frontiers | Frontiers in Ecology and Evolution

TYPE Original Research
PUBLISHED 26 January 2023
DOI 10.3389/fevo.2023.1107987

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OPEN ACCESS

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SPECIALTY SECTION
This article was submitted to Conservation and Restoration Ecology, a section of the journal Frontiers in Ecology and Evolution

RECEIVED 25 November 2022
ACCEPTED 10 January 2023
PUBLISHED 26 January 2023

CITATION
Köhler M, Schmidt A, Hölzel N, Baasch A and Tischew S (2023) Positive long-term effects of year-round horse grazing in orchid-rich dry calcareous grasslands–Results of a 12-year study.
Front. Ecol. Evol. 11:1107987.
doi: 10.3389/fevo.2023.1107987

Positive long-term effects of year-round horse grazing in orchid-rich dry calcareous grasslands–Results of a 12-year study

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Introduction: Dry calcareous grasslands are among the most species-rich habitats worldwide but strongly endangered by abandonment causing a severe decline of characteristic species such as orchids. To counteract further degradation, economically sustainable restoration tools such as megaherbivore grazing, that aim to substitute extinct wild grazers, should be considered. However, the long-term effects on target species of dry grasslands, and in particular for orchid populations, is still unclear.

Methods: To contribute to this knowledge gap, we applied vegetation surveys (5m × 5m), as well as large-scale census-based orchid observation and mapping of habitat structures (50m × 50m) in a year-round grazing scheme of a Natura 2000 site in Central Germany over 12 years. The horses and their grazing activity were observed *via* GPS telemetry. We fitted linear mixed models to evaluate whether *Ophrys apifera* density was affected by horse feeding frequency, habitat structure variables (bare soil patches, woody plant cover), grassland type or years.

Results: A The main results were that the target dry calcareous grassland vegetation significantly increased in species numbers and cover. The total abundance of *O. apifera* increased from 1,237 (2013) and 1,893 (2018), to 4,652 (2021) individuals. *Ophrys apifera* density was positively affected by horse feeding frequency as well as grazing-induced enhanced bare soil patches but underlying mechanisms varied between the three classified grassland types.

Discussion: Our results indicate that low-intensity year-round horse grazing as a relatively new restoration tool in dry calcareous grasslands has the potential to enhance floristic biodiversity in general, and particularly *O. apifera* density in the long run. Furthermore, we showed that highvalue xeric grasslands with outstanding orchid abundances can be integrated into the year-round grazing system and that there is no need of fencing off such sections.

KEYWORDS

***Ophrys apifera*, Orchidaceae, plant conservation, management, Konik horses, Natura 2000, remote sensing**

1. Introduction

Dry calcareous grasslands are among the most species-rich habitats of the European cultural landscape (Poschlod and WallisDeVries, 2002; Wilson et al., 2012). They are an essential refugium for low-competitive and often endangered species, such as orchids. Due to their high importance, these grasslands are to be maintained and developed *via* the European Natura 2000 network (Habitats Directive 92/43/EEC). Many dry calcareous grasslands currently show severe management deficits, mainly grass and/or shrub encroachment, due to the widespread cessation of domestic (seasonal) livestock grazing during the last century that has led to a loss of habitat function and biodiversity (Poschlod and WallisDeVries, 2002).

In the last two decades, year-round grazing systems with large herbivores aiming to substitute extinct wild grazers (Vera, 2000; Bunzel-Drüke et al., 2008; Svenning et al., 2016; Pedersen et al., 2020) are increasingly applied to counteract further degradation of nutrient-rich (Gilhaus et al., 2014) and nutrient-poor acidic grasslands or heathlands (Schwabe et al., 2013; Rupprecht et al., 2016; Henning et al., 2017a,b). For these habitats, large herbivores are known to shape the pasture through their specific feeding behavior and utilization (Putfarken et al., 2008; Gilhaus et al., 2014) creating diverse vegetation structures, appropriate biomass removal and improved light conditions at the soil surface through reduced litter layer and woody plant cover (Bokdam and Gleichnam, 2000; Hejcman et al., 2005; Borer et al., 2014). Periodic creation of bare soil patches by feeding and trampling can successfully reactivate the seed bank or provide better recruitment conditions especially for rare species with a high light requirement in the germination and establishment phase (Tischew et al., 2017; Elias et al., 2018), such as orchids (Hutchings, 2010).

EU Natura 2000 legislation has identified calcareous grasslands shaped by human intervention such as grazing and mowing as prime habitat for orchids (Olmeda et al., 2019). At the same time, orchids are believed to be very sensitive to disturbance (e.g., Catorci et al., 2013). Grazing before or during flowering is generally assumed to be (at least at some point) harmful to orchid species due to the mechanical destruction of sensitive leaves and inflorescences (Calaciura and Spinelli, 2008; Catorci et al., 2013). Hence, orchid-rich dry calcareous grasslands are often not integrated into grazing concepts due to expected damage by feeding and trampling through grazing animals, but are mown instead. Especially in the case of year-round grazing, negative grazing effects on orchid species are expected in the winter and spring months (Olmeda et al., 2019), as many species form leaf rosettes during this time. As a consequence, the most commonly applied management of orchid-rich habitats currently is single mowing or grazing within a vegetation season, ideally, after flowering and fruit set (e.g., Jersáková et al., 2015), while more frequent or year-round grazing is mostly considered as harmful and unsuitable. This point of view is often neglecting that grazing could provide open canopy gaps that are important for the regeneration of low-competitive and light demanding orchid species such as *Ophrys apifera*. This addresses the long-debated question in conservation of whether disturbance affects rare species generally in a negative or, in adjusted intensities, in a positive way and which mechanisms operate in this context in the long run (Grubb, 1977). However, only few studies investigated the dynamics of orchid populations under grazing regimes over several years revealing contrasting results. Hutchings (2010) recorded an increase of *Ophrys sphegodes* after the beginning of seasonal sheep grazing in a 32-year study, whereas Catorci et al. (2013) proclaimed spring grazing as threat for orchid species in general in a replicate study after 30 years. So far, Köhler et al. (2016) was the only study finding positive effects on the orchid species *O. apifera* in a year-round grazing system in a calcareous grassland. However, this study covered only 5 years and has raised questions about the long-term effects of year-round megaherbivore grazing on target species of calcareous grasslands.

This current study represents the rare case of a validation of findings from the early years of a large-scale real-life field experiment. In addition to the much longer observation period of 12 years, we observed in details the effects of habitat structures (litter, bare soil, herb layer and woody plant cover) and horse feeding frequency on the development of *O. apifera*. Factors crucial for target orchid development were determined in three different calcareous grassland types (xeric, dry, and dry-mesic). We addressed the following questions:

1. How does the small-scale dry calcareous grassland vegetation develop in terms of the number and abundance over the 12-year grazing period?
2. How does the population of the most important orchid target species *O. apifera* develop in the different calcareous grassland types over the grazing period and how is the density of the orchid affected by horse feeding frequency or habitat structures?

