.g., deworming), they have close contacts to humans and breeders form batches (according to sex and ages). We here consider takhi as being wild managed – a similar concept to rewilding - because of the species conservation status, the way takhi are managed (non-intervention, no selection by humans) and the habitat management objectives.

2.2. Characterization of the functional trait structure of plant communities

We used flora inventories and environmental parameters already



Sources:
Parc National des Cévennes
IGN

22/07/2024
C.Mutillod

Fig. 1. Study area and sites localization in the *Parc National des Cévennes* (South of France) with the six grazed sites by sheep (in blue), takhi (in green) and domestic horses (in yellow) in 2022.

surveyed in 2022 (Mutillod et al., 2024). Systematic random sampling – i.e., by using a grid randomly drawn on a map from north to south - was done on the six selected sites, where a total of 208 plots were inventoried. All plots were located 200m apart to avoid autocorrelation effect and the number of plots was proportional to the surface of the site. A plot consisted of a 1 m^2 quadrat to inventory all the flora at the species level, and a 100 m^2 (5.64m radius) circle where environmental parameters were measured. We used the subsample of sampling plots having the most similar environmental parameters based on the k-means cluster analysis ($n = 97$, sheep: $n = 45$, takhi: $n = 34$, domestic horses: $n = 18$) (see Mutillod et al., 2024 for further details) to focus on the herbivore type effects that could be concealed by environmental parameters resulting from other management choices (e.g., land depressions that are mostly cultivated, mowed for hay production or intensively grazed in domestic herd management, but open to animals and grazed as the rest of the site within the 'as wild' management).

We selected traits from the sampled species within the TRY database - https://www.try-db.org/(Kattge et al., 2020) - request number 27697 - being attentive to the synonyms that can be used for the same species using flora and taxonomic references (Tison et al., 2014; Gargominy et al., 2021).

We investigated on eleven traits commonly studied and that can be linked to the grazing effects (Bullock et al., 2001; Díaz et al., 2001, 2007; Cornelissen et al., 2003; Catorci et al., 2012; Lebbink et al., 2023). Six traits were extracted from the TRY database: Leaf Dry Matter Content (LDMC), plant height vegetative, woodiness (0: non woody, 0.5: semi-woody, 1: woody), nutrient requirement (eutrophic, mesotrophic, oligotrophic, hemiparasitic), Raunkiaer life forms (Raunkiaer, 1934), growth form (forbs, herbaceous legume, graminoid, woody). Five other traits: life cycle (annual, perennial monocarpic, perennial polycarpic), habit (erect, prostrate), architecture (leafy stem, rosette, tussock), spinescence (yes, no), leaf blade fragmentation (entire, compounded) were added using the flora (Tison et al., 2014).

To sort values and information within the TRY database, we used the *rtry package* (Lam et al., 2024) on R (R Core Team, 2022). We first kept information on mature plants as they were observed in that stage during the field work by removing observations of juvenile plants, saplings and unknown plant development status. Then, we filtered the dataset according to longitude ($<35 \sim$ Turkish, $>15 \sim$ Maroc) and latitude (<60 South Sweden, >0 equatorial line), removing also lines with NAs, to avoid values of species that could have been introduced outside their range distribution - ancillary data "*Latitude*" (DataID 59) and "*Longitude*" (DataID 60). We excluded outliers according to values with error risk ≥ 3 (the trait record has a maximum distance of 3 standard deviations than the species mean values), and duplicates. We visually checked the congruence (i.e., same order of magnitude) of the values obtained from the database and those measured in the field (see following part) to check their applicability (Lavorel et al., 2008).

155 of the 171 plants (including five for which we could only determine the genera - but no other detected species for these genera)

were found within the TRY database (Fig. 2). Among these 155, all the traits were finally filled for 118 species after completing with field measurements (height, LDMC), closest species information from TRY database or information provided by floras. Mean values for *Rhinanthus pumilus* are mean values measured in field (see following part). Mean values of *Teucrium rouyanum* are obtained from *Teucrium polium* in the TRY database because it is an autonomous amphidiploid probably between *Teucrium aureum* and a diploid taxon close to *Teucrium polium* showing only slight differences on chalice teeth (Tison et al., 2014). Vegetative plant height of *Koeleria vallesiana* was taken from the closest species *K. pyramidata* and concordance checked comparing to floras indications. Other missing trait information for few species (e.g. Raunkiaer life form, nutrient requirement) were reported according to information provided by floras (Tison et al., 2014; Tela Botanica, 2024).

We checked with the total percent cover of each modality if at least 80 % of the community was filled with traits information (Pakeman and Quested, 2007) and we finally obtained 90 plots in total (Table 1, sheep $n = 42$, takhi $n = 31$ and domestic horses $n = 17$).

We first performed a multivariate analysis (Hill & Smith) with *Ade4* package (Chessel et al., 2004) to verify the possible correlation between traits (Suppl. Material S1) before to use them all in the following analyses.

To evaluate vegetation responses to grazing, we calculated Community Weighted Mean (CWM), multi-traits functional diversity indices, and relative abundances. CWM were calculated for each continuous and semi-quantitative variable: LDMC, plant height and woodiness, using the dbFD function of the FD package (Laliberté et al., 2014). We calculated three multi-traits functional diversity indices (functional richness, functional evenness and functional divergence, built to be complementary (Villéger et al., 2008)) using the *alpha.fd.multidim* function of the *mFD package* (Magneville et al., 2022). Functional richness (FRic) (Villéger et al., 2008) is "*the volume of multidimensional space occupied by all species in a community within functional space*" (Mouillot et al., 2013). Functional evenness (FEve) is the regularity of the distribution abundance in the volume, and the functional divergence (FDiv) reflects the divergence in the distribution of abundance in the same volume (Villéger et al., 2008).

Three shrub species were excluded – not changing the 80 % of the filled community - for CWM and functional diversity indices (*Amelanchier ovalis, Crataegus monogyna, Prunus spinosa*) because inventoried only as germination or short saplings within the herbaceous layers but showing height values within the shrub layer in the TRY database.

We calculated the relative abundances of each species and then for each category of the eight qualitative traits in order to characterize the communities under the different type of grazing.

Table 1
Replication statement.

Scale of inference	Scale at which the factor of interest is applied	Number of replicates at the appropriate scale
Community	Community: 118 species	90 plots: sheep $n = 42$, takhi $n = 31$ and domestic horses $n = 17$
Species	Four species	5 plots/site; 6 sites Vegetative height was measured on five individuals in each plot, total $n = 25$ per species per grazed sites, total $n = 150$ per species. LA, SLA and LDMC were measured on two individuals (leaves) on each plot, $n = 10$ leaves per species per grazed sites, total $n = 60$ per species. All individuals measured were not bitten by herbivores and showed no obvious sign of parasitism.

To compare CWM, functional diversity indices and relative abundances for each qualitative traits, we run Generalized Linear Mixed Models (GLMM) - using the *glmmTMB* package (Brooks et al., 2017) and checking the accuracy of the models with the *DHARMa* package (Hartig, 2022) - with herbivore type as fixed effect and utilization rate (i.e., estimated grazing pressure for each plot) as random effect. GLMM allow to take into account an additional structure in the data set – the grazing pressure in our case. The grazing pressure was estimated observing the use of the herbaceous stratum (0: no sign of grazing to 5: heavily grazed) according to the work of Ruiz-Mirazo et al. (2011). We put the utilization rate as random effect to avoid possible confounding effect. GLMM are then followed by pairwise comparison tests (*emmeans* package) with Holm adjustment to limit error type I.

