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Published in:
Applied Vegetation Science

DOI:
10.1111/avsc.12718

Publication date:
2023

Document version
Publisher's PDF, also known as Version of record

Document license:
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Citation for published version (APA):
Grazing by semi-feral cattle and horses supports plant species richness and uniqueness in grasslands

Christoffer Bonavent1 | Kent Olsen2 | Rasmus Ejrnæs3 | Camilla Fløjgaard3 | Morten D. D. Hansen2 | Signe Normand4 | Jens-Christian Svenning5 | Hans Henrik Bruun1

1Department of Biology, University of Copenhagen, Copenhagen Ø, Denmark
2Natural History Museum Aarhus, Aarhus C, Denmark
3Department of Ecoscience, Aarhus University, Aarhus C, Denmark
4Department of Biology, Aarhus University, Aarhus C, Denmark
5Department of Biology, Center for Ecological Dynamics in a Novel Biosphere (ECONOVO) & Center for Biodiversity Dynamics in a Changing World (BIOCHANGE), Aarhus University, Aarhus C, Denmark

Correspondence
Hans Henrik Bruun, Department of Biology, University of Copenhagen, Universitetsparken 15, 2100 Copenhagen Ø, Denmark.
Email: hhbruun@bio.ku.dk

Funding information
Danmarks Grundforskningsfond; Villum Fonden

Co-ordinating Editor: Péter Török

Abstract

Question: How does naturalistic grazing (trophic rewilding with large herbivores), in contrast to mowing and free succession (no grazing), affect plant community composition and species richness in temperate grassland grazed by semi-feral cattle and horses?

Location: Mols Laboratory, Denmark.

Methods: We investigated grazing exclosures in the rewilding area of the Mols Laboratory, four years after its establishment. We focused on moist to dry grassland vegetation, that is, excluding scrub and woodland. Each experimental block consisted of five 5 × 9 m plots, representing four fenced treatments, that is, summer-only grazing, winter-only grazing, full enclosure with annual autumn mowing and full enclosure with passive succession. The matrix (the fifth treatment) was grazed by large herbivores at close-to-natural densities, that is, regulated bottom-up by the carrying capacity of the area. Hence, even the seasonal grazing treatments were grazed at close-to-natural animal density. Quantitative plant community composition was assessed using the point-intercept method in 25 × 25 cm quadrats, supplemented with biomass calibration models based on additional quadrats, in which above-ground plant biomass was harvested after recording and the material sorted to species and weighed. Uniqueness was assessed as the sum of inverse range sizes for constituent species (unicity).

Results: We found an appreciably higher plant species richness in grazing treatments than under both annual mowing and full enclosure, but only minor differences between seasonal grazing treatments. Uniqueness was highest in year-round and winter-only grazing and lowest in summer-only grazing. The forb:graminoid ratio tended to be high in the winter-only grazing treatment, whereas annual mowing was associated with dominance of graminoids over forbs. Full-exclosure plots had accumulation of litter.
1 | INTRODUCTION

Grazing by large herbivorous mammals is a key process shaping vegetation structure and habitat conditions for plants and other organisms (Bakker et al., 2016; Malhi et al., 2016; Galetti et al., 2018). In European conservation management, the aim is conventionally to mimic traditional practices in agriculture and livestock husbandry, for example extensive haymaking and summer grazing (Varga et al., 2016). In reality, however, actual conservation management is often strongly constrained by the opportunities compatible with modern high-input–high-output farming and agri-environment support schemes (Newton et al., 2012). Either way, conservation management practice is not always rooted in ecological theory and often fails to deliver the desired outcomes for biodiversity (Maxwell et al., 2020; Kindvall et al., 2022). Attempts to apply first principles to grazing management can be comprised under the term “naturalistic grazing,” which may be characterized as landscape-scale conservation management, which differs from other types of extensive grazing by: (1) herbivore density being resource-regulated bottom-up, not human-controlled at a specific level; (2) grazing being seen as a natural process and, therefore, as a restoration target in itself; and (3) consequently, direct human intervention is reduced to a minimum (Hodder et al., 2005). Naturalistic grazing can be viewed as an implementation of the broader concept of trophic rewilding (sensu Svenning et al., 2016), focused on large grazers and their functions (e.g., Pedersen et al., 2020). Although “naturalistic grazing” is considered open-ended with regard to effects on herbivore populations and vegetation, monitoring the effects is crucial to our understanding of how grazing as a natural process works and interacts with other natural conditions and processes (e.g., Thomassen et al., 2023).