2. Materials and methods

2.1. Study site and study species

The study area comprises the 90 ha horse pasture in the nature reserve and Natura 2000 site "Tote Täler südwestlich Freyburg" in Central Germany (51°13′*N*; 11°46′*E*), *ca.* 250 m above sea level (see also Köhler et al., 2016). The climate is slightly continental with mild winters and warm, relatively dry summers (mean annual temperature: 8.3°C; mean annual precipitation: 565 mm). Shallow loess Luvisols on middle Muschelkalk prevail in the hilly region (Reichhoff et al., 2001).

The study area, surrounded by deciduous forests and arable land, is characterized by a plain, semi-open landscape formed by large-scale dry calcareous grasslands (Festuco-Brometea), patches of shrubs and trees as well as scattered old orchards and several historical small-sized sparsely vegetated quarries (Köhler et al., 2016). From 1950 to 1992 the area was used as a Soviet military training ground. After that period sheep herding was introduced to maintain the calcareous grasslands, but habitat quality decreased because of irregular grazing management with too low stocking rates and biomass removal, leading to highly grass encroached stands dominated by tall grasses such as *Arrhenatherum elatius*, *Bromus erectus* and *Brachypodium pinnatum* (Köhler et al., 2016). As a consequence, the floristic species composition typical of the habitat type 6210* orchid-rich semi-natural dry grasslands on calcareous substrates decreased in extent and quality. Further habitat information is given in Köhler et al. (2016).

In the study area, *O. apifera* Huds., the Bee Orchid has one of the largest regional populations. The critically endangered species of submediterranean distribution occurs on basophilic dry grasslands and light-rich forests (Jäger, 2017) but also is a major colonizer of former quarries and road verges (Gardiner and Vaughan, 2009). Currently, the species is expanding its range to the north, probably due to climate warming (in Saxony-Anhalt since about 1990: Meysel, 2011; in Poland since 2010: Osiadacz and Kręciała, 2014). *Ophrys apifera* is a long-lived perennial wintergreen geophyte and terrestrial orchid that is self-pollinating (Darwin, 1877) at its northern range of distribution (study area), but otherwise bee pollinated by the solitary bee genus *Eucera* (Kullenberg and Bergström, 2008). Plants produce one inflorescence with heights of 20–40 cm and 1–12 blossoms in May–June, fruit set begins in June–July (Ziegenspeck, 1936; Jäger, 2017). The plants emerge from tubers in early autumn and leaves continue to grow slowly during winter making the species exposed to grazing for a rather long period.

Leaves die back during flowering. Reproduction occurs by seeds and vegetatively (Lang, 1980).

2.2. Grazing management

In 2009, a year-round grazing system was introduced to manage the *ca.* 90 ha calcareous grassland (Köhler et al., 2016). The Konik Polski horses formed a herd with on average 18 adult horses (one stallion, 17 mares) and five foals. This results in a stocking rate of 0.3 livestock units (LU)/ha/a (assuming that one adult horse is counted as 1 LU and one foal 0.5 LU). In the first years of grazing, higher stocking rates up to 0.4 LU/ha/a helped repressing the encroachment with tall grasses and could be lowered with the improvement of the site. Additionally, single years of higher biomass production due to higher precipitation required slightly higher stocking rates. The robust breed was able to cope with near-natural conditions such as a very low level of additional winter feeding or rare veterinary intervention (further management information see Köhler et al., 2016).

2.3. Data collection and species classification

2.3.1. Small-scale observations of dry calcareous grassland vegetation

To study the vascular plant species composition of the target vegetation, we randomly established eight permanent 5 m × 5 m vegetation survey plots on the strongly grass encroached parts of the pasture in 2009. We conducted vegetation surveys in June/July annually from 2009 to 2015, and in 2018, and 2020. The calculation of conservation value for vascular plant species is based on the red-lists for Germany (Metzing et al., 2018) and Saxony-Anhalt (Frank et al., 2020). Nomenclature of vascular plants follows Jäger (2017).

We classified vascular plant species into the following ecological groups: target forbs, target grasses (both categories were selected according to the characteristic species of calcareous grasslands following the Habitats Directive), other dry grassland species (including rare ecotone species), mesic grassland species, ruderals and woody plants (Jäger, 2017; species list see Supplementary Table SA1). Each species only belongs to one group.

2.3.2. Large-scale observations of *Ophrys apifera*, habitat structures and horse feeding frequency

Ophrys apifera and habitat structures were observed on grid cells. To stratify habitat structure in orchid census observation grid cells, three vegetation types were classified according to the habitat types of the EU Habitats Directive. Differences in vegetation cover and bare soil patches served as proxies for soil depth and grassland productivity. Xeric calcareous grasslands (xeric) on shallow soils harbored characteristic species of basophilic grasslands of the Alysso-Sedion albi, code 6110* and a range of xeric grassland species such as *Galatella linosyris*, *Teucrium botrys* or *T. chamaedrys* with a total area of 11 ha and 13.6% of the pasture, respectively (red sites in Figure 1). Dry calcareous grasslands (dry) covered 64 ha (76.5%) of the pasture and were dominated by *B. pinnatum*, *Festuca rupicola* or *Scabiosa ochroleuca* (Semi-natural dry grasslands and scrubland facies on calcareous substrates Festuco-Brometalia, code 6210*, green sites in Figure 1). Dry-mesic calcareous grasslands (dry-mesic) on slightly deeper and more productive soils

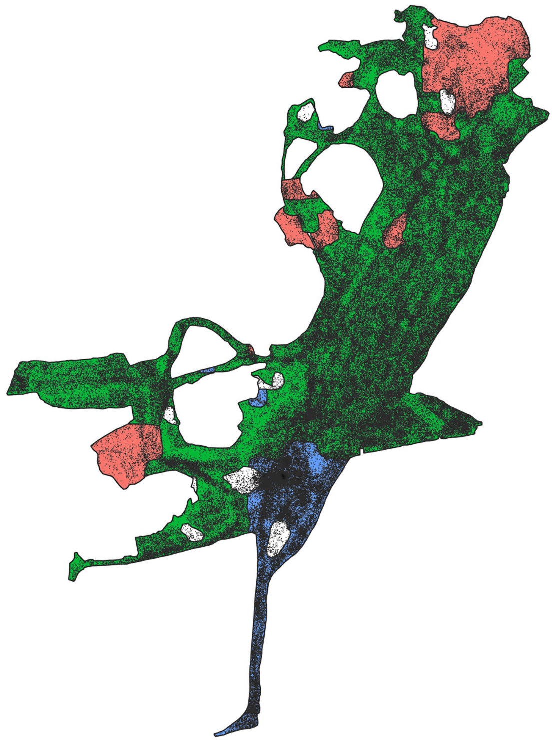

FIGURE 1
Heat map of horse feeding frequency from April–March from 2011 to 2021 (black points correspond to GPS positions). Cover of calcareous grassland types are marked red (xeric), green (dry) and blue (dry-mesic). White sites refer to dense patches of high woody vegetation and forests without remarkable grassland vegetation.

were characterized by dry as well as mesic grassland species such as *A. elatius*, *F. rupicola* or *Origanum vulgare*. In the study area, floristic species composition contains not only submediterranean but also a range of continental species. That vegetation type was found on 8 ha (9.9%) of the pasture (blue sites in Figure 1). The study area was divided into 449 50 m × 50 m grid cells using ArcGIS, of which 121 grid cells were randomly selected proportionally to the size of the three calcareous grassland types (number of grid cells on xeric: 17, dry: 96, dry-mesic: 8). Grid cells with larger patches of high woody vegetation and forests (white sites in Figure 1) were excluded from the selection procedures as not appropriate for *O. apifera*. The selected grid cells covered 32% (27.4 ha) of the *ca.* 90 ha pasture.