2.3. Intraspecific trait variability

To explore the possible effects of herbivore type on intraspecific trait variability, we selected four species and four traits to focus on. Species selection was made based on a recent previous work (Mutillod et al., 2024) and on their abundance/frequency within studied sites during the 2022 inventory. *Anthyllis montana* is abundant in all the studied sites and is a Fabaceae, *Bromopsis erecta* is also abundant and frequent, it is a Poaceae and a bioindicator species of sheep grazing (Mutillod et al., 2024). *Potentilla verna* is a Rosaceae, frequent within all grazed sites and bioindicator of takhi grazing (Mutillod et al., 2024). *Rhinanthus pumilus* an Orobanchaceae; hemiparasite, was common only within takhi and

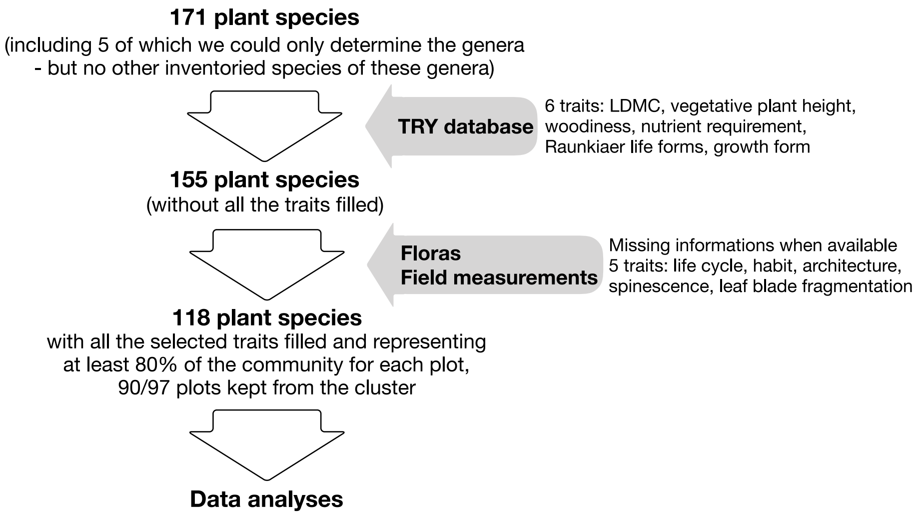


Fig. 2. Followed framework from traits extraction to data analyses.

domestic horse grazed sites; it is a bioindicator species of the takhi grazing (Mutillod et al., 2024). We choose three leaf traits easily measurables in field and in laboratory following standardized protocols (Pérez-Harguindeguy et al., 2013): vegetative plant height (m), Leaf Area (LA) (mm^2), Specific Leaf Area (SLA) (mm^2.mg^{-1}) and LDMC (g. g^{-1}) (petiole excluded). These traits are often studied within grazing effect studies (Díaz et al., 2007; Lebbink et al., 2023) because they are linked to resource acquisition, and plant responses to environmental variability and stress tolerance (Wilson et al., 1999; Garnier et al., 2001; Pérez-Harguindeguy et al., 2013). Five plots per grazed sites were chosen among the ones having similar environmental parameters (avoiding areas with high shrub cover, land depressions) and intermediate utilization rate (avoiding non- or heavy grazed area, utilization rates were measured in 2022 and visually checked by the same person in 2023). For all measurements, we selected healthy plants, with no evidence of herbivory or pathogen damage, and representative of the typical range of plant size observed within the local population. Vegetative plant height was measured in spring 2023 on five individuals for each species on each plot (Table 1, total for each species $n = 150$: $n = 25$ per grazed sites). LA, SLA and LDMC were measured on two individuals for each plot ($n = 10$ leaves per species per grazed sites, $n = 60$ per species). LA was measured by scanning leaves and using Image J software to calculate the surface (Schneider et al., 2012). Leaves were weighted – with a precision of 0.001g - when fresh (kept at temperature <4 °C and measured within 48h) and after being at the oven for 70 °C during 72h.

To evaluate the herbivore type effect, we realized GLMM with herbivore type as fixed effect, plot numbers and grazed sites as random effects, followed by pairwise comparison tests with Sidak adjustment.

3. Results

3.1. Functional trait structure of plant communities

Functional diversity indices show different answers depending of the grazer type (Fig. 3 A, B, C). The functional richness is significantly the lowest under sheep grazing (mean ± sd; 0.071 ± 0.083 *vs* domestic horses: estimate = 0.712, $p = 0.0001$, *vs* takhi: estimate = −0.367, $p = 0.033$). Intermediate values were measured for takhi grazing (0.093 ± 0.066; *vs* domestic horses: estimate = 0.345, $p = 0.033$) and the highest under domestic horse grazing (0.147 ± 0.085). Functional evenness is significantly lower under domestic horse grazing (0.336 ± 0.144) than takhi grazing (0.448 ± 0.112) and sheep grazing (0.416 ± 0.123) (*vs* takhi estimate = −0.111, p-value = 0.01; *vs* sheep estimate = −0.08, p-value = 0.049). Functional divergence (Fig. 3 C) is significantly higher under takhi (0.909 ± 0.043) and sheep grazing (0.902 ± 0.068; $p > 0.1$) than domestic horses (0.856 ± 0.108, *vs* takhi: estimate = −0.081, $p = 0.004$; *vs* sheep: estimate = −0.068, $p = 0.01$).

Vegetative plant height CWM (Fig. 4 A) shows no difference between grazers (sheep: 0.230 ± 0.105; takhi: 0.247 ± 0.06; domestic horses: 0.246 ± 0.067; p-values >0.1). LDMC CWM (Fig. 4 B) are similar for sheep (0.343 ± 0.039) and takhi (0.341 ± 0.039) (p-value >0.1), but is significantly lower for domestic horses (0.314 ± 0.022) (*vs* sheep: estimate = −0.029, $p = 0.019$; *vs* takhi: estimate = −0.029, $p = 0.019$). Woodiness CWM (Fig. 4 C) is significantly higher for takhi (0.193 ± 0.127) than for sheep (0.114 ± 0.115; estimate = −0.080, $p = 0.015$) and domestic horses (0.091 ± 0.115; estimate = −0.103, $p = 0.015$). No difference was showed between sheep and domestic horses ($p > 0.1$).

All the functional structures of plant communities under the three types of grazing show high relative abundances of perennial polycarpic, hemicryptophytes, graminoids, erect, tussock, with entire leaf blade plants, with oligotrophic to mesotrophic nutrient requirements (Table 2). However, there are significantly higher relative abundances of plants with entire leaf blade under sheep grazing than under domestic horses or takhi grazing. Some differences are also measured within Raunkiaer life forms, there are significantly more chamaephytes under takhi grazing than sheep or domestic horse grazing. There are also more geophytes within domestic horses grazed sites, and more hemicryptophytes under sheep grazing than takhi grazing. Otherwise, there are similar relative abundances of phanerophytes and therophytes species. Sheep and takhi grazing effects show also differences concerning growth forms and architecture, with significantly more forbs, herbaceous legumes, and plants with leafy stem and rosette under takhi grazing, and more graminoids, tussocks species relative abundances under sheep grazing. Domestic horse grazing shows intermediate values, except for rosette, which are significantly higher than under sheep grazing. There are significantly more hemiparasitic plants under takhi grazing than under sheep or domestic horses grazing. They are significantly more oligotrophic species under sheep and takhi grazing than under domestic horses, they are also significantly less eutrophic and mesotrophic species under takhi and sheep grazing respectively when compared to domestic horses (Table 2).

No difference was measured between habit and life cycle under the three different grazing. For spinescence, we can only note that there are slightly more spiny plants when grazed by domestic horses, but this is

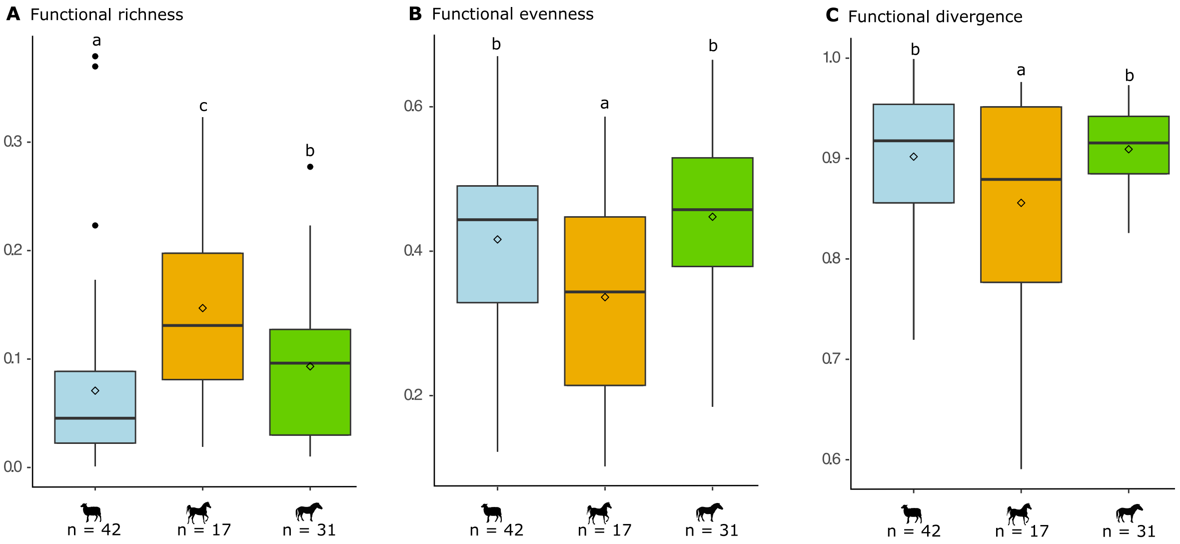


Fig. 3. Multi-traits diversity indices: functional richness, functional evenness, functional divergence depending of the grazer (sheep in blue $n = 42$, takhi in green $n = 31$ and domestic horses in yellow $n = 17$). Black lines represent median values per groups of plots. Black empty diamonds represent the mean value for each group of plots depending of the grazer type.