In large contiguous landscapes, habitat use by large herbivores often shows substantial variation in diurnal, seasonal and between-year patterns. Animal activity tends to be concentrated in certain areas, while large areas may be much more extensively used, for example wet areas may be avoided during winter, but preferred in spring and summer (Górecka-Bruzda et al., 2020). Traditional European livestock husbandry had, and continues to have, the growth and survival of domestic animals as its core purpose. Therefore, summer-only grazing on pastures and winter feeding of stable herds was traditionally the norm in Denmark, in particular for cattle, while some horses have traditionally been left on pastures year-round (Fritzøe, 2004). The pattern of summer-only grazing is strongly reinforced in modern North-European livestock husbandry, in which standard practice is to turn livestock out at very high density (usually >400 kg ha⁻¹, and sometimes exceeding 1000 kg ha⁻¹) during a short period of intensive grazing at the peak of the growing season (typically May through September or shorter; Ejrnæs et al.). One way of investigating the resulting impact on vegetation of the annual timing of herbivore activity is to compare areas, to which animal access is restricted to certain parts of the year (Bullock et al., 2001).

Modern European grasslands are often highly dominated by grasses. The relatively low prevalence of forbs may, however, be a legacy effect of past megafauna extinctions. It has been hypothesized that megafauna once sustained much higher abundance of forbs in grasslands (Bråthen et al., 2021). The shift in dominant growth form has likely been exacerbated by the more recent demise of large herbivores from European landscapes at large, and natural areas in particular. The shift has probably propagated to higher trophic levels, that is, mega-diverse consumer taxa, for example arthropods and fungi (Brunbjerg et al., 2018). Flower-visiting...
insects have attracted particular attention, partly because this functional group is particularly threatened by both land-use intensification and abandonment, and partly because some anthophilous insect taxa have shown dramatic declines in species richness and abundance (e.g. Hallmann et al., 2017; Warren et al., 2021). The ratio in vegetation of forbs to graminoids has therefore been particularly highlighted, as most forbs have flowers offering resources to anthophilous insects, while graminoids all have wind-pollinated flowers.

The response of vegetation structure to grazing regime will likely involve changes in quantitative plant community composition, with the activities of large herbivores promoting the abundance of certain species, while limiting others. We therefore applied the point-intercept method to quantitatively recording vegetation structure (Jonasson, 1988; Godínez-Alvarez et al., 2009; Bonham, 2013). Non-destructivity is a virtue of the method, which was desired in the current setup of long-term monitoring plots, also surveyed for other groups of organisms. However, because of differences in plant architecture, the intercept-based abundance does not translate directly to biomass-based abundance. We therefore made calibration models per species and/or functional groups, based on an additional set of quadrats, first subjected to point-intercept recording, next to total harvest and dry-mass estimation per species.

Plant community species richness, or alpha diversity, is of core interest to evaluations of vegetation under contrasted grazing regime, although results may depend on the actual quadrat size applied. From the perspective of gamma diversity in the region or country, however, community unicity — the regional rarity of constituent species — is of higher relevance. One way to evaluate the contribution of individual communities to regional gamma diversity is the ‘Sum of inverse range-sizes’ (Guerin & Lowe, 2015; Ejrnæs et al., 2018), in which constituent species are given decreasing weight with increasing regional occupancy. Also, from the perspective of biodiversity conservation, community unicity may be more relevant than alpha diversity, for example even locally species-poor communities may be of high regional conservation value, if they tend to consist of relatively rare species.

Our overarching aim was to assess differences in grassland vegetation structure, community richness and unicity (the prevalence of less widespread species) as a snapshot after four years of naturalistic year-round grazing, as compared to seasonal grazing regimes, to mechanical mowing and to free succession after grazing abandonment and mowing regimes. Specifically, we aimed at investigating:

1. Does plot-scale plant species richness vary between year-round grazing, seasonal grazing (all at naturalistic herbivore density), mowing and passive succession?
2. Does forb to graminoid ratio vary between year-round grazing, seasonal grazing (all at naturalistic herbivore density), mowing and passive succession?
3. Does plant community unicity vary between year-round grazing, seasonal grazing (all at naturalistic herbivore density), mowing and passive succession?

A subordinate aim was the methodological issue of non-destructive assessment of quantitative plant community composition and the sufficiency of the point-intercept method as compared to biomass estimation.