In April of 2013, 2018 and 2021, the number of *O. apifera* individuals at leaf rosette stage was counted in every grid cell in March. Since a few grid cells did not reach full plot size due to pasture fence boundaries, *O. apifera* density was calculated for each grid cell to equal the slightly different grid cell sizes. In 2011, 2012, 2014, 2018, and 2020, habitat structure data (percent cover of litter layer, bare soil patches, herb layer and woody plants) was collected on the grid cells *via* field surveys. Starting in January 2010, the position and activity of the free-ranging horses on the pasture were recorded using remote sensing *via* a GPS PLUS-4 collar (Vectronic Aerospace GmbH Berlin). As the horses showed gregorial behavior, one collar on a female horse recorded spatio-temporal information in 10-min intervals in WGS 84 and UTC time as well as angle and acceleration differences in 2-min intervals *via* a two-axis accelerometer. Inaccuracy of GPS signals due to atmospheric conditions or satellite errors may have resulted in some imprecision of our data. In order to interpret the collar activity data, we collected direct observational behavioral data in the field that was matched to the collar data *via* consistent timestamps (every minute for 881 h on 52 days from 2010 to 2012). During our direct behavioral observations, we did not detect abnormal behavior of the telemetered horse. A discriminant analysis was applied to classify the main behavioral groups feeding, resting and walking of the recorded telemetry data according to the direct observations in the field. As feeding, which always includes walking, was assumed to have the highest impact on the growth cycle of the target orchid species, we selected the horses´ feeding frequency to explain orchid development (Figure 1). The amount of horse feeding frequency data was calculated in each grid cell for one m^2 in ArcGIS (amount of GPS positions classified into feeding per grid cell/grid cell area), as the grid cells cutting the pasture margins showed slightly reduced sizes.

2.4. Statistical analysis

We used non-parametric Friedman tests to test for differences of total species numbers, species numbers and covers within the ecological groups of the small-scale observations of dry calcareous grassland vegetation through time.

Linear mixed models (LMM) were fitted to evaluate whether the density of *O. apifera* was affected by horse feeding frequency, habitat structure variables (bare soil patches, woody plant cover), grassland type or years (Table 1), using lme4 1.1–21 (Bates et al., 2015) and MuMIn 1.43.17 for multi-model selection and averaging (Bartoń, 2020). The cover of the herb as well as litter layer had to be excluded from the modeling process to avoid strong inter-correlations among the predictors ($|r| > 0.6$, Pearson's correlation analysis, $r_{\text{bare soil} \sim \text{herb layer}} = -0.735$, $r_{\text{bare soil} \sim \text{litter layer}} = -0.683$). Moreover, we included all two-way interactions. To achieve normally distributed residuals and avoid heteroscedasticity, we inverse-transformed the density data prior to statistical analysis. Assumptions were checked graphically as recommended by Smith et al. (2009). Possible dependence in the data due to repeated measurements in the same permanent grid cells was controlled by incorporating grid number as random variable in the models. Multi-model selection was based on Akaike information criterion (AIC). For model averaging, we selected all models with $\Delta AIC < 4$ compared to the best model according to AIC.

We implemented all statistical analyzes in R version 4.0.2 (R Core Team, 2020), all telemetry data analyzes in SPSS version 20.0 (IBM Corp. Released, 2011; ArcGIS® 10.1 Software by Esri, 2012).

3. Results

3.1. Development of dry calcareous vegetation under year-round grazing (small scale)

In total, we observed 134 vascular plant species within the eight 5 m × 5 m vegetation survey plots during the entire period of observation, among them 13 endangered red list species (Supplementary Table SA1). Total mean species number significantly increased from 30.3 ± 3.5 to 38.5 ± 2.9 (mean ± SE; df = 8, Qui-square = 41.717, $p < 0.001$, Friedman test).

Different ecological species groups showed varying effects in response to horse grazing. In total, 35 target for species were recorded on all plots with significantly increasing species numbers from 9.9 ± 1.5 to 14.5 ± 1.5 (mean ± SE; Figure 2). In addition, mean number of other dry grassland species and ruderals significantly increased, whereas mesic grassland species significantly decreased (Figure 2). Mean number of target grasses and woody plants remained constant.

From 2009 to 2020, cumulative cover of target forbs, e.g., *Asperula cynanchica*, *Hippocrepis comosa*, *Potentilla neumanniana*, *S. ochroleuca* or *Thesium linophyllon*, as well as other dry grassland species and ruderals significantly increased by 18.1, 4.4 and 2.6%, respectively (Figure 3). On the contrary, cover of ecological species groups indicating abandonment of dry calcareous grasslands such as target grasses and mesic grassland species significantly decreased by 24.2 and 5.6%, respectively (Figure 3). Grass encroachment was mainly built of the target grass species *B. pinnatum* and *B. erectus*. Mean cover of woody plants remained constant on the small-scale plots (Figure 3).

3.2. Development of the target orchid species *Ophrys apifera* under year-round grazing (large scale)

3.2.1. Habitat structures and horse feeding frequency

For large-scale grid cell observation, the study site was stratified in three different grassland types covering xeric, dry and dry-mesic

TABLE 1 Results of the linear mixed-effect model for effects of horse feeding frequency, woody plant cover, bare soil patches, year (three-level factor) and grassland type (three level factor) on density of the target orchid species *Ophrys apifera*.

Density *Ophrys apifera*	Estimate	SE	*P*
Intercept	−41.727	11.673	<0.001
Mean woody plant cover	−6.374	2.465	0.010
Mean horse feeding frequency	42.843	10.879	<0.001
Mean cover bare soil patches	8.144	2.806	0.004
Dry grassland type	−41.735	12.065	0.001
Dry-mesic grassland type	−45.078	17.317	0.009
Year 2021	29.042	6.605	<0.001
Mean horse feeding frequency: dry grassland type	−50.294	11.130	<0.001
Mean horse feeding frequency: dry-mesic grassland type	−44.216	11.556	<0.001
Dry-mesic grassland type: year 2021	−27.434	11.115	0.014

Estimates of model-averaged coefficients are shrinkage estimates including all selected models from model averaging (full model average). Non-significant factors are not displayed but can be found in Supplementary Table SA2. Intercept: Year 2013, xeric grassland type.