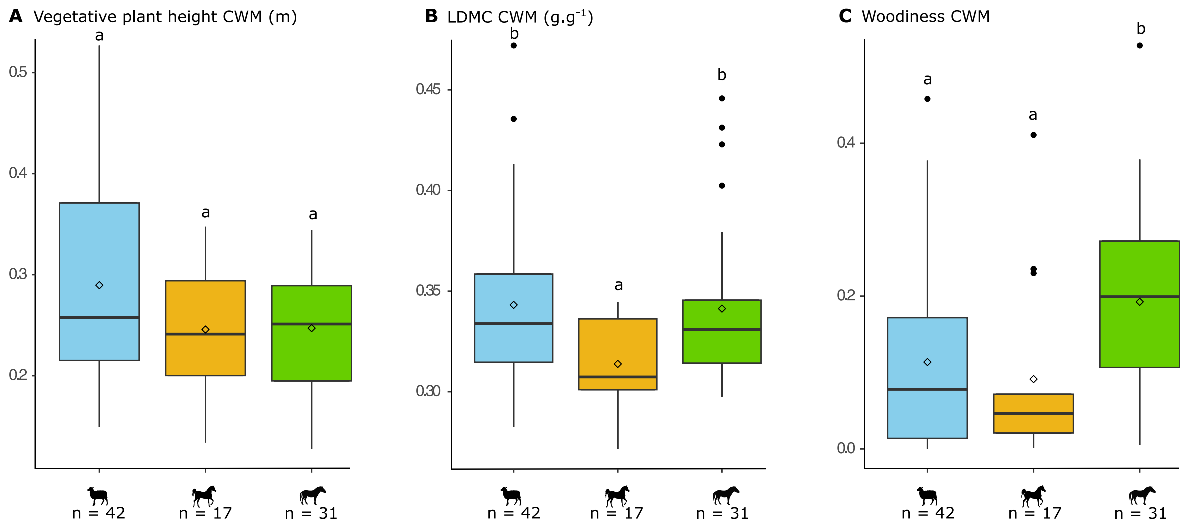


Fig. 4. Community Weighted Mean of A. LDMC (g.g^{-1}), B. Vegetative plant height (m), C. Lignification degree (woodiness) depending of the grazer (sheep in blue n = 42, takhi in green n = 31 and domestic horses in yellow n = 17). Black lines represent median values per groups of plots. Black empty diamonds represent the mean value for each group of plots depending of the grazer type.

not significant (Table 2).

3.2. *Intraspecific trait variability*

Vegetative plant height of *Rhinanthus pumilus* is significantly higher under domestic horse grazing (19.95 ± 4.90) than takhi (15.00 ± 3.65) (estimate = −4.95, p = 0.001) (Fig. 5 D). No difference in plant height was measured concerning other species ($p > 0.09$) (Fig. 5 A, B, C).

The Leaf Dry Matter Content of *Anthyllis montana* is significantly higher under takhi grazing (263.01 ± 25.48) than under domestic horse grazing (255.99 ± 86.00) (estimate = 0.101, p = 0.029) (Fig. 5 E). *Bromopsis erecta* LDMC mean value for takhi (449.83 ± 58.26) is slightly higher than the one under domestic horse grazing (392.86 ± 103.65) (estimate = 57, p = 0.065) (Fig. 5 F). Mean values of *Potentilla verna* LDMC are significantly higher for sheep (388.11 ± 35.00) and domestic horses (377.80 ± 33.57) than takhi (335.99 ± 52.44) (respectively: estimate = 0.101, p = 0.003; estimate = −0.075, p = 0.038) (Fig. 5 G).

No significant difference is shown for Leaf Area values ($p > 0.1$) (Fig. 5I–K, L) although *B. erecta* values for sheep (256.04 ± 122.20) and domestic horses (257.58 ± 102.79) were slightly higher than the one for takhi (167.07 ± 71.57) (respectively estimate = 88.97, p = 0.08 and estimate = −90.51, p = 0.073) (Fig. 5 J).

The Specific Leaf Area of *B. erecta* measured under takhi grazing (17.02 ± 5.57) is significantly lower than under sheep grazing (19.48 ± 1.93) (estimate = 0.176, p-value = 0.049) (Fig. 5 N). The SLA values of *A. montana* under takhi grazing (16.25 ± 2.73) tend to be lower than under domestic horse grazing (18.24 ± 4.42) (estimate = −0.143, p = 0.051) (Fig. 5 M).

For all the other comparisons and species, no significant differences were detected ($p > 0.09$) (Fig. 5H–O, P).

4. Discussion

4.1. *Horse grazing helps conserve the functional trait structure of multi-centennial sheep grazed dry grassland in the short term*

Despite similar pool species, the previous study using a taxonomic approach (Mutillod et al., 2024), has shown significant differences in community composition between takhi *vs* sheep and domestic horses, at the cluster level. Species richness, evenness and heterogeneity were significantly higher under takhi than sheep grazing. Species richness was also higher under domestic horse grazing than sheep. Intermediate values were measured for evenness and heterogeneity under domestic horse grazing. Takhi have also significantly promoted dicots rather than monocots.

Nevertheless, our present results show that the functional trait structure of grassland plant communities growing under takhi and domestic horses are quite similar, and also similar to the reference under sheep grazing. These plant communities are characterized and dominated by perennial polycarpic plants, with oligotrophic to mesotrophic nutrient requirement, hemicryptophytes, graminoids, plants with entire leaf blades, not spiny, erect and mainly forming tussock. Low plants are favored by grazing (Díaz et al., 2007; Garrido et al., 2019) and maximum height is usually negatively related to grazing pressure (Atkinson et al., 2024). So, the results showing no difference for CMW of the plant height seems logical since we worked at similar grazing pressure in similar grassland types. However, we find slight but significant differences between the functional trait structures of these plant communities. These differences can be explained by dietary selectivity, herbivore size (which corroborate previous results (Lundgren et al., 2024)) and management practices of the herd. Moreover, even if not native from the area or present since a long time as sheep, both type of horses help conserve the dry grasslands plant community, and their different effects can be linked to their functional traits and not their nativeness (Lundgren et al., 2024).

4.2. *Fine differences of functional diversity indices between horse and sheep grazing*

The functional richness is lower under sheep grazing which is a result corroborated by a previous study focusing on differences between sheep and cattle grazing (Tóth et al., 2018). Here, sheep grazing promotes plants with more entire leaf (not compounded), graminoids and thus species with tussock architecture, and plants with intermediate values in terms of nutrient requirements. It has already been showed that smaller ungulates select more palatable species and so promote species with low nutritional value, such as graminoids (Catorci et al., 2012; van der Plas et al., 2016; Potter et al., 2022; Lundgren et al., 2024). Dietary selectivity is linked to physiological and morphological difference between sheep and horses, such as ruminant *vs* monogastric, which also influences daily intake (higher for horses than sheep) and so the space use (Hofmann, 1989; Clauss, 2013; Clauss et al., 2015). Differences of muzzle size, teeth and jawbone can influence selectivity (Janis and Ehrhardt, 1988) and probably cause different plant damages, and horses are maintaining both short lawns and tall grass area (Fleurance et al.,

Table 2
Mean ± sd values of relative abundances according to each category of qualitative traits (unless for traits with only two categories) under the three grazing types (sheep n = 42, takhi n = 31 and domestic horses n = 17), and the results of their comparisons (estimate and p-value).