2 | MATERIALS AND METHODS

2.1 | Study site

The Mols Laboratory is an ecological research station, owned by the Natural History Museum, Aarhus. The 120-ha estate is located in the glacially shaped hilly landscape of Mols Bjerge at 56.23° N latitude and 10.58° E longitude. The area covers steep gradients in soil moisture, nutrient status and vegetation openness. Roughly half of the area is covered by open habitats, the other half by scrub and forests, with all types in a mosaic with gradients both between open and closed-canopy habitats and between dry and moist habitats. The most frequent open habitat type, as categorized under the European Habitats Directive, is Species-rich Nardus grasslands (6230). Despite this common designation, quite large variation in topography and dominant species between different parts of the area is evident, foremost between hilly glacial gravelly till and sandy marine foreland shaped by the higher sea-level of the Littorina transgression (Atlantic time; 6800–3900 BCE). This contrast is presumably mainly linked to hydrology, with the marine foreland being somewhat impacted by exfiltration of groundwater from the hills.

In 2016, under the name of “Rewilding Mols,” a perimeter fence was established surrounding the 120-ha estate and 13 heads of Galloway cattle and 12 Exmoor ponies were released, supplemented six months later by a stallion. Since then, the herds have lived under conditions attempted to be as close to natural as possible, that is, naturalistic grazing. This “near-natural” aim entails that population size is determined by the carrying capacity, that is, bottom-up by the primary productivity of the area, without any human interference with fecundity. It also means that when populations are under pressure from food shortage, no supplemental feeding is provided. Resource limitation is likely to kick in during the late winter months, at which time weak individuals would die under fully natural conditions. However, in order to minimize possible suffering of the animals and to comply with Danish animal welfare legislation, all individual horses and cattle are continuously evaluated, following a scoring protocol based on body condition and behavior. Individuals failing to meet a pre-set threshold are removed from the area (Natural History Museum, 2017). This so-called “reactive” population management has led to a dynamic development in population size, with the population of large herbivores growing to a total of 44 cattle and 25 ponies in the summer of 2019, and subsequently decreasing to the current level of 12 cattle and 26 ponies (Natural History Museum, 2020, 2021). In terms of large herbivore biomass, these numbers are equivalent of a peak at c. 210 kg ha⁻¹, a drop to c. 60 kg ha⁻¹ and, since then, a stable level around 100 kg ha⁻¹ (Oskar Liset Pryds Hansen, unpublished estimates). The described human
intervention is also what makes the cattle and horse populations qualify as "semi-feral" (or "kept wild"), as opposed to fully feral populations of former livestock, in which regulation by resource shortage may take place without any human intervention. In the TRAIL framework (Pedersen et al., 2020), the "Rewilding Mols" project qualifies as "partial rewilding," because no predatory mammals are included. Wolves have access, but the area is not sufficiently large to sustain a sedentary wolf, let alone a pack.

With the purpose of monitoring the effects of the naturalistic grazing regime, 22 randomly selected blocks for permanent vegetation monitoring were established in the spring of 2017. Each block — $5 \times 9$ m of reasonably homogeneous vegetation — contained four treatment plots, that is, summer-only grazing (exclusion November through April), winter-only grazing (exclusion May through October), annual autumn mowing (full exclusion with one annual cut during September–October and the thatch removed) and passive succession (full exclusion), all embedded in the matrix of year-round grazing. A year-round grazing plot was demarcated immediately outside the block containing the four treatment plots. Shrubs (but not trees) were initially removed from the mown plots in order to allow cutting by machinery, but not from the other treatments. Fencing did not prevent access to plots by herbivores such as red deer, roe deer and hare, only horse and cattle.

2.2 | Vegetation recording

In order to select grassland blocks, all monitoring blocks were initially surveyed in order to establish the dominant vegetation type. Out of the initially established 22 blocks, one was discontinued, four were located in closed-canopy forest, four were almost entirely covered by dense scrub and four had scrub–grassland mosaics with too high scrub cover for the point-intercept method to be practically applicable in all treatment plots, leaving nine blocks with mostly open grassland vegetation (Figure 1).