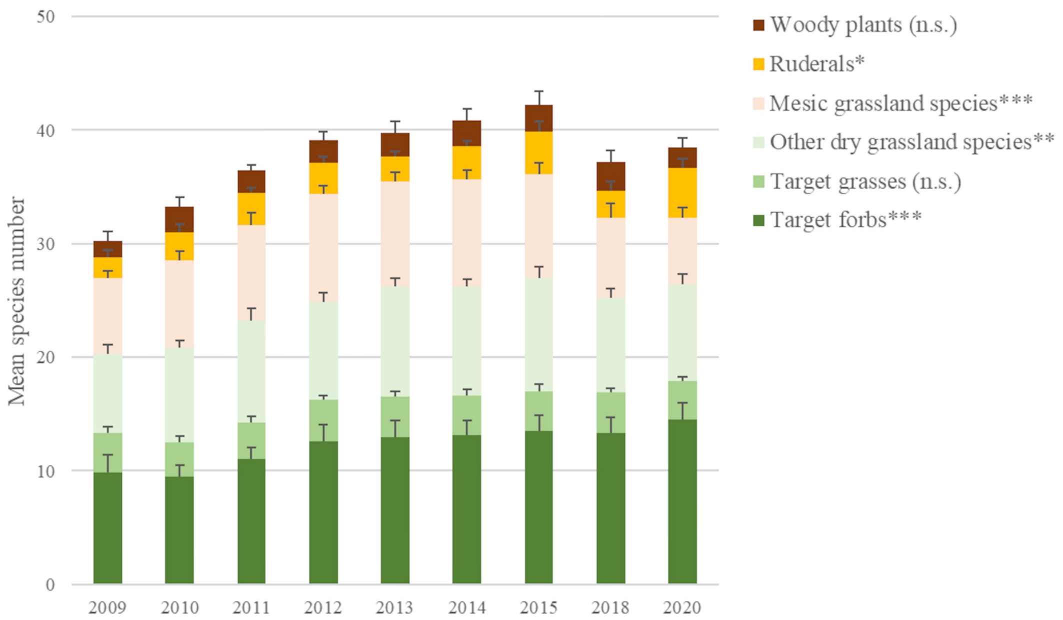

FIGURE 2
Mean vascular plant species number on grazed vegetation survey plots (5m×5m, *n*=8). Significant changes in ecological groups over 9 observational years (2009 to 2015, 2018, 2020) are marked with asterisks (n.s. not significant, *p<0.05, **p<0.01, ***p<0.001; Friedman tests: Target forbs: df=8; Qui-square=37.479; p<0.001; target grasses: df=8; Qui-s. = 5.539; p=0.699; other dry grassland species: df=8; Qui-s. = 25.071; p=0.002; mesic grassland species: df=8; Qui-s. = 31.212; p<0.001; ruderals: df=8; Qui-s. = 15.550; p=0.049; woody plants: df=8; Qui-s. = 11.250; p=0.188). Error bars indicate standard error.

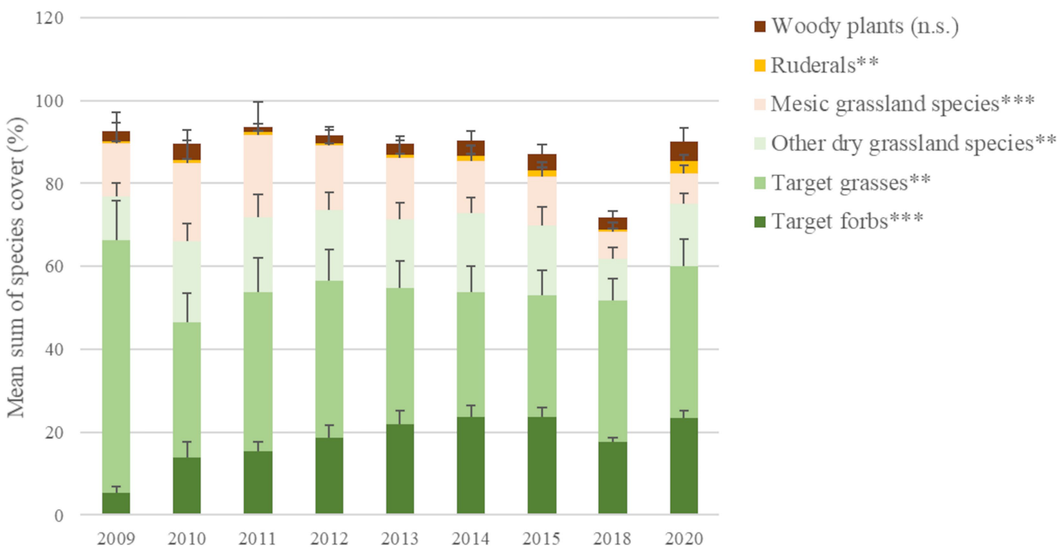

FIGURE 3
Mean cumulative cover of vascular plant species in grazed vegetation surveys (5m×5m, *n*=8). Significant changes in ecological groups over 9 observational years (2009 to 2015, 2018, 2020) are marked with asterisks (n.s. not significant, *p<0.05, **p<0.01, ***p<0.001; Friedman tests: Target forbs: df=8; Qui-s. = 36.800; p<0.001; target grasses: df=8; Qui-s. = 23.933; p=0.002; other dry grassland species: df=8; Qui-s. = 25.700; p=0.001; mesic grassland species: df=8; Qui-s. = 30.407; p<0.001; ruderals: df=8; Qui-s. =21.201; p=0.007; woody plants: df=8; Qui-s. = 12.865; p=0.117). Error bars indicate standard error.

calcareous grasslands. Litter layer decreased in all calcareous grassland types but most in the dry grassland grid cells. Highest reduction occurred in the first years of grazing, before reaching a stable level of 15–20% in 2018 and 2020 (Figure 4). Area of bare soil patches showed highest values of about 55% in xeric grasslands from the beginning of the survey, whereas in both, dry and dry-mesic grasslands, values were half these maximum values but increased over time (Figure 4). In general, litter layer decreased while herb layer increased. Highest increase in herb layer occurred in the dry grasslands, while dry-mesic grasslands remained constant at *ca.* 60–70% cover (Figure 4). Herb layer in xeric grasslands only slightly increased with significant values since 2018. According to the large-scale observation, woody plant cover was slightly higher in xeric grassland grid cells than in dry or dry-mesic grasslands where horse feeding frequency was highest (Figures 4, 5). In