Traits		Herbivore types	Mean %	± sd	Comparison	Estimate	P-value	Significance	Group
Leaf blade fragmentation	Entire	Sheep	92.443	10.324	Sheep vs Takhi	0.099	**0.020**	*	b
		Domestic horses	85.736	15.934	Sheep vs Domestic horses	0.108	**0.037**	*	a
		Takhi	84.329	12.967	Takhi vs Domestic horses	0.009	0.857		a
Spinescence	No	Sheep	93.532	11.209	Sheep vs Takhi	−0.021	1.000		a
		Domestic horses	94.907	6.524	Sheep vs Domestic horses	−0.031	1.000	.	a
		Takhi	95.435	9.495	Takhi vs Domestic horses	−0.009	1.000		a
Habit	Erect	Sheep	91.546	9.882	Sheep vs Takhi	0.032	0.784		a
		Domestic horses	89.010	8.334	Sheep vs Domestic horses	0.014	1.000		a
		Takhi	87.055	9.964	Takhi vs Domestic horses	−0.018	1.000		a
Raunkiaer	Chamaephyte	Sheep	17.954	15.849	Sheep vs Takhi	−12.67	**0.008**	**	a
		Domestic horses	16.061	18.297	Sheep vs Domestic horses	1.89	0.702		a
		Takhi	30.620	19.062	Takhi vs Domestic horses	14.56	**0.012**	*	b
	Geophyte	Sheep	0.019	0.094	Sheep vs Takhi	−1.47	0.112		a
		Domestic horses	0.674	1.103	Sheep vs Domestic horses	−3.56	**0.0001**	***	b
		Takhi	0.085	0.234	Takhi vs Domestic horses	−2.09	**0.005**	**	a
	Hemicryptophyte	Sheep	80.891	15.944	Sheep vs Takhi	12.20	**0.009**	**	b
		Domestic horses	79.780	16.478	Sheep vs Domestic horses	1.11	0.819		ab
		Takhi	68.687	19.040	Takhi vs Domestic horses	−11.09	0.064	.	a
	Phanerophyte	Sheep	0.815	2.738	Sheep vs Takhi	2.80	0.445		a
		Domestic horses	2.827	6.732	Sheep vs Domestic horses	−4.64	0.263		a
		Takhi	0.052	0.197	Takhi vs Domestic horses	−7.44	0.195		a
	Therophyte	Sheep	0.320	0.889	Sheep vs Takhi	−0.452	0.611		a
		Domestic horses	0.658	1.342	Sheep vs Domestic horses	−0.676	0.557		a
		Takhi	0.556	0.830	Takhi vs Domestic horses	−0.224	0.663		a
Life cycle	Annual	Sheep	0.320	0.889	Sheep vs Takhi	−0.452	0.611		a
		Domestic horses	0.658	1.342	Sheep vs Domestic horses	−0.676	0.557		a
		Takhi	0.556	0.830	Takhi vs Domestic horses	−0.224	0.663		a
	Perennial monocarpic	Sheep	0.017	0.110	Sheep vs Takhi	−1.802	0.350		a
		Domestic horses	0.054	0.224	Sheep vs Domestic horses	−1.163	0.825		a
		Takhi	0.103	0.277	Takhi vs Domestic horses	0.639	0.825		a
	Perennial polycarpic	Sheep	99.663	0.889	Sheep vs Takhi	0.003	0.568		a
		Domestic horses	99.288	1.337	Sheep vs Domestic horses	0.004	0.568		a
		Takhi	99.341	0.942	Takhi vs Domestic horses	0.001	0.767		a
Growth form	Forbs	Sheep	11.588	10.534	Sheep vs Takhi	−0.783	**0.0003**	***	a
		Domestic horses	16.111	11.603	Sheep vs Domestic horses	−0.486	0.070	.	ab
		Takhi	22.515	15.093	Takhi vs Domestic horses	0.297	0.217		b
	Herbaceous legume	Sheep	7.174	9.656	Sheep vs Takhi	−0.792	**0.006**	**	a
		Domestic horses	11.069	16.258	Sheep vs Domestic horses	−0.169	0.574		ab
		Takhi	15.241	12.985	Takhi vs Domestic horses	0.623	0.103		b
	Graminoid	Sheep	71.671	16.275	Sheep vs Takhi	15.99	**0.001**	**	b
		Domestic horses	64.595	16.162	Sheep vs Domestic horses	7.08	0.183		ab
		Takhi	55.676	19.981	Takhi vs Domestic horses	−8.92	0.183		a
	Woody	Sheep	9.568	11.466	Sheep vs Takhi	0.294	0.837		a
		Domestic horses	8.225	9.984	Sheep vs Domestic horses	0.024	0.941		a
		Takhi	6.568	9.036	Takhi vs Domestic horses	−0.269	0.871		a
Architecture	Leafy stem	Sheep	24.043	16.200	Sheep vs Takhi	−10.32	**0.031**	*	a
		Domestic horses	27.265	15.820	Sheep vs Domestic horses	−3.22	0.503		ab
		Takhi	34.365	18.419	Takhi vs Domestic horses	7.10	0.323		b
	Rosette	Sheep	3.983	5.240	Sheep vs Takhi	−8.60	**0.0005**	***	a
		Domestic horses	7.990	6.253	Sheep vs Domestic horses	−0.734	**0.008**	**	b
		Takhi	9.929	9.588	Takhi vs Domestic horses	0.126	0.634		b
	Tussock	Sheep	71.974	16.452	Sheep vs Takhi	16.27	**0.0005**	***	b
		Domestic horses	64.745	16.072	Sheep vs Domestic horses	7.23	0.178		ab
		Takhi	55.706	19.984	Takhi vs Domestic horses	−9.04	0.178		a
Nutrient requirement	Eutrophic	Sheep	2.731	4.266	Sheep vs Takhi	0.317	0.162		ab
		Domestic horses	4.788	7.506	Sheep vs Domestic horses	−0.270	0.207		b
		Takhi	1.983	2.690	Takhi vs Domestic horses	−0.587	**0.027**	*	a
	Hemiparasitic	Sheep	0.007	0.026	Sheep vs Takhi	−4.252	**<0.0001**	****	a
		Domestic horses	0.004	0.017	Sheep vs Domestic horses	0.531	0.705		a
		Takhi	0.491	0.740	Takhi vs Domestic horses	4.783	**0.0003**	***	b
	Mesotrophic	Sheep	9.011	12.214	Sheep vs Takhi	−0.379	0.190		a
		Domestic horses	20.121	18.940	Sheep vs Domestic horses	−0.957	**0.013**	*	b
		Takhi	11.464	12.845	Takhi vs Domestic horses	−0.578	0.190		ab
	Oligotrophic	Sheep	88.251	13.235	Sheep vs Takhi	0.016	0.699		b
		Domestic horses	75.087	18.695	Sheep vs Domestic horses	0.200	**0.001**	***	a
		Takhi	86.062	13.297	Takhi vs Domestic horses	0.184	**0.004**	**	b

2012).

On the other hand, functional evenness is higher under takhi and sheep grazing than domestic horses. Grazing by takhi significantly modifies the community by making the distribution of the abundance in trait space of the species as regular as under sheep grazing. Takhi control unpalatable tall grasses when compared to sheep and domestic horses, which could also be due to the presence of more hemiparasitic species. It has already been proven that *Rhinantus* spp. can play an important role in vegetation structure and community dynamics, reducing interspecific competition by parasitizing competitive species (especially grasses but