Field work was carried out in two periods: September 1–16, 2020 and August 2–20, 2021. In the first year, destructive sampling was done to parameterize models calibrating above-ground biomass from point-intercept data. In this round, sampling quadrats in treatment plots were put in the periphery of the established circular monitoring plots (see Appendix S1) and subjected to point-intercept vegetation recording, after which the above-ground biomass was cut as close to the soil surface as possible, immediately sorted into fractions by plant species (with standing litter as a separate fraction) and dried at $55^\circ$C until constant weight. The resulting data were used to create calibration models per species or functional groups for the prediction of plant species above-ground biomass from non-destructive point-intercept counts. In the second year, non-destructive recording was done in sample quadrats, which on this occasion were located inside the circular monitoring plots. Quadrats were, again, surveyed using the point-intercept method, as in the first round, but without any biomass harvest. The resulting records of the second year were (1) used as-is, (2) subjected to prediction of species’ or functional group biomass using the regression models developed upon data from the first year.

Due to time constraints, only six of the nine blocks were included in the first round of field work and were thus included in the construction of calibration models (i.e. block numbers 60, 62 and 70 were not sampled). Similarly, mown plots were not sampled, as they were in the process of being mown while the vegetation surveys were carried out. Including newly mown plots would have compromised the reliability of calibration models. In the second year, the field work took place one month earlier, allowing point-intercept recordings in the annually mown plots.

FIGURE 1 Satellite image of the Mols Laboratory property with locations of the nine sampled blocks marked.
The total sample size for the two periods of fieldwork were: six blocks by four treatment plots is 24 quadrats in the first period (in 2020) and nine blocks by five treatment plots is 45 quadrats in the second period (in 2021).

Point–intercept vegetation recording was done using a quadratic frame with a regular 5 × 5 cm point grid within a sampling area of 25 × 25 cm, that is, 25 regularly spaced sampling points, at each of which a 0.8 cm thick wooden stick was inserted vertically. The frame was elevated above the herbaceous canopy on 50 cm legs. All leaves and stems of plants intercepted by the stick were recorded with species' identity. Dead plant parts were recorded as litter. If the main part of a plant was alive, all its parts was recorded as live. If the main part of the plant was withered, it was recorded as litter. Contact points with bryophytes were also recorded, but were not used in the regression models.

2.3 | Plant diversity metrics

Species richness per quadrat (alpha diversity) was assessed as one of the simplest metrics of biodiversity.

An index of community unicity was calculated based on species’ occupancy within Denmark, that is, Atlas Flora Danica, AFD (Hartvig & Vestergaard, 2015). These data consist of presence and absence records of all vascular plants in 1300 grid cells, each 5 × 5 km, dispersed across the country. Each species i recorded in a quadrat was given a value equivalent to the inverse of its range size and the resulting values summed per quadrat, thus
\[
\sum_{i=1}^{S} \frac{1}{n_{\text{intercepts} - \text{AFD grid cells with species } i \text{ present}}},
\]
in which S is the number of species in a given quadrat.

The ratio of forbs to graminoids was included as an indicator of floral resources available to anthophilous insects, thus
\[
\frac{n_{\text{intercepts - forbs}}}{n_{\text{intercepts - graminoids}}},
\]
or the equivalent for biomass estimates.

Finally, the amount of leaf litter was used as an indication of the degree to which the grazing regime qualified as naturalistic. The expectation would be that — if herbivore population size was controlled bottom-up — there would be no litter accumulation from year to year, as the plant biomass produced during one growing season would be almost exhaustively consumed during the subsequent winter and, thus, before the plant biomass production increases again in the following growing season.

2.4 | Statistical analysis of point-intercept data

First, an overall model of intercepts per vascular plant species as a function of above-ground biomass was built as a generalized linear model. Next, the residual variation of this model was investigated using analysis of variance with dry mass per point-intercept as the dependent variable and species identity, block and treatment as factors, using data from 24 quadrats recorded in 2020. This was done to investigate the assumption that species identity would explain variation in the ratio between number of intercepts and biomass. Subsequently, a linear regression model per plant species was made. This was done only for plant species with three or more data points (22 in total), and additionally for genera with more than one species present and for functional groups meeting the same criterion.

The functional groups were: broad-leaved graminoids (leaf blades >2 mm), narrow-leaved graminoids (leaf blades <2 mm), Juncus effusus-type rushes (for which intercepts with stems were recorded, as they bear no leaf blades), forbs, woody plants (trees and shrubs, incl. Calluna vulgaris and Cytisus scoparius). Initially, separate models were built for forbs with basal leaves, for example rosettes, versus post-and-flag-type forbs, but model estimates were very similar, so the two groups were combined to produce a single model with comparable \( R^2 \) and lower standard error. A separate model was built for standing dead litter. No data transformations were used. All regressions models were forced through the origin, because otherwise — when predicted biomass was accrued per plot over species — total biomass per plot would gain a spurious strong positive relationship with plot species richness.