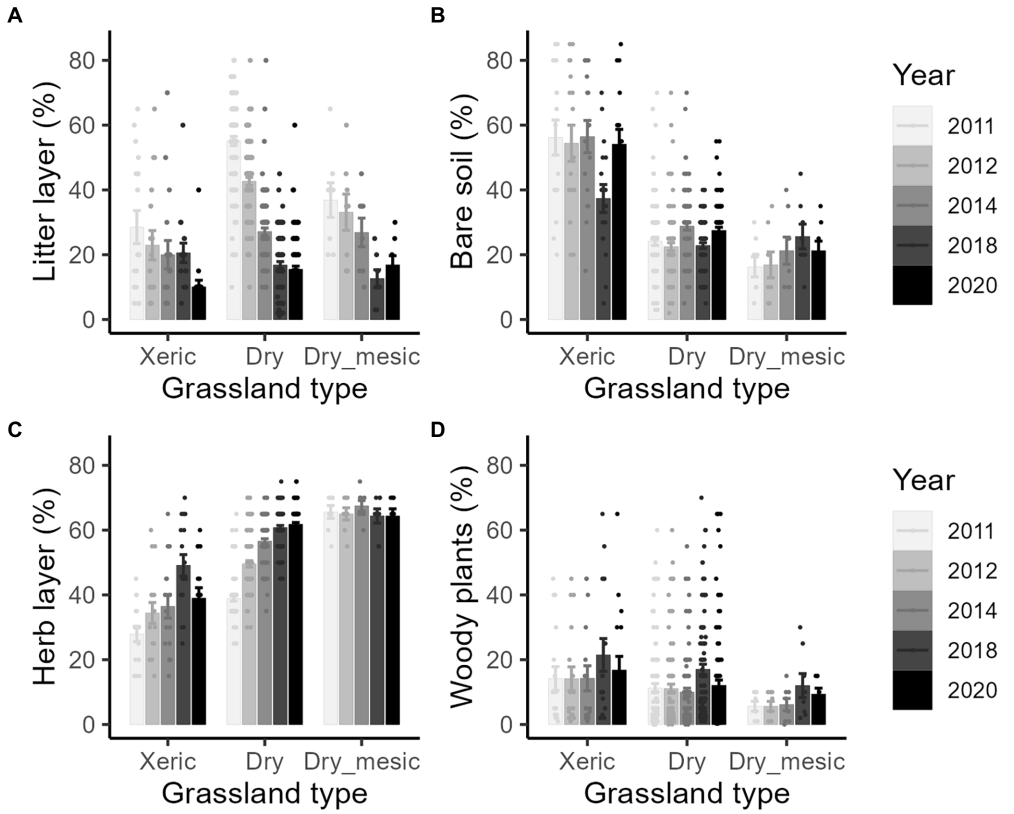

FIGURE 4
Mean values (± SE) of percent cover of habitat structures litter layer **(A)**, bare soil **(B)**, herb layer **(C)** and woody plants **(D)** on the grid cells (50m×50m) in the year-round horse pasture in the different calcareous grassland types (*n*=121; xeric *n*=17, dry *n*=96, dry-mesic *n*=8) in the years 2011, 2012, 2014, 2018 and 2020. Points correspond to the respective data sets.

all vegetation types woody plant cover remained constant at about 15% until 2017 and only slightly increased in 2018.

Horse feeding frequency in xeric grassland grid cells showed lowest means and did not markedly change over the entire grazing period (Figures 1, 5). In grid cells harboring dry calcareous grasslands horse feeding frequency was twice as high compared to xeric grasslands, while highest horse feeding frequency was recorded in dry-mesic grassland grid cells with varying mean values over the period of observation (Figures 1, 5). In 2020, lower values correspond with the partial absence of horses (due to low fodder availability related to the extreme drought).

3.2.2. Development of *Ophrys apifera* and effects of habitat structures and horse feeding frequency

The total number of recorded individuals of the target orchid species *O. apifera* in the 121 grid cells continuously and significantly increased from 1,237 in 2013 and 1,893 in 2018, to 4,652 in 2021. Hence, the total number of individuals clearly increased, and was estimated to be at least 10,000 individuals in the entire pasture in 2021.

Ophrys apifera density significantly varied in the different calcareous grassland types showing highest values in xeric, medium in dry and lowest in dry-mesic grassland grid cells (Table 1; Figure 6). Within the observation period, density doubled in xeric (almost) and dry grassland (significantly) grid cells from 2018 to 2021 (Figure 6). Density in dry-mesic grasslands remained stable from 2013 to 2021. The total number of *O. apifera* individuals was highest in dry, and twice as high as in xeric grassland grid cells.

Horse feeding frequency affected the density of *O. apifera* positively but showed varying effects between grassland types (Table 1; Figures 7, 8; Supplementary Table SA2). In xeric grasslands, grid cells with higher horse feeding frequency also had a higher *O. apifera* density compared to xeric grassland grid cells of low horse feeding frequency. In contrast, in dry-mesic grasslands which generally exhibited the highest horse feeding frequency (compared to the xeric and dry grassland type), the grid cells with a higher *O. apifera* density tended to be frequented less often. The increase of *O. apifera* on dry grasslands covered a relatively broad range of horse feeding frequency and contributed most to the overall increase of individuals (Figure 7). A high cover of bare soil patches was predicted to have the second largest positive effect. In contrast, grid cells with a higher woody plant cover were predicted to show a lower density of *O. apifera*. High horse feeding frequency was negatively correlated with woody plant cover ($r_{\text{woody plant cover} \sim \text{horse feeding frequency}} = -0.382$, $p = <0.001$, Pearson's correlation coefficient).

4. Discussion

4.1. Year-round grazing effects on small-scale dry calcareous vegetation

We investigated the number and cover of characteristic dry calcareous grassland species over a study period of 12 years in a year-round horse grazing regime. We found a constant increase particularly of target forbs which only decreased in cover due to the severe drought