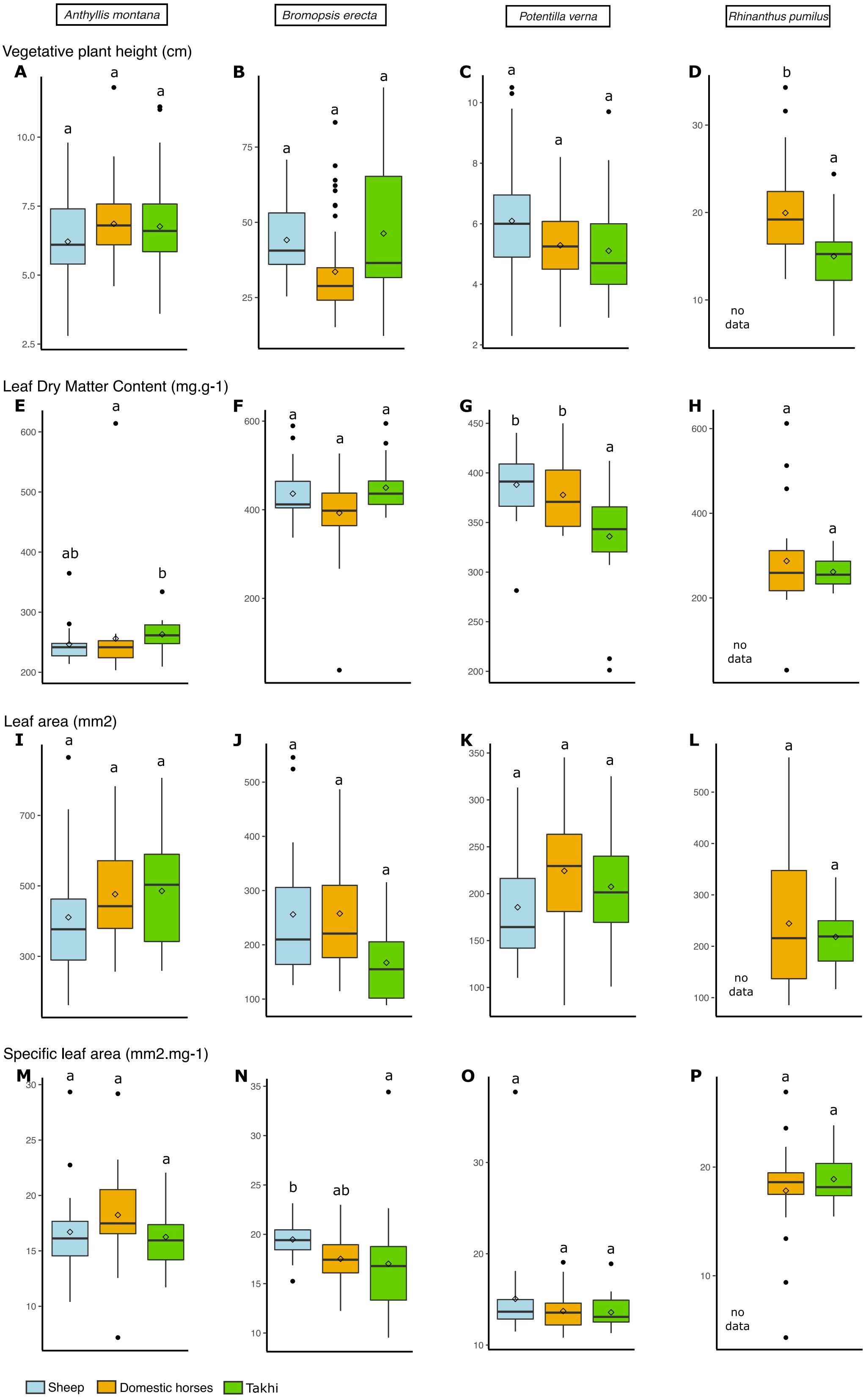


Fig. 5. A. B. C. D. Vegetative plant height (cm); E. F. G. H. Leaf Dry Matter Content (mg.g^{-1}); I. J. K. L. Leaf Area (mm^2); M. N. O. P. Specific Leaf Area (mm^2.mg^{-1}) measured for *Anthyllis montana, Bromopsis erecta, Potentilla verna* under sheep (in blue), takhi (in green) and domestic horses (in yellow) grazing; and *Rhinanthus pumilus* under takhi and domestic horses grazing. Black lines represent median values per groups of plots. Black empty diamonds represent the mean value for each group of plots depending of the grazer type.

also legumes) and so promoting subordinates (Press and Phoenix, 2005; Cameron et al., 2006). They can also play a role in nutrient cycling (Ameloot et al., 2008). Their presence and high density could create a positive feedback on the rest of the plant community (Heer et al., 2018).

We also find differences in functional divergence, even if in all cases we measured high values, with significantly higher values under sheep and takhi grazing compared to domestic horses. High values mean a high rate of utilization of the available niche space and so, allows high ecosystem stability and functioning (Mason et al., 2005). The plant community growing under domestic horse grazing could be less stable because the modification of the disturbance - using domestic horses instead of sheep - is more recent (i.e., 4 years), resulting in more abundant functionally similar species. This highlights the importance to follow the changes of these communities over time. Our results are not similar to a previous study which showed no difference in functional evenness nor functional divergence between herbivores (Tóth et al., 2018).

4.3. *Horses managed "as wild" promote chamaephyte biological types*

'As wild' takhi horses significantly promote forbs, herbaceous legumes, and plants having compounded leaf blade, rosette and leafy stem architecture, and show less hemicryptophytes relative abundances than the sheep grazed community.

Woodiness CWM is positively influenced by takhi grazing and this is linked to the higher relative abundance of chamaephyte species (such as *Coronilla minima, Genista* spp., *Linum suffruticosum, Thymus serpyllum*), which are ligneous species. A previous study done in dry grasslands of the Apennines, with grazing pressures about 0.8–0.9 LU.ha^{-1} (higher than our), showed that domestic horses did not promote chamaephytes compared to sheep, probably due to their lower resistance to trampling by large herbivores (Catorci et al., 2012). In our study, the chamaephytes could be promoted by takhi because of their control on graminoid species, that could be reinforced by the presence of more hemiparasitic species, their intermediate trampling disturbance and some of their natural behavior (including space use) linked to their management 'as wild'. It is assumed that trampling is more important when herbivores are larger: larger herbivores have relatively shorter legs and so shorter steps than small herbivores, consequently they trample a greater area of ground per unit distance travelled (Cumming and Cumming, 2003; Hobbs and Searle, 2005). In our study, we have three different sizes of large herbivores: domestic horses are bigger animals (arabian horses ~400 kg) than takhi (~300 kg) or sheep (~75 kg), resulting in trampling differences (both sub-species of horses are not shod). Managed 'as wild', takhi express natural behaviors. With no prophylactic treatment, takhi probably do not have the exact same diet as domestic horses, because they may search for specific nutriments or therapeutic properties (as was already shown for several species (Krief, 2011; Amit et al., 2013)). Moreover, potential physiological differences (such as nutritional requirements, digestion) between domestic horses and takhi may further explain the observed differences in effects.

4.4. *Possible effects of defecation pattern and behavior on plant traits*

We also find significant differences regarding LDMC CWM, with a higher value for sheep and takhi compared to domestic horses. Tóth et al. (2018) also found higher values for sheep compared to cattle. Leaves showing high LDMC values tend to be tough, less palatable (Al Haj Khaled et al., 2006), while often, low LDMC values are associated with productive and commonly highly disturbed environments (Pérez-Harguindeguy et al., 2013). The particular behaviors of horses managed 'as wild' concern defecation and the use of space. The localization of dung piles and the volume of each dung differing between herbivores (Finn and Giller, 2002) could explain why we find relatively more oligotrophic species within the studied plots under sheep and takhi grazing than under domestic horse grazing. While sheep defecate in localized places close to their resting area (Taylor et al., 1987), in extensive grazing, horses defecate almost everywhere and do not always show the use of latrines (Lamoot et al., 2004; Köhler et al., 2016). This behavior is observed for both domestic and as wild horses. However, takhi – especially males at reproduction age – do scent marking. They defecate on other male or female dung, which can lead to huge dung piles (King and Gurnell, 2007). Dung piles can have major effect on the vegetation close to the piles as well as on the surroundings (Zalba and Loydi, 2014). The presence of different social groups within takhi herd can also lead to a different use of space and differences in temporal activities depending of the groups (Saïdi, 1998; Saïdi and Mende, 1999). This can separate consumption, defecation and urination, and trampling effects within the grazed area and influence both the presence of chamaephytes and the nutrient requirement of plant species, thus leading to a higher LDCM CWM under takhi grazing.

4.5. *Domestic horse grazing slightly promotes geophytes biological types*

Domestic horses slightly promote geophytes, such as *Filipendula vulgaris, Muscari neglectum, Ornithogalum umbellatum, Ranunculus bulbosus*. It has been shown that grazed area compared to non-grazed area have more geophytes (Noy-Meir and Oron, 2001), but high pressure can lead in geophyte decrease (De Bello et al., 2005). The reason why we measured more geophytes under domestic horses grazing can be explained by several factors, such as the diminution of the graminoid cover by horses, leaving space for other types of plants – as corroborated by our results with a tendency to have more forbs than under sheep grazing - the toxicity and/or non appetent species, and particularly the slightly higher disturbance linked to trampling. Horses also favor plants having rosette architecture because they select taller plants such as graminoid when compared to sheep. Sheep exhibit a higher selectivity for ground-covering and prostate plants. As previously explained, both domestic horse size and differences in behaviors could explain the difference in some Raunkiaer's life form responses with differences in disturbance regime. The relative abundance of entire leaf blade is lower under both horses (domestic and 'as wild') than under sheep grazing because they promote – significantly or not – other type of plants than graminoids.

4.6. *Changes in grazing practices did not influence therophytes biological types*

At last, we find no difference concerning therophytes relative abundances, contrary to another study comparing sheep and domestic horse grazing but with higher grazing pressures than ours (Catorci et al., 2012). In 2022 a severe drought began early during the growing season and this could have impacted the germination and development of annual species and so alleviate possible differences. Furthermore, we studied dry grasslands composed mainly of perennial species, and the long history of grazing and the dry environment can explain the lack of strong responses to modifications in grazing herbivore (Milchunas et al., 1988; Díaz et al., 2007).

4.7. *Changes in grazing practices did not influence intraspecific variability*

The study of the intraspecific variability for four species does not show any general pattern. Each species and traits - when there are differences – have different responses to the type of grazers. These results are similar to previous study, because responses to grazing vary depending on the traits studied and the acquisition strategy of the species (Streit et al., 2022).