Second, for the 45 quadrats sampled in 2021, calibrated biomass values per species per plot were calculated from point-intercept data and summed over species present in plots (total biomass, plus forb and graminoid biomass separately). For each species present in a plot, the best available model was used, that is, first choice was a species-specific model, second choice a genus-specific model, third choice a model for functional group and, in case none of these were available, a general model based on all point-intercepts was used.

2.5 | Statistical analysis of treatment data

Generalized linear models (GLMs) were used to assess the effect of grazing treatment on the two biodiversity metrics, richness and unicity, and on both forb:graminoid ratio and litter estimates, while considering block, topographic position and treatment. Block was nested in topographic position, which was either hilly terrain or marine foreland. GLMs with Poisson errors and log-link function were used for species richness and for litter (standing dead intercepts), whereas ordinary Gaussian regression was used for the forb:graminoid ratio.

For litter and for forb:graminoid ratio, the procedure was run for raw intercept counts and for calibrated biomass in parallel.

3 | RESULTS

3.1 | Biomass calibration model

The initial GLM of harvested dry mass per point-intercept across species and plots showed the expected positive linear relationship, but with much unexplained variation (\( R^2 = 0.517 \)). In the subsequent ANOVA, species identity was by far the most important factor.
accounting for the residual variation, that is, explaining 56.4% of total deviance. In contrast, treatment explained less than 2% of the total deviance. Thus, there was a significant degree of variation in (bio-)mass per point intercept across species, justifying the attempt to make single-species calibration models.

In the 24 quadrats recorded in 2020, a total of 60 plant species were found, of which 35 occurred in more than three quadrats. For 22 species, linear regression models of single-species biomass on intercepts were significant ($p$-value ≤ 0.05). Statistically significant models with fair $R^2$ values were also constructed for five genera, each represented by more than one species, that is, Agrostis, Carex, Galium, Festuca and Juncus (effusus-type), the four functional types as well as for total biomass and for standing litter. The regression models are presented in the Appendix S2: Table S1.

### 3.2 Grazing treatments

The total number of species per treatment found across plots differed quite markedly, with full exclosure having the fewest species in total (Table 1). Similarly, the average species density, that is, number of species per plot (mean alpha diversity), varied being treatments, with winter-only and year-round grazing showing the highest levels (Table 1).

In the 2021 data, treatment accounted for a rather small fraction of total deviance as compared to block and topographic position. Only for unicity did treatment overall seem to have an appreciable effect (Table 2). When broken into individual treatment groups, species richness per plot (log-transformed) was relatively high in winter-only and year-round grazing, while it was low in full exclosure. When treatment, topographic position and block were considered, the model accounted for 66% of the total deviance in richness between quadrats. Treatment overall accounted for 11% explained deviance (Table 2), without being statistically significant ($p = 0.08$).

A similar pattern was seen for unicity, for which winter-only grazing on average had a more than 50% higher level than full exclosure (Table 2). Here, the model could account for 61% of the total deviance, with treatment overall being statistically significant and accounting for 17% of total deviance.

<table>
<thead>
<tr>
<th>Treatment</th>
<th>Gamma diversity</th>
<th>Richness (average alpha diversity)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Winter-only grazing</td>
<td>50</td>
<td>11.22 SE 0.51</td>
</tr>
<tr>
<td>Year-round grazing</td>
<td>49</td>
<td>11.33 SE 0.45</td>
</tr>
<tr>
<td>Summer-only grazing</td>
<td>42</td>
<td>9.89 SE 0.33</td>
</tr>
<tr>
<td>Annual mowing</td>
<td>41</td>
<td>8.89 SE 0.36</td>
</tr>
<tr>
<td>Full exclosure</td>
<td>37</td>
<td>7.89 SE 0.47</td>
</tr>
</tbody>
</table>

Note: Statistical differences for richness between treatments are presented in Table 2.

No statistically significant effects of treatment on the forb:graminoid ratio were found. Nonetheless, we find the tendency for annual mowing to have the lowest ratio noteworthy. For explanatory models based on calibrated biomass estimates, the patterns for forb:graminoid ratio and litter were very similar. The models showed lower explained deviance for litter and higher for the forb:graminoid ratio.

