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RESEARCH ARTICLE

Fallow deer foraging alone does not preserve the vegetation of traditionally sheep-grazed calcareous grasslands

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Abstract

1. The goal of this study was to evaluate to what extent wild ungulates (fallow deer) can contribute to the maintenance of semi-natural calcareous grasslands, which are a threatened habitat type (natura 2000 code *6210).
2. In a 10-year exclosure experiment, we tested the effects of ungulate foraging using three treatments: (A) control with combined foraging of herded sheep and wild fallow deer, (B) sheep exclosure with only deer foraging and (C) total exclosure with no foraging.
3. Treatments not grazed by sheep (B, C) were characterized by significantly declining species numbers, litter accumulation and shrub encroachment. Despite high population densities, the effect of fallow deer alone (B) was weak: Succession of woody species was only partly inhibited, while annuals, short-growing and rosette-building plant species were strongly suppressed by litter accumulation.
4. Only the combination of sheep and fallow deer foraging preserved vegetation structure and species richness and led to a promotion of target species.
5. *Synthesis and applications*. We conclude that we need to continue the traditional land-use forms such as sheep grazing in order to maintain calcareous grasslands. However, we should also raise our awareness for wild animals and analyse more in depth their potential contribution to the conservation management of open habitats.

KEYWORDS
calcareous grassland, conservation management, fallow deer, litter, rewilding, sheep, shrub encroachment, succession

1 | INTRODUCTION

Species-rich semi-natural grasslands are dependent on continuous biomass removal (Valkó et al., 2018), which reduces plant competition for light and prevents litter accumulation. This creates favourable conditions for several less competitive, short-growing and light-demanding species (Borer et al., 2014) leading to high species numbers and supporting endangered target species. Biomass was traditionally removed by grazing, mowing or burning.

These land use forms were widely abandoned in low-productivity grasslands due to drastic changes in land use in Central Europe over the last century (Poschlod et al., 2005). This resulted in a radical decline of species-rich semi-natural habitats with negative consequences for biodiversity. This process especially affected semi-dry calcareous grasslands that occupy shallow infertile soils on limestone substrates (WallisDeVries et al., 2002). Today, they are endangered throughout Central Europe (Finck et al., 2017). Due to their high richness in specialized and endangered plant and animal species, calcareous grasslands are protected habitats under the EU Habitats Directive in Europe (Ssymank et al., 1998). The main threats for such grasslands are abandonment, land-use intensification and conversion into forest or arable land. Traditionally, sheep pasture has been the predominant management practice that is crucial for maintaining diverse calcareous grasslands (WallisDeVries et al., 2002). Today, it is difficult to preserve this habitat by grazing for cultural and socio-economic reasons, such as the low profitability of sheep breeding caused by declining meat and wool prizes in the course of highly competitive globalized trade since the 20th century (Poschlod et al., 2005). Even with support by EU-funded agri-environmental schemes, it is often difficult to continue livestock grazing. Therefore, conservationists and land managers are searching for new ways to maintain calcareous grasslands in an adequate and cost-effective way.

During the past two decades, rewilding concepts emerged as an alternative to traditional pastoral management of conservation areas (Pereira & Navarro, 2015). The concept of rewilding is based on the assumption that throughout Pleistocene times, large herbivores played a predominant role in maintaining open and semi-open habitats in Central Europe (Bakker et al., 2016). A great diversity of large herbivores was found in Europe that was strongly reduced at the end of the last glacial period, most likely by humans (Sandom et al., 2014), and completely eradicated in the Holocene until the 16th century. The ecological role of wild large herbivores was taken over by domestic livestock that was free-roaming in the landscape until the 19th century (WallisDeVries et al., 2002). Trophic rewilding theory (e.g. Svenning et al., 2016) claims that, in the Central European landscape, large herbivore populations are needed to preserve open or semi-open habitats to substitute the declining influence of domestic livestock. Whether wild large herbivores alone are able to maintain patches of open habitats in the naturally forest-dominated Central European landscape is heavily debated (Nogués-Bravo et al., 2016; Vera, 2000) and, in general, there is a significant lack of empirical studies addressing this issue. In European rewilding projects, most often domesticated animals such as cattle and horses are set free in year-round grazing schemes to substitute the ecological function of their wild ancestors (Bunzel-Drüke et al., 2008; Svenning et al., 2016). Such projects often proved to be quite successful in restoring and maintaining open habitats such as heath and various types of grasslands (e.g. Köhler et al., 2016; Rupprecht et al., 2016).