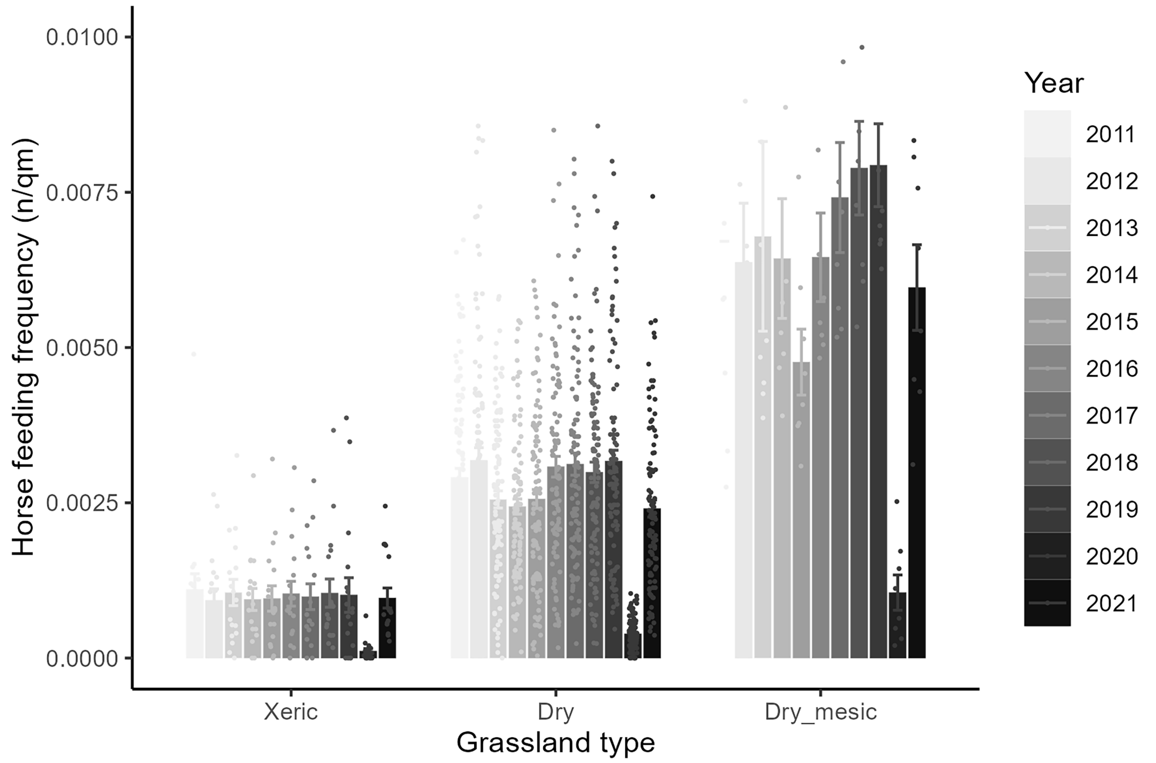

FIGURE 5
Mean values (± SE) of horse feeding frequency per qm on the grid cells in the different calcareous grassland types (*n*=121; xeric *n*=17, dry *n*=96, dry-mesic *n*=8) from April–March from 2011–2021. Lower values in 2020 referred to partial absence of horses (due to low fodder availability related to the extreme drought). Points correspond to the respective single data sets.

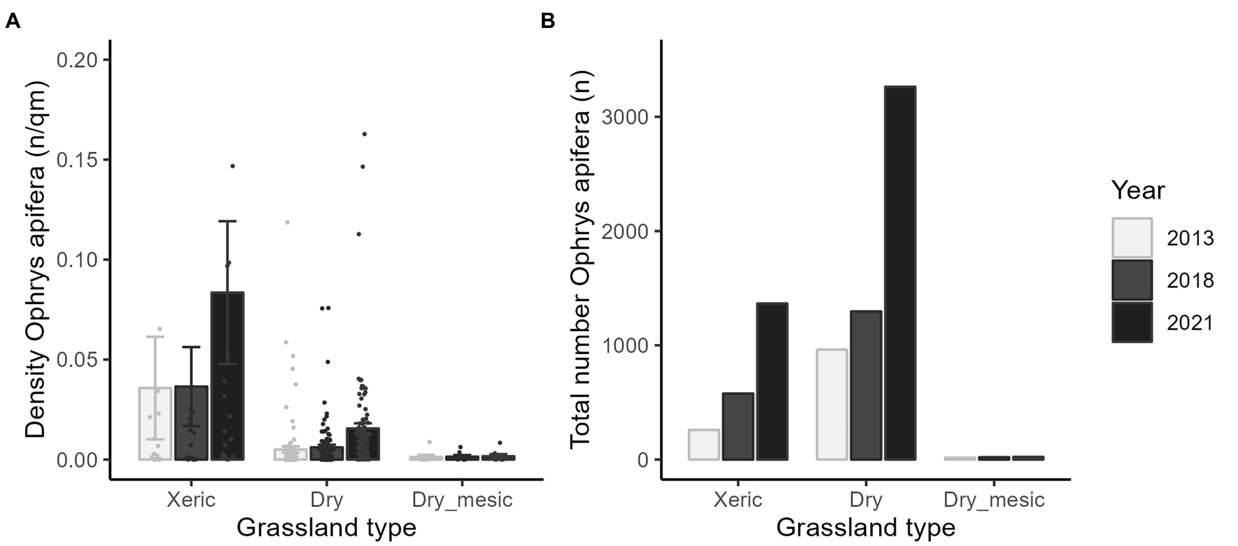

FIGURE 6
Mean values (± SE) of the density **(A)** and total number **(B)** of *Ophrys apifera* on the grid cells in the different calcareous grassland types (*n*=121; xeric *n*=17, dry *n*=96, dry-mesic *n*=8) in the years 2013, 2018 and 2021. Values 0.546, 0.440 and 0.347 **(A)** and 407 **(B)** are not displayed. Points correspond to the respective data sets.

in Central Germany in 2018, whereas the cover of target grasses significantly decreased. Low competitive dry grassland species depending on bare soil patches benefited from grazing and increased. This finding emphasizes that the typical floristic species composition can be maintained and even improved by year-round grazing not only over short periods (Köhler et al., 2016), but also in the long run. Several studies have reported a positive impact of year-round equid grazing on the abundance of target species of dry sandy grasslands (Süss and

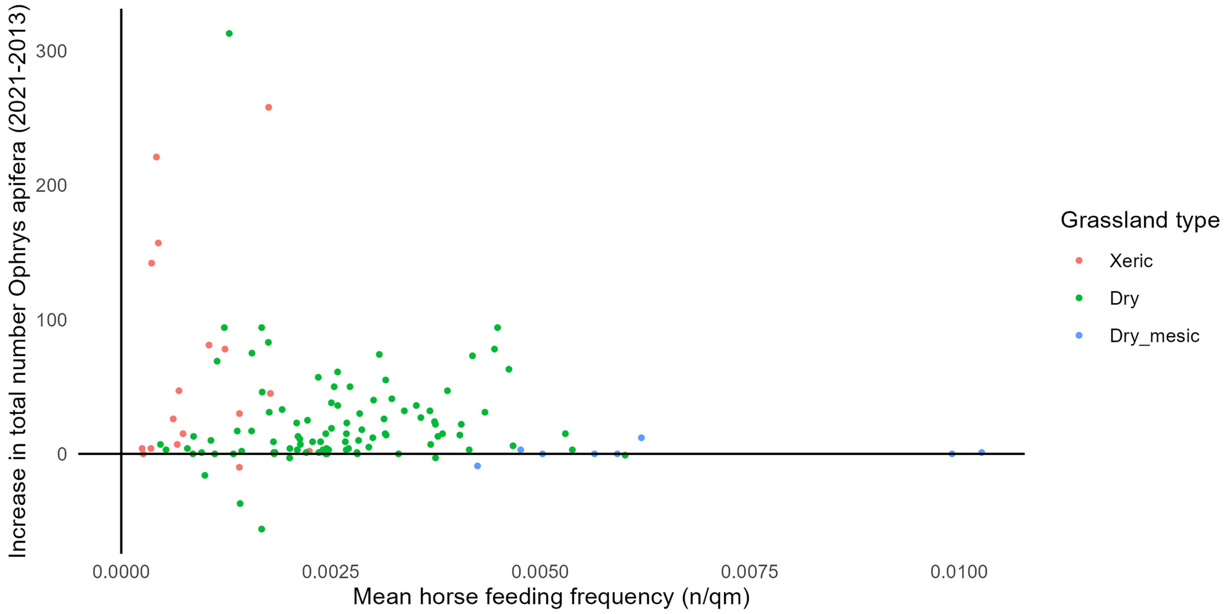

FIGURE 7
Increase in total number of *Ophrys apifera* from 2013 to 2021 and mean horse feeding frequency from April–March from 2011–2021 on the grid cells in the different calcareous grassland types (*n*=121; xeric *n*=17, dry *n*=96, dry-mesic *n*=8).