The assessed biodiversity metrics featured high within-group variation from the treatment means (Figures 2–5). This is an indication that local environmental conditions and legacy effects of initial plant community composition prior to setting up exclosures strongly influence plant communities, which was also reflected in the high proportion of deviance explained by topographic position and block in GLMs (Table 2). The deviance is especially high for the forb:graminoid ratio, as in accordance with field observations, where some quadrats featured an almost complete dominance of either forbs or graminoids.

### 4 DISCUSSION

Natural grazing by semi-feral horses and cattle was found to support higher plant species richness and higher prevalence of less widespread species (unicity) in grassland vegetation, as compared to annual mowing and to full exclosure of large herbivores. Also, we saw a tendency for the prevalence of forbs over graminoids to be higher, which may result in increased floral resource availability to anthophilous insects. At first glance, this result may seem trivial, since temperate grasslands as an ecosystem are inherently dependent on the disturbance regime maintained by the activities of megafauna (Janis et al., 2002; Pärtel et al., 2005; Kuneš et al., 2015). It is nevertheless, in our view, an important result, as it highlights the detrimental effect on grassland plant diversity of the now widespread grazing abandonment or mechanical biomass harvest. Since wild grazers, such as red deer, roe deer and hare, had free access to the fenced plots in our study area and were observed there, our full exclosure treatment mimics the standard conditions in most temperate European landscapes, where populations of wild herbivores are kept at very low densities, that is, the maximum acceptable to agriculture and silviculture (Fløjgaard et al., 2022). In accordance, we found accumulation of litter in full-exlosure plots. Thick layers of litter change light and microclimate conditions at the soil surface, deteriorating conditions for plant recruitment and survival (Jensen & Gutekunst, 2003) and reducing the richness of arthropod assemblages (van Klink et al., 2015). Although grazing and haymaking may share more similarities than dissimilarities (Pykälä, 2000), our results indicate that annual autumn mowing does not support the same plant species richness and abundance of forbs as grazing.

One more reason not to overemphasize differences in vegetation response between grazing treatments obtained from exclosure plots is that larger grazed landscapes are likely to encompass areas used more and less intensively by the large herbivores at different times of
<table>
<thead>
<tr>
<th>Treatment intercept and effects</th>
<th>Deviance explained</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Treatment (%)</td>
</tr>
<tr>
<td></td>
<td>All variables (%)</td>
</tr>
<tr>
<td><strong>Richness (log-link)</strong></td>
<td></td>
</tr>
<tr>
<td>Full exclosure (model intercept)</td>
<td>2.30***</td>
</tr>
<tr>
<td>Mowing</td>
<td>0.12</td>
</tr>
<tr>
<td>Year-round grazing</td>
<td>0.36*</td>
</tr>
<tr>
<td>Winter-only grazing</td>
<td>0.35*</td>
</tr>
<tr>
<td>Summer-only grazing</td>
<td>0.23</td>
</tr>
<tr>
<td>Deviance explained</td>
<td>11.12</td>
</tr>
<tr>
<td></td>
<td>65.73</td>
</tr>
<tr>
<td><strong>Unicity</strong></td>
<td>0.0083***</td>
</tr>
<tr>
<td>Winter-only grazing</td>
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</tr>
<tr>
<td>Year-round grazing</td>
<td>0.0034 (p = 0.07)</td>
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<tr>
<td>Winter-only grazing</td>
<td>0.0047*</td>
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<tr>
<td>Summer-only grazing</td>
<td>0.0019</td>
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<tr>
<td>Deviance explained</td>
<td>17.08*</td>
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<tr>
<td></td>
<td>60.9</td>
</tr>
<tr>
<td><strong>Forb:graminoid ratio (point intercept)</strong></td>
<td>0.47</td>
</tr>
<tr>
<td>Winter-only grazing</td>
<td>0.01</td>
</tr>
<tr>
<td>Year-round grazing</td>
<td>0.23</td>
</tr>
<tr>
<td>Deviance explained</td>
<td>3.94</td>
</tr>
<tr>
<td></td>
<td>41.97</td>
</tr>
<tr>
<td><strong>Litter (point intercept, log-link)</strong></td>
<td>4.46***</td>
</tr>
<tr>
<td>Winter-only grazing</td>
<td>-0.58 ***</td>
</tr>
<tr>
<td>Year-round grazing</td>
<td>-0.84***</td>
</tr>
<tr>
<td>Deviance explained</td>
<td>-1.03***</td>
</tr>
<tr>
<td></td>
<td>-0.77***</td>
</tr>
<tr>
<td>Deviance explained</td>
<td>26.09**</td>
</tr>
<tr>
<td></td>
<td>65.16</td>
</tr>
<tr>
<td><strong>Forb:graminoid ratio (modelled biomass)</strong></td>
<td>0.77</td>
</tr>
<tr>
<td>Winter-only grazing</td>
<td>-0.13</td>
</tr>
<tr>
<td>Year-round grazing</td>
<td>0.7</td>
</tr>
<tr>
<td>Deviance explained</td>
<td>5.73</td>
</tr>
<tr>
<td></td>
<td>52.03</td>
</tr>
<tr>
<td><strong>Litter (modelled biomass)</strong></td>
<td>16.71***</td>
</tr>
<tr>
<td>Winter-only grazing</td>
<td>-7.32*</td>
</tr>
<tr>
<td>Year-round grazing</td>
<td>-9.5**</td>
</tr>
<tr>
<td>Deviance explained</td>
<td>-10.72**</td>
</tr>
<tr>
<td></td>
<td>-8.97**</td>
</tr>
<tr>
<td>Deviance explained</td>
<td>25.57**</td>
</tr>
<tr>
<td></td>
<td>60.56</td>
</tr>
</tbody>
</table>