Thus, *Anthyllis montana* shows significantly lower LDMC for domestic horses when compared to takhi which means that leaves are less tough: this could be linked to higher productivity and a more disturbed habitat (Pérez-Harguindeguy et al., 2013) under domestic horses grazing. However, for *Potentilla verna*, the contrary is measured, with leaves being tougher under sheep and domestic grazing than under takhi grazing. They are probably more resistant to grazing disturbance due to their tussock-like form.

Bromopsis erecta SLA is significantly lower under takhi grazing than sheep grazing (with intermediate values for domestic horses) which could be explained by the higher takhi consumption of this plant. Low SLA can be related to carbon investment in quantitatively important secondary compounds (such as tannin of lignin) and with habitat with poor resources (Pérez-Harguindeguy et al., 2013). Even if there are no significant differences concerning *B. erecta* LDMC and LA the difference measured for SLA is the result of a tendency to have higher LDMC and lower LA.

We also detect differences concerning plant height for *Rhinanthus pumilus* only, with higher values under domestic horses grazing than takhi grazing. Plant height is considered as a strong indicator of plant resource use strategies (Cornelissen et al., 2003). Higher plant density – as was recorded under takhi grazing (Mutillod et al., 2024) - could lead to intraspecific competition which can be important within plant communities (Adler et al., 2018), and explain the reduced plant height.

The fact that we did not measure significant differences between most of the traits for the different species is mainly due to the high intra-modality variation than the inter-modality variation. This observation is corroborated by previous study, which have also shown the importance of micro-environmental conditions (Harzé et al., 2016). Even if we worked on the most similar plots, we cannot exclude interaction with micro-environmental conditions, such as light, soil temperature and depth, availability of nutrients (Wellstein et al., 2013; Harzé et al., 2016), induced both by micro-topology but also by the herbivores themselves, that could modify the plant trait responses within each modality.

5. Conclusions and perspectives

While the intraspecific variability on the four quantitative traits measured on four species do not show a general pattern, the differences between the different type of herbivores and management highlighted with a taxonomic approach (Mutillod et al., 2024) are also partly reflected in the functional trait structure of the communities.

Despite maintaining the same habitat and similar plant functional types, the three types of herbivores affect the functional trait structure of the communities differently. Even among horse sub-species, differences are significant for some traits, which could be linked to horse physiological and morphological differences (e.g., nutritional requirements, herbivore size) and to herd management (domestic *vs* 'as wild'). Although specific to a particular ecosystem and time, these findings can inform ecosystem management decisions and highlight the value of horses (Öckinger et al., 2006; Köhler et al., 2016; Bonavent et al., 2023) and of 'as wild' management in conserving steppe-like grasslands of high cultural heritage and biodiversity value in other places in the world.

Nevertheless, further research is needed to understand how different management practices (domestic vs. wild) affect ecosystems, particularly regarding animal behavior and physiological traits. Future studies could benefit from incorporating additional plant traits, such as thickness, tensile strength, hairiness, secondary metabolites, flowers traits, and root characteristics, especially when measured on-site (Sanson et al., 2001).

Furthermore, investigating how these traits influence ecosystem functions (e.g., carbon sequestration, pollination) will enhance our understanding of their ecological implications (Lavorel, 2013; Atkinson et al., 2024).

CRediT authorship contribution statement

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

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.

Acknowledgments

We would like to thank the *Ministère de l'Education Nationale, de l'Enseignement supérieur et de la Recherche* for the funding. Our gratitude also goes to *Association Takh* and the *Parc National des Cévennes* for the operational support and the authorization to conduct out our study within the designated protected areas. We are grateful to the domestic horses (Gaëtan L.) and sheep breeders (Benjamin L. and Mickaël J.) for allowing us to carry out our study in their enclosures and for providing us with the information about the animals, herd management and the land history. We are thankful to Nicolas Guillon and Pedro Augusto Thomas for their help during the field work, particularly in determinating and measuring plant traits. Many thanks to Daniel Pavon from the *Institut Méditerraéen de Biodiversité et d'Ecologie* and Frédéric Andrieu from the *Conservatoire Botanique National Mediterranéen* for their training in plant identification and for helping us identify certain species. We thank all the TRY database contributors for their precious measurements. We are thankful to Marie-Lise Benot from INRAE Université de Bordeaux for her advices, and the three anonymous reviewers who greatly contributed to improve this article.

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.jenvman.2025.126378.

Data availability

Data and R script supporting the findings will be available on request.

References

Adler, P., Raff, D., Lauenroth, W., 2001. The effect of grazing on the spatial heterogeneity of vegetation. Oecologia 128, 465–479.

Adler, P.B., Smull, D., Beard, K.H., Choi, R.T., Furniss, T., Kulmatiski, A., Meiners, J.M., Tredennick, A.T., Veblen, K.E., 2018. Competition and coexistence in plant communities: intraspecific competition is stronger than interspecific competition. Ecol. Lett. 21, 1319–1329.

Al Haj Khaled, R., Duru, M., Decruyenaere, V., Jouany, C., Cruz, P., 2006. Using leaf traits to rank native grasses according to their nutritive value. Rangel. Ecol. Manag. 59, 648–654.

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 Soil 311, 255–268.

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.

Atkinson, J., Gallagher, R., Czyżewski, S., Kerr, M., Trepel, J., Buitenwerf, R., Svenning, J.-C., 2024. Integrating functional traits into trophic rewilding science. J. Ecol. 1–18.

Bakker, E.S., Ritchie, M.E., Olff, H., Milchunas, D.G., Knops, J.M.H., 2006. Herbivore impact on grassland plant diversity depends on habitat productivity and herbivore size. Ecol. Lett. 9, 780–788.

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. Appl. Veg. Sci. 26, e12718.

Borchardt, P., Oldeland, J., Ponsens, J., Schickhoff, U., 2013. Plant functional traits match grazing gradient and vegetation patterns on mountain pastures in SW Kyrgyzstan. Phytocoenologia 43, 171–181.

Brooks, M.E., Kristensen, K., Benthem, K.J., van, Magnusson, A., Berg, C.W., Nielsen, A., Skaug, H.J., Mächler, M., Bolker, B.M., 2017. glmmTMB balances speed and flexibility among packages for zero-inflated generalized linear mixed modeling. R J. 9, 378.

Bullock, J.M., Joe, F., Mark, J.S., Jonathan, S., Sarah, J.C., Steve, J.G., Richard, T., 2001. A plant trait analysis of responses to grazing in a long-term experiment. J. Appl. Ecol. 38, 253–267.

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.

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.

Catorci, A., Gatti, R., Cesaretti, S., 2012. Effect of sheep and horse grazing on species and functional composition of sub-Mediterranean grasslands. Appl. Veg. Sci. 15, 459–469.

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.

Ceballos, G., García, A., Ehrlich, P.R., 2010. The sixth extinction crisis loss of animal populations and species. Journal of Cosmology 8, 1821–1831.

Chessel, D., Dufour, A.B., Thioulouse, J., 2004. The ade4 Package - I : One-Table Methods 4.

Chillo, V., Ojeda, R.A., Capmourteres, V., Anand, M., 2017. Functional diversity loss with increasing livestock grazing intensity in drylands: the mechanisms and their consequences depend on the taxa. J. Appl. Ecol. 54, 986–996.

Clauss, M., 2013. Digestive physiology and feeding behaviour of equids – a comparative approach. Horse Health Nutrition - European Equine Health Nutrition Congress 25–33.

Clauss, M., Steuer, P., Erlinghagen-Lückerath, K., Kaandorp, J., Fritz, J., Südekum, K.-H., Hummel, J., 2015. Faecal particle size: digestive physiology meets herbivore diversity. Comp. Biochem. Physiol. Mol. Integr. Physiol. 179, 182–191.

Cornelissen, J.H.C., Lavorel, S., Garnier, E., Díaz, S., Buchmann, N., Gurvich, D.E., Reich, P.B., ter Steege, H., Morgan, H.D., van der Heijden, M.G.A., Pausas, J.G., Poorter, H., 2003. A handbook of protocols for standardised and easy measurement of plant functional traits worldwide. Aust. J. Bot. 51, 335.

Cowie, R.H., Bouchet, P., Fontaine, B., 2022. The sixth mass extinction: fact, fiction or speculation? Biol. Rev., 12816 brv.

Crosnier, C., Granger, C., 2004. Le parc national des Cévennes : la population rurale à l'épreuve de la gestion des milieux ouverts. Environnement Et Sociétés Rurales En Mutation : Approches Alternatives.