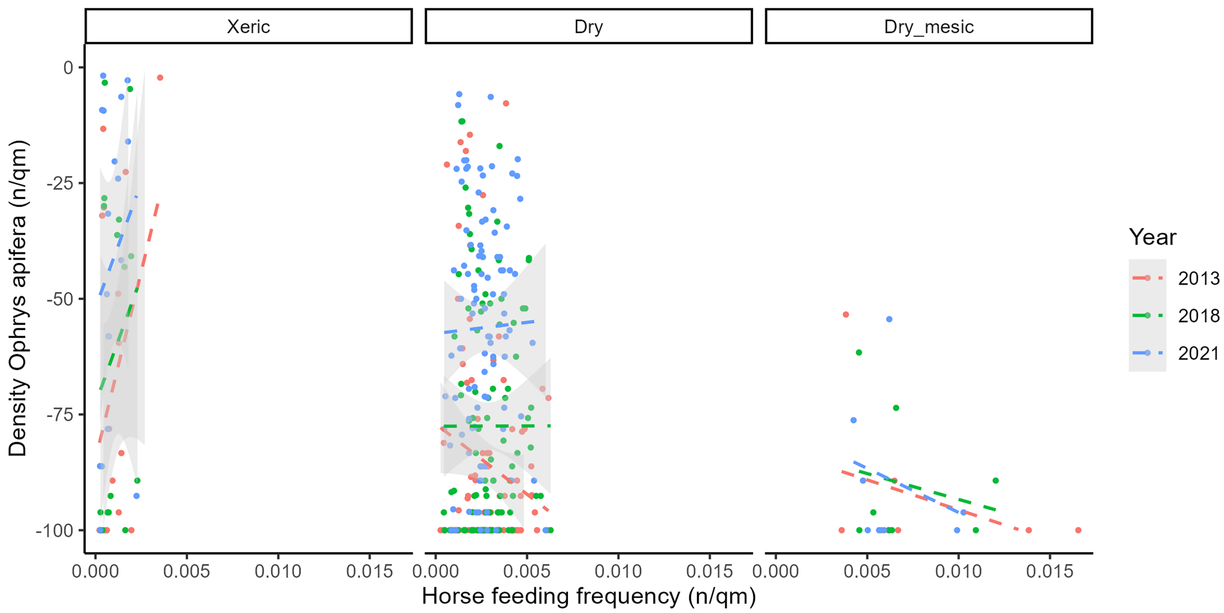

FIGURE 8
Effect of horse feeding frequency on inverse-transformed density of *Ophrys apifera* in the different calcareous grassland types in 2013, 2018 and 2021 (*n*=121; xeric *n*=17, dry *n*=96, dry-mesic *n*=8). Shaded area represents 95% confidence intervals.

Schwabe, 2007; Schwabe et al., 2013; Henning et al., 2017a) assuming that a sufficient, adapted stocking rate is guaranteed as undergrazing can lead to ruderalization or tall species dominance (Sýkora et al., 2009; Moinardeau et al., 2021). Concerning faunistic diversity, forb enhancement of grassland is usually beneficial to insects as forbs provide both nesting and foraging sites (Bonari et al., 2017), and in the consequence beneficial to higher trophic animal species like birds (Lovász et al., 2021; Schmidt et al., 2022).

Compared to other grazing animal species such as cattle, sheep or goats, equids can compensate low-quality forage through increased, nearly permanent feeding (Duncan et al., 1990; own observation data). As equids show a preference for grass species, grasses are disproportionately more frequently used compared to forbs. Grass species, almost indigestible for many herbivores due to silicate inclusion in the cells and lignifying fibers, can be digested by equids because of their digestive system geared to fiber utilization and high-crowned teeth protecting from abrasion (coevolution of grasses and grazers beginning in the Tertiary; Stebbins, 1981; Bunzel-Drüke et al., 2008). These characteristics make horses well suited to reduce grass encroachment in dry grasslands (Süss and Schwabe, 2007; Schwabe et al., 2013).

We found that ruderals significantly increased only in the long-term observation period, probably due to enhanced disturbance and more bare soil patches created by the continuous reduction of herb and litter layers through grazing in the long run. The observed short-lived, small-growing, thermophilic ruderal species such as *Arenaria serpyllifolia*, *Cerastium pumilum* or *Draba verna* are seen as intrinsic part of pastures that enhance their biodiversity (Elias et al., 2018; Köhler et al., 2020) as well as nectar and pollen supply for insects, but do not affect the species assemblage of dry grasslands due to the low increase of cover. Extended nitrophilous ruderal patches that are often discussed as problematic in grazed areas, have not been observed in our study, most likely due to the generally low nutrient levels. Generally, the different types of zoochory leading to species dispersal inside the pasture are seen as the main driver of long-time establishment success of target species (Kiss et al., 2021), emphasizing the benefits of grazing compared to mowing.

4.2. Large-scale effects of year-round grazing on *Ophrys apifera*

We evaluated the long-term effects of year-round horse grazing on the target orchid species *O. apifera* in a dry calcareous grassland using data on habitat structures and horse feeding frequency. We found a continuous significant increase of the counted *O. apifera* individuals on most observed grid cells from 2013 to 2021. This important finding means that low-intensity horse grazing is generally suitable for orchid species maintenance and promotion on large-scale, plain dry calcareous grasslands. The orchid species' ability to cope with permanent grazing has already been demonstrated by Köhler et al. (2016) for a 5-year grazing period. In this study, we confirm these results for a 12-year period and clarified relevant mechanisms in the different calcareous grassland types. Across all three calcareous grassland types, horse feeding frequency had an overall positive effect on the density of *O. apifera* individuals. However, *O. apifera* abundance varied inside the pasture due to differently appropriate site conditions. Particularly, the increase of bare soil patches and the reduction of litter layers induced by feeding and trampling led to lower competition through the surrounding vegetation and to enhanced light availability on the ground (Borer et al., 2014) creating niches for orchid recruitment and seedling establishment (Shefferson et al., 2020). In addition, biomass and particularly grass cover reduction also diminished vegetation competition.

Sites characterized by shallow soils, a high share of bare soil patches and low vegetation cover that harbor xeric calcareous grassland species showed highest initial *O. apifera* abundance at the beginning of the study. Here, lowest horse feeding frequencies were recorded over the observation period, as grazers probably avoided grassland patches with both low fodder availability and quality (Gilhaus et al., 2014). However, under this condition of generally very low grazing intensity, the higher the feeding frequency, the more positive it affected *O. apifera* density due to the better reduction of litter layer and the dynamic creation of bare soil patches. Hence, these high-value xeric grasslands can be integrated into the grazing system contrary to often recommended fencing off (Calaciura and Spinelli, 2008; Catorci et al., 2013), at least in large-scaled pastures (>10, better >50 ha; Bunzel-Drüke et al., 2008) where sites of higher productivity are preferentially grazed.