Note: The full-exclosure treatment is used as the intercept, while the other treatments are shown with their effect relative to the intercept value. Deviance is listed as the percentage explained by the GLM model relative to the NULL model for (1) treatment alone and (2) for both treatment, topographic position and block (all variables). Levels of significance are: *, p < 0.05; **, p < 0.01; ***, p < 0.001.

FIGURE 2: Boxplot of richness by treatment. Mean values are indicated by the red dots, the black bars show the median values and the white boxes contain all values between the lower and upper quartiles. Year-round grazing and winter-only grazing are statistically significantly different from full exclosure (p < 0.05).
Even if it would be possible to experimentally demonstrate plant community properties typical of either year-round, winter-only and summer-only grazing, it may be hypothesized that all these characteristics would be created or maintained in the landscape at large by such animal behavior, thereby promoting overall habitat heterogeneity. More specifically, summer-only grazing might be a natural grazing regime in naturally nutrient-rich meadows, which are flooded during winter, while winter-only grazing may be a frequently occurring natural regime in grassland, heathland and open woodland on nutrient-poor higher grounds, which may be less immediately attractive to large herbivores during summer. We also acknowledge that our study only takes a snapshot of effects that may depend on legacy effects of previous land use (Stroh et al., 2021), such as the grazing and scrub-clearance regime that prevailed in the area before 2016. Also we cannot rule out that the patterns observed are transient in the dynamic interaction between herbivore population dynamics and interannual variation in weather conditions, such as the irregular occurrence of severe summer droughts (Stampfli et al., 2018).

It should be emphasized that modern European grassland management as an agri-environmental practice often occurs as intense summer grazing at high stocking rates (Fløgaard et al., 2022). This practice is very different from our summer-only grazing treatment (c. 100 kg ha⁻¹), in which animal densities are thought to approach natural densities set by winter forage-carrying capacity. Also, the presence of two large herbivore species — horse and cattle — contributes complexity in the effect of grazing and other activities on other groups of organisms.

Several recent studies have reported a positive effect of year-round grazing on plant species richness and — in particular — the prevalence of rare or threatened species (Köhler et al., 2016; Rupprecht et al., 2016). Temperate European landscapes have seen major habitat changes over recent decades and centuries affecting plant species and communities, including the effective disappearance of first, large wild herbivores and second, free-roaming livestock (Bruun & Fritzbøger, 2002; Finderup Nielsen et al., 2021). Naturalistic grazing appears to be key in restoring habitat conditions lost in this long-term land-use change and intensification. Although, in the present study, we were not able to encompass the grassland-scrub-forest ecotone, the heterogeneity arising from naturalistic grazing is probably important to many species showing declining trends in human-dominated landscapes (e.g. Maes et al., 2014).
A tendency for naturalistic grazing to promote forbs over graminoids has recently been reported elsewhere (Henning et al., 2017; Dvorský et al., 2022). Despite graminoids lending their name to the grassland ecosystem, forbs are essential to the phylogenetic and functional diversity of grassland communities, and are particularly important to flower-seeking insects. It has been hypothesized that grass dominance in temperate open biomes is a relatively recent phenomenon (Bråthen et al., 2021) and, no doubt, grass dominance has been promoted by agricultural grassland management (Dengler et al., 2020). Possibly, the change of dominance towards forbs may be an effect of animal trampling as much as their forage preference (Striker et al., 2011). Although differences in forb:graminoid ratio between our treatments were not statistically significant given the variation between plots, we note that the highest levels of forb relative abundance was found in the three grazing treatments. We also note that certain forb species may be sensitive to grazing, but in a larger grazing landscape probably would find habitat in browsing shelter between thorny shrubs or fallen logs.