Cumming, D.H.M., Cumming, G.S., 2003. Ungulate community structure and ecological processes: body size, hoof area and trampling in African savannas. Oecologia 134, 560–568.

De Bello, F., Lepš, J., Sebastià, M., 2005. Predictive value of plant traits to grazing along a climatic gradient in the Mediterranean. J. Appl. Ecol. 42, 824–833.

de Bello, F., Lavorel, S., Díaz, S., Harrington, R., Cornelissen, J.H.C., Bardgett, R.D., Berg, M.P., Cipriotti, P., Feld, C.K., Hering, D., Martins da Silva, P., Potts, S.G., Sandin, L., Sousa, J.P., Storkey, J., et al., 2010. Towards an assessment of multiple ecosystem processes and services via functional traits. Biodivers. Conserv. 19, 2873–2893.

Díaz, S., Noy-Meir, I., Cabido, M., 2001. Can grazing response of herbaceous plants be predicted from simple vegetative traits? J. Appl. Ecol. 38, 497–508.

Díaz, S., Lavorel, S., McINTYRE, S., Falczuk, V., Casanoves, F., Milchunas, D.G., Skarpe, C., Rusch, G., Sternberg, M., Noy-Meir, I., Landsberg, J., Zhang, W., Clark, H., Campbell, B.D., 2007. Plant trait responses to grazing ? A global synthesis. Glob. Change Biol. 13, 313–341.

European Environment Agency, 2019. In: EUNIS Habitat Classification 2012 Amended 2019. https://eunis.eea.europa.eu/habitats/993.

Finn, J.A., Giller, P.S., 2002. Experimental investigations of colonisation by north temperate dung beetles of different types of domestic herbivore dung. Appl. Soil Ecol. 20, 1–13.

Fleurance, G., Edouard, N., Collas, C., Duncan, P., Farruggia, A., Baumont, R., Lecomte, T., Dumont, B., 2012. How do horses graze pastures and affect the diversity of grassland ecosystems?. In: Forages and Grazing in Horse Nutrition. Wageningen Academic, pp. 147–161.

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.

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., et al., 2018. Ecological and evolutionary legacy of megafauna extinctions. Biol. Rev. 93, 845–862.

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. Rapport UMS PatriNat (OFB-CNRS-MNHN). Muséum national d'Histoire naturelle, Paris, p. 63.

Garnier, E., Laurent, G., Bellmann, A., Debain, S., Berthelier, P., Ducout, B., Roumet, C., Navas, M.-L., 2001. Consistency of species ranking based on functional leaf traits. New Phytol. 152, 69–83.

Garrido, P., Mårell, A., Öckinger, E., Skarin, A., Jansson, A., Thulin, C., 2019. Experimental rewilding enhances grassland functional composition and pollinator habitat use. J. Appl. Ecol. 56, 946–955.

Gill, J.L., 2014. Ecological impacts of the late Quaternary megaherbivore extinctions. New Phytol. 201, 1163–1169.

Gottlieb, L., Schäfer, B.A., Buttenschøn, R.M., 2024. European bison (Bison bonasus) increase plant species richness in forest habitats. For. Ecol. Manag. 561, 121891.

Hart, E.E., Haigh, A., Ciuti, S., 2023. A scoping review of the scientific evidence base for rewilding in Europe. Biol. Conserv. 285, 110243.

Hartig, F., 2022. _DHARMa: residual diagnostics for hierarchical (Multi-Level/mixed) regression models_. R package version 0.4.6.

Harzé, M., Mahy, G., Monty, A., 2016. Functional traits are more variable at the intra- than inter-population level: a study of four calcareous dry-grassland plant species. Floristisch-soziologische Arbeitsgemeinschaft e. V. (FlorSoz).

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. Perspect. Plant Ecol. Evol. Systemat. 32, 22–29.

Herrero-Jáuregui, C., Oesterheld, M., 2018. Effects of grazing intensity on plant richness and diversity: a meta-analysis. Oikos 127, 757–766.

Hobbs, N.T., Searle, K.R., 2005. A reanalysis of the body mass scaling of trampling by large herbivores. Oecologia 145, 462–464.

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

IUCN, 2021. In: The IUCN Red List of Threatened Species. Version 2021-3. https://www.iucnredlist.org. (Accessed 27 April 2022).

Janis, C.M., Ehrhardt, D., 1988. Correlation of relative muzzle width and relative incisor width with dietary preference in ungulates. Zool. J. Linn. Soc. 92, 267–284.

Jepson, P., 2016. A rewilding agenda for Europe: creating a network of experimental reserves. Ecography 39, 117–124.

Jia, S., Wang, X., Yuan, Z., Lin, F., Ye, J., Hao, Z., Luskin, M.S., 2018. Global signal of top-down control of terrestrial plant communities by herbivores. *Proceedings of the National Academy of Sciences* **115**. Proceedings of the National Academy of Sciences, pp. 6237–6242.

Kattge, J., Bönisch, G., Díaz, S., Lavorel, S., Prentice, I.C., Leadley, P., Tautenhahn, S., Werner, G.D.A., Aakala, T., Abedi, M., Acosta, A.T.R., Adamidis, G.C., Adamson, K., Aiba, M., Albert, C.H., et al., 2020. TRY plant trait database – enhanced coverage and open access. Glob. Change Biol. 26, 119–188.

King, S.R.B., Gurnell, J., 2007. Scent-marking behaviour by stallions: an assessment of function in a reintroduced population of Przewalski horses (Equus ferus przewalskii). J. Zool. 272, 30–36.

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. Agric. Ecosyst. Environ. 234, 48–57.

Kovacsics-Vári, G., Sonkoly, J., Tóth, K., McIntosh-Buday, A., Díaz Cando, P., Törő-Szijgyártó, V., Balogh, N., Guallichico Suntaxi, L.R., Espinoza Ami, F.D., Demeter, L., Tóthmérész, B., Török, P., 2023. Intensity-dependent effects of cattle and sheep grazing in sand grasslands — does livestock type really matter? Appl. Veg. Sci. 26, e12727.

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.

Laliberté, E., Legendre, P., Shipley, B., 2014. FD: measuring functional diversity from multiple traits, and other tools for functional ecology. R package version 1, 0-12.1.

Lam, O.H.Y., Kattge, J., Tautenhahn, S., Boenisch, G., Kovach, K.R., Townsend, P.A., 2024. 'rtry': an R package to support plant trait data preprocessing. Ecol. Evol. 14, e11292.

Lamoot, I., Callebaut, J., Degezelle, T., Demeulenaere, E., Laquière, J., Vandenberghe, C., Hoffmann, M., 2004. Eliminative behaviour of free-ranging horses: do they show latrine behaviour or do they defecate where they graze? Appl. Anim. Behav. Sci. 86, 105–121.

Lavorel, S., 2013. Plant functional effects on ecosystem services. J. Ecol. 101, 4–8.

Lavorel, S., Garnier, E., 2002. Predicting changes in community composition and ecosystem functioning from plant traits: revisiting the Holy Grail: plant response and effect groups. Funct. Ecol. 16, 545–556.

Lavorel, S., Grigulis, K., McIntyre, S., Williams, N.S.G., Garden, D., Dorrough, J., Berman, S., Quétier, F., Thébault, A., Bonis, A., 2008. Assessing functional diversity in the field – methodology matters. Funct. Ecol. 22, 134–147.

Lebbink, G., Risch, A.C., Schuetz, M., Firn, J., 2023. How plant traits respond to and affect vertebrate and invertebrate herbivores—Are measurements comparable across herbivore types? Plant Cell Environ. 47, 5–23.

Lezama, F., Baeza, S., Altesor, A., Cesa, A., Chaneton, E.J., Paruelo, J.M., 2014. Variation of grazing-induced vegetation changes across a large-scale productivity gradient. J. Veg. Sci. 25, 8–21.

Louthan, A.M., Doak, D.F., Goheen, J.R., Palmer, T.M., Pringle, R.M., 2014. Mechanisms of plant–plant interactions: concealment from herbivores is more important than abiotic-stress mediation in an African savannah. In: Proceedings of the Royal Society B: Biological Sciences, vol. 281. Royal Society, 20132647.

Lundgren, E.J., Bergman, J., Trepel, J., 2024. Functional traits—not nativeness—shape the effects of large mammalian herbivores on plant communities. Science 383, 531–537.

Magneville, C., Loiseau, N., Albouy, C., Casajus, N., Claverie, T., Escalas, A., Leprieur, F., Maire, E., Mouillot, D., Villéger, S., 2022. mFD: an R package to compute and illustrate the multiple facets of functional diversity. Ecography 2022.

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.

Proceedings of the National Academy of Sciences **113**. Proceedings of the National Academy of Sciences, pp. 838–846.