Sites, that were initially less suited for orchid occurrence due to heavy grass encroachment and thick litter layers, were characterized by higher vegetation cover of dry calcareous grasslands. These sites were significantly more frequented by the horses due to higher fodder availability and quality. On this grassland type, that had by far the largest area share (80.9%), *O. apifera* density was significantly lower at the beginning of grazing compared to xeric grasslands. But, surprisingly, it also increased significantly and contributed most to the increase in numbers of individuals due to enhanced habitat quality. The benefits of grazing for the development of *O. apifera* in this grassland type were most effective at a medium horse feeding frequency, since grazing frequency did not show an explicit effect on the individual density. On grid cells with a higher grazing frequency, positive grazing effects seemed to be able to outbalance negative effects such as trampling and feeding on *O. apifera*.

Grid cells of the dry-mesic calcareous grassland type were *per-se* sub-optimal sites for orchid occurrence as characterized by deeper soils, supporting more mesic, higher-competitive species. On these (rather small) sites of the pasture, horse feeding frequency showed significantly highest values probably due to higher protein forage compared to dry and xeric grasslands (Gilhaus et al., 2014). But even on these sites, *O. apifera* individual density was stabilized during the horse grazing experiment. Here, grid cells with lower or medium horse feeding frequency maintained *O. apifera* populations, while at higher horse feeding frequency a slightly negative effect was observed (Figure 8).

In contrast to other studies reporting direct negative grazing effects on orchids by feeding and trampling (Calaciura and Spinelli, 2008; Catorci et al., 2013; Cleavitt et al., 2016), we found positive effects of year-round grazing. Horses that intentionally graze orchid inflorescences or leaves were not observed in our study (field observation). *Vice-versa*, horse grazing was shown to maintain or create habitat structures that supported the strong population increase of the target orchid species. A crucial factor for this development was the increase of bare soil patches mainly induced by grazing and trampling. The establishment of many orchid species is not limited by seed but microsite availability (Shefferson et al., 2020). Hutchings (2010) reported site disturbance as a key driver of species recruitment *of O. sphegodes* and Gardiner and Vaughan (2009) outlined that site disturbance at road verges enhanced *O. apifera* abundance. The regular and dynamic creation of bare soil patches might be the main advantage of large herbivore grazing in comparison to mowing or small-scale rudimentary grazing. Intermediate disturbance often initiates positive processes such as species establishment and should not only be discussed as generally problematic in conservation and restoration ecology (Grubb, 1977).

In contrast to other reports of the failure of year-round horse grazing to counteract woody plant encroachment (e.g., Cosyns et al., 2001), our study revealed that woody plant cover only slightly increased under grazing impact in the long term, indicating the potential of horses to prevent significant increase of woody plant cover in low precipitation habitats with relatively low initial woody plant cover. In addition, only a few potentially invasive, stoloniferous woody species were present on the pasture (Köhler et al., 2016) and additional mineral supply was limited enhancing the intensity of browsing (especially bark peeling) to meet the mineral requirements particularly in the winter months (Putfarken et al., 2008). Moreover, only marginal areas needed additional restoration treatment such as mechanical shrub removal to achieve restoration targets compared to other similar pasture regimes (e.g., Henning et al., 2017a). For the positive development of target bird communities, remaining individual shrubs as well as groups of shrubs and small forest patches should be considered as beneficial (Köhler et al., 2016; Lovász et al., 2021).

Besides grazing, there might be other factors influencing orchid density. *Ophrys apifera* shows a general increase and range extension probably due to climate warming in Saxony-Anhalt and Central Europe since the 1990s (Hutchings, 2010; Meysel, 2011; Osiadacz and Kręciała, 2014). Increases to such an extent have not been observed in other pastures in Saxony-Anhalt but the species often even decreased due to poor management. A not yet published dataset of the regional working group Arbeitskreis Heimische Orchideen Saxony-Anhalt e.V. shows clearly that in an area managed by mowing the number of *O. apifera* individuals remained stable over the same period, but did not increase. Yet, clarifying studies about climate impact on population growth and range expansion of *O. apifera* are missing. Fast population development in the pasture may also derive from relatively short reproduction cycles between germination and first appearance of *O. apifera*. Ziegenspeck (1936) suggested that the species can produce leaves after only 1 or 2 years.

4.3. Conclusion

Our results indicated that year-round horse grazing as a relatively new grassland restoration tool has the potential to enhance floristic biodiversity of dry calcareous grasslands not only in the short, but also in the long term. Particularly, the development of orchid species has to be evaluated differentially, when assessing the restoration success. Since pastures usually consist of heterogeneous vegetation types with varying suitability for orchid establishment, practitioners should not only rely on mean values concerning the entire pasture to regulate management but also on decrease and increase of individuals in individual vegetation types as the potential for local new establishment can strongly vary. In our study site, numbers of *O. apifera* increased most significantly in the prevailing medium dry calcareous grassland type and this type contributed most to the overall increase of individuals. Furthermore, our study clearly showed that even high-value xeric grasslands with very high orchid abundances can be integrated into the year-round grazing system also in the long term, and there is no need to the often recommended fencing off (exclosure) of such particularly valuable areas. Our study also revealed that short-term, especially one-year-only evaluation of restoration schemes can be misleading, particularly at slow-changing indicators such as dry calcareous vegetation types and at slow-growing and longer-lived species or those exhibiting high interannual population fluctuations such as many orchid species. Long-term monitoring schemes should be implemented to meet these requirements and to obtain found results on the effects of restoration and management measures.

Data availability statement

The raw data supporting the conclusions of this article will be made available by the authors, without undue reservation.

Ethics statement

Ethical review and approval was not required for the animal study because our work was a purely observational study and no ethical approval was needed. The GPS collar that provided our horse feeding frequency data was fitted and regularly controlled on one female horse without using any external devices such as sedation. In order to access the telemetry data, no direct animal contact was needed. Written informed consent was obtained from the owners for the participation of their animals in this study.

Author contributions

MK and ST developed the research questions and plot selection. MK collected the data and wrote the manuscript. MK and AS analyzed the data. AS, AB, NH, and ST contributed critically to the drafts and gave final approval for publication. All authors contributed to the article and approved the submitted version.

Funding

Funding was provided by the European Agricultural Fund for Rural Development (EAFRD) and the state of Saxony-Anhalt (407.1.7–60128/323009000054, 323010000089, 323012000034, and 630116000006) and by the Graduate Scholarship Program of Saxony-Anhalt. We acknowledge support by the German Research Foundation (Deutsche Forschungsgemeinschaft DFG) -project number 491460386 - and the Open Access Publishing Fund of Anhalt University of Applied Sciences.

Acknowledgments

The authors thank Georg Hiller and Frank Meysel as well as all students who helped with the data collection in the field, particularly horse observations, the Nature Conservation Authority Burgenlandkreis for implementing the financial support of the pasture, the Agrar GmbH Crawinkel for implementing the management, the owner of the site Naturstiftung David – Die Stiftung des BUND Thüringen and further cooperation partners.

Conflict of interest

The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

Supplementary material

The Supplementary material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fevo.2023.1107987/full#supplementary-material

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