From a methodical standpoint, our results indicate that the application of the model-derived biomass estimates in most cases does not change the overall patterns also revealed by the intercept-based analyses. It would therefore seem that the supposed differences in species morphology were, in most cases, not large enough to generate significantly different results in terms of species composition. Furthermore, the application of the calibration models to the number of intercepts constitutes a complicating step in the analysis, due to the error propagation that results from using model estimates in a function. While this does not mean that the model-derived results are invalid, it may be both more efficient and accurate to use the intercept-based results. It can therefore be argued that the use of biomass calibration models may not be necessary for comparisons to be made between treatments, unless results from methodologically different studies are compared.

Grazing is a natural ecosystem process and, thus, restoring naturalistic grazing using feral animals may be seen as restoration goal in itself, notwithstanding the effects on biodiversity. Nevertheless, the present study demonstrates that naturalistic grazing as a management tool may indeed create habitat for regionally uncommon species of conservation concern and probably enhance resource availability to flower-seeking insects.
**AUTHOR CONTRIBUTIONS**

Kent Olsen and Morten D. D. Hansen organized the establishment and maintenance of the experimental treatments, with running input from Jens-Christian Svenning, Signe Normand, Rasmus Ejrnæs and Camilla Flejgaard; Hans Henrik Bruun and Christoffer Bonavent designed the specific study; Christoffer Bonavent did the data collection; Christoffer Bonavent and Hans Henrik Bruun analysed the data; Hans Henrik Bruun and Christoffer Bonavent wrote the first draft; all authors contributed to interpretation of results and writing the text.

**ACKNOWLEDGEMENTS**

The technical staff at the Mols Laboratory are warmly thanked for their kind assistance during the field work. We are also indebted to Oskar Liset Pryds Hansen, Bjarke Madsen and Simon D. Schowanek, who were instrumental in the design, establishment and early maintenance of the experimental blocks at the Mols Laboratory. JCS considers this work a contribution to the Center for Ecological Dynamics in a Novel Biosphere (ECONOVO), funded by the Danish National Research Foundation (grant DNRF173) and his VILLUM Investigator project “Biodiversity Dynamics in a Changing World”, funded by VILLUM FONDEN (grant 16549).

**DATA AVAILABILITY STATEMENT**

The raw data are openly available in the Dryad repository at https://doi.org/10.5061/dryad.bnzs7h4g2.

**ORCID**

Rasmus Ejrnæs [https://orcid.org/0000-0003-2538-8606](https://orcid.org/0000-0003-2538-8606)
Camilla Flejgaard [https://orcid.org/0000-0002-5829-8503](https://orcid.org/0000-0002-5829-8503)
Signe Normand [https://orcid.org/0000-0002-8782-4154](https://orcid.org/0000-0002-8782-4154)
Jens-Christian Svenning [https://orcid.org/0000-0002-3415-0862](https://orcid.org/0000-0002-3415-0862)
Hans Henrik Bruun [https://orcid.org/0000-0003-0674-2577](https://orcid.org/0000-0003-0674-2577)

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**SUPPORTING INFORMATION**

Additional supporting information can be found online in the Supporting Information section at the end of this article.

**Appendix S1.** Additional details on the field work protocol.

**Appendix S2.** Parameters from calibration models estimating biomass from point intercepts, with separate models for single species, genera, functional groups, total biomass and standing litter.

**How to cite this article:** Bonavent, C., Olsen, K., Ejrnæs, R., Fløjgaard, C., Hansen, M.D.D., Normand, S. et al. (2023) Grazing by semi-feral cattle and horses supports plant species richness and uniqueness in grasslands. *Applied Vegetation Science*, 26, e12718. Available from: https://doi.org/10.1111/avsc.12718