Mason, N.W.H., Mouillot, D., Lee, W.G., Wilson, J.B., 2005. Functional richness, functional evenness and functional divergence: the primary components of functional diversity. Oikos 111, 112–118.

Matches, A.G., 1992. Plant response to grazing: a review. J. Prod. Agric. 5, 1–7.

McIntyre, S., Lavorel, S., Landsberg, J., Forbes, T.d. a., 1999. Disturbance response in vegetation – towards a global perspective on functional traits. J. Veg. Sci. 10, 621–630.

Meteoblue, 2025. In: Simulation De Données Climatiques Et Météorologiques Historiques Pour Causse Méjean. https://www.meteoblue.com/fr/meteo/historyclimate/climatemodelled/causse-méjean_france_2994720. (Accessed 28 April 2025).

Milchunas, D.G., Sala, O.E., Lauenroth, W.K., 1988. A generalized model of the effects of grazing by large herbivores on grassland community structure. In: The American Naturalist, vol. 132. The University of Chicago Press, pp. 87–106.

Mouillot, D., Graham, N.A.J., Villéger, S., Mason, N.W.H., Bellwood, D.R., 2013. A functional approach reveals community responses to disturbances. Trends Ecol. Evol. 28, 167–177.

Mutillod, C., Buisson, E., Tatin, L., Mahy, G., Dufrêne, M., Mesléard, F., Dutoit, T., 2024. Managed as wild, horses influence grassland vegetation differently than domestic herds. Biol. Conserv. 290, 110469.

Noy-Meir, I., Oron, T., 2001. Effects of grazing on geophytes in Mediterranean vegetation. J. Veg. Sci. 12, 749–760.

Öckinger, E., Eriksson, A.K., Smith, H.G., 2006. Effects of grassland abandonment, restoration and management on butterflies and vascular plants. Biol. Conserv. 133, 291–300.

Olff, H., Ritchie, M.E., 1998. Effects of herbivores on grassland plant diversity. Trends Ecol. Evol. 13, 261–265.

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

Pakeman, R.J., Quested, H.M., 2007. Sampling plant functional traits: what proportion of the species need to be measured? Appl. Veg. Sci. 10, 91–96.

Pérez-Harguindeguy, N., Díaz, S., Garnier, E., Lavorel, S., Poorter, H., Jaureguiberry, P., Bret-Harte, M.S., Cornwell, W.K., Craine, J.M., Gurvich, D.E., Urcelay, C., Veneklaas, E.J., Reich, P.B., Poorter, L., Wright, I.J., et al., 2013. New handbook for standardised measurement of plant functional traits worldwide. Aust. J. Bot. 61, 167.

Potter, A.B., Hutchinson, M.C., Pansu, J., Wursten, B., Long, R.A., Levine, J.M., Pringle, R.M., 2022. Mechanisms of dietary resource partitioning in large-herbivore assemblages: a plant-trait-based approach. J. Ecol. 110, 817–832.

Press, M.C., Phoenix, G.K., 2005. Impacts of parasitic plants on natural communities. New Phytol. 166, 737–751.

Pringle, R.M., Abraham, J.O., Anderson, T.M., Coverdale, T.C., Davies, A.B., Dutton, C.L., Gaylard, A., Goheen, J.R., Holdo, R.M., Hutchinson, M.C., Kimuyu, D.M., Long, R.A., Subalusky, A.L., Veldhuis, M.P., 2023. Impacts of large herbivores on terrestrial ecosystems. Curr. Biol. 33, R584–R610.

R Core Team, 2022. A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria. https://www.R-project.org/.

Raunkiaer, C., 1934. The life forms of plants and statistical plant geography. Being the Collected Papers of C. Raunkiær.

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

Rodríguez, A., Ibanez, M., Chocarro, C., Sebastià, M.-T., 2023. Livestock species rather than grazing intensity shape plant guild proportions in interaction with multiple environmental drivers in grassland from the Pyrenees. Appl. Veg. Sci. 26, e12724.

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). Agric. Ecosyst. Environ. 141, 13–22.

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. Mappemonde 53, 7.

Sanson, G., Read, J., Aranwela, N., Clissold, F., Peeters, P., 2001. Measurement of leaf biomechanical properties in studies of herbivory: opportunities, problems and procedures. Austral Ecol. 26, 535–546.

Schneider, C.A., Rasband, W.S., Eliceiri, K.W., 2012. NIH Image to ImageJ: 25 years of image analysis. In: Nature Methods, vol. 9. Nature Publishing Group, pp. 671–675.

Streit, H., Menezes, L.S., Pillar, V.D., Overbeck, G.E., 2022. Intraspecific trait variation of grassland species in response to grazing depends on resource acquisition strategy. J. Veg. Sci. 33, e13129.

Svenning, J.-C., 2020. Rewilding should be central to global restoration efforts. One Earth 3, 657–660.

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, 113. Proceedings of the National Academy of Sciences, pp. 898–906.

Svenning, J.-C., Lemoine, R.T., Bergman, J., Buitenwerf, R., Roux, E.L., Lundgren, E., Mungi, N., Pedersen, R.Ø., 2024. The late-Quaternary megafauna extinctions: patterns, causes, ecological consequences and implications for ecosystem management in the anthropocene. Cambridge Prisms: Extinction 2, e5.

Taylor, J.A., Robinson, G.G., Hedges, D.A., Whalley, R.D.B., 1987. Camping and faeces distribution by Merino sheep. Appl. Anim. Behav. Sci. 17, 273–288.

Tela Botanica, 2024. In: Tela botanica. https://www.tela-botanica.org/?in=flore&s=.

Tison, J.M., Jauzein, P., Michaud, H., 2014. *Flore De La* France *Méditerranéenne Continentale*turriers. Naturalia publications.

Török, P., Penksza, K., Tóth, E., Kelemen, A., Sonkoly, J., Tóthmérész, B., 2018. Vegetation type and grazing intensity jointly shape grazing effects on grassland biodiversity. Ecol. Evol. 8, 10326–10335.

Török, P., Lindborg, R., Eldridge, D., Pakeman, R., 2024. Grazing effects on vegetation: biodiversity, management, and restoration. Appl. Veg. Sci. 27, e12794.

Torres, A., Fernández, N., zu Ermgassen, S., Helmer, W., Revilla, E., Saavedra, D., Perino, A., Mimet, A., Rey-Benayas, J.M., Selva, N., Schepers, F., Svenning, J.-C., Pereira, H.M., 2018. Measuring rewilding progress. Phil. Trans. Biol. Sci. 373, 20170433.

Tóth, E., Deák, B., Valkó, O., Kelemen, A., Miglécz, T., Tóthmérész, B., Török, P., 2018. Livestock type is more crucial than grazing intensity: traditional cattle and sheep grazing in short-grass steppes. Land Degrad. Dev. 29, 231–239.

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.

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.

Villéger, S., Mason, N.W.H., Mouillot, D., 2008. New multidimensional functional diversity indices for a multifaceted framework in functional ecology. Ecology 89, 2290–2301.

Violle, C., Navas, M.-L., Vile, D., Kazakou, E., Fortunel, C., Hummel, I., Garnier, E., 2007. Let the concept of trait be functional. Oikos 116, 882–892.

Wellstein, C., Chelli, S., Campetella, G., Bartha, S., Galiè, M., Spada, F., Canullo, R., 2013. Intraspecific phenotypic variability of plant functional traits in contrasting mountain grasslands habitats. Biodivers. Conserv. 22, 2353–2374.

Wentao, M., Shiming, T., Le, Q., Weibo, R., Fry, E.L., De Long, J.R., Margerison, R.C.P., Yuan, C., Xiaomin, L., 2023. Grazing reduces plant sexual reproduction but increases asexual reproduction: a global meta-analysis. Sci. Total Environ., 162850

Wilson, P.J., Thompson, K., Hodgson, J.G., 1999. Specific leaf area and leaf dry matter content as alternative predictors of plant strategies. New Phytol. 143, 155–162.

Young, H.S., McCauley, D.J., Helgen, K.M., Goheen, J.R., Otárola-Castillo, E., Palmer, T. M., Pringle, R.M., Young, T.P., Dirzo, R., 2013. Effects of mammalian herbivore declines on plant communities: observations and experiments in an African savanna. J. Ecol. 101, 1030–1041.

Zalba, S., Loydi, A., 2014. The influence of feral horses dung piles on surrounding vegetation. Management of Biological Invasions 5, 73–79.

Zimmermann, W., 2005. Przewalski's horses on the track to reintroduction-various projects compared. Zeitschrift des Kölner Zoo 183–209.