Much less is known about if and how much wild deer populations can contribute to the preservation of open habitats in temperate forest landscapes. So far, most studies have focused on ecological consequences of deer overabundance on forest structure, tree species composition and regeneration (e.g. Côté et al., 2004; Goetsch et al., 2011). However, there are also studies indicating that old-growth forest floor richness may increase with deer herbivory intensity (e.g. Hegland & Rydgren, 2016). Few studies address the effects of deer foraging on open heath and grassland habitats (Riesch et al., 2019, 2020; Schütz et al., 2003). All of these studies focused on the potential of red deer *Cervus elaphus* for the preservation of open habitats, while there are so far no such studies on the effects of introduced fallow deer *Dama dama*. Fallow deer were distributed in Central Europe during warmer periods of the Pleistocene and have been reintroduced from the Mediterranean area as a game animal in the 15th to 17th century (Bunzel-Drüke et al., 2008). Today, there are dense local populations kept and supervised by hunters. Fallow deer are comparable to sheep in foraging habits, since they share more or less the same dietary niche. Both species are ruminants ranging between grazers and intermediate feeders, in contrast to browsers such as roe deer *Capreolus capreolus* (Bunzel-Drüke et al., 2008; Spitzer et al., 2020). Among European deer species, fallow deer are considered to be the most adapted to foraging on grasses. However, they show a broad food spectrum and their forage preferences vary strongly according to seasonal and spatial forage availability (Spitzer et al., 2020).

In the Teutoburger Wald, a midmountain range in northwest Germany, a very dense population of fallow deer has established with strong impact on the vegetation. As a consequence, in forests of that area, successful regeneration of trees is completely dependent on fencing. Similarly, in open calcareous grasslands, the succession of woody species is strongly retarded by fallow deer browsing, reflected in bonsai-like growth forms (Figure 1). These observations led to the idea that fallow deer foraging may be sufficient to maintain orchid-rich calcareous grasslands in former limestone quarries and may potentially make sheep pasture management superfluous. To test for the effects of fallow deer and sheep foraging, we performed an exclosure experiment to answer the following questions:

1. How does fallow deer foraging alone affect shrub and tree encroachment?
2. How strongly do species diversity, composition, and above-ground biomass differ between the combined foraging of sheep and fallow deer vs. foraging by fallow deer alone?
3. Is fallow deer foraging alone a suitable method to maintain species-rich calcareous grasslands?

2 | MATERIALS AND METHODS

2.1 | Study area

The study site is located near the town Lengerich in northwest Germany (52°10′31.555″N, 7°54′9.029″E). Climate is sub-oceanic with average temperatures ranging from 2.3°C in January to 18.4°C in July and annual precipitation of around 850 mm (measured at Bielefeld, DWD, 2021). The climate is characterized by humid conditions throughout the year with mild winters and relatively cool, precipitation-rich summers. The study site comprises about 400 ha and is part of the low mountain range Teutoburger Wald, which originates from cretaceous limestone. The mountains are covered

FIGURE 1 Pictures of heavy fallow deer browsing and consequent bonsai-like growth forms of trees.

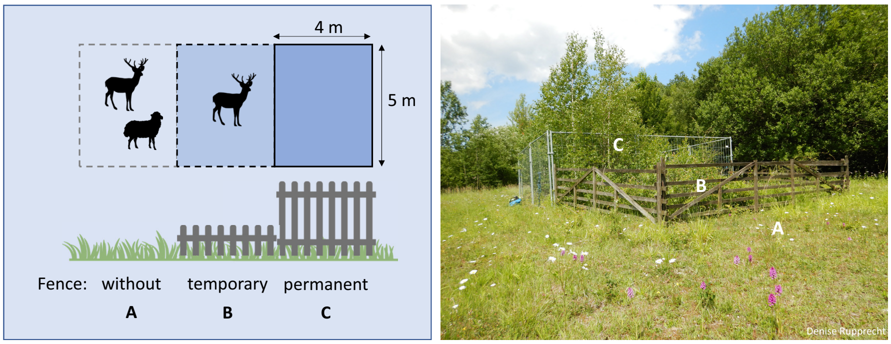

FIGURE 2 Structure of the experimental block design. There are three treatments: (a) a control, which is accessible to wild fallow deer and sheep, with purple flowering orchid *Anacamptis pyramidalis* in the foreground, (b) a sheep exclosure, which is only accessible to wild fallow deer and (c) a total exclosure, which is inaccessible to both animals.

by broad-leaved forests with dominant European Beech *Fagus sylvatica* intermingled with patches of open grassland. To the north and the south, the forests of the Teutoburg mountains are embedded in intensively used agricultural landscapes.

All study plots are situated in calcareous grassland patches (0.6–3.5 ha in size) within former quarry sites where limestone was extracted until the 1990s. Six of the exclosure plots are situated in an abandoned part of a large active quarry and four are situated in surrounding ex-quarry sites. Due to the shallow and highly permeable stony soils (Rendzic Leptosols), site conditions are generally nutrient-poor and dry. A few decades after abandonment of the quarry sites typical species-rich vegetation of calcareous grasslands developed, containing also rare and endangered specialist species such as orchids (e. g. *Anacamptis pyramidalis*, *Ophrys apifera*) and gentians (*Gentianopsis ciliata*, *G. germanica*). Today, they are listed as habitat type of the natura 2000 network (code *6210), which is threatened throughout Germany (Finck et al., 2017). Moreover, the ex-quarry sites are under special protection as conservation area of the Natura 2000 network (DE-3813-302 'Nördliche Teile des Teutoburger Waldes mit Intruper Berg'). To maintain this highly valuable vegetation, a grazing regime was introduced in 2001. Since then, a flock of about 500 sheep is herded in the area by a shepherd for several days once or twice a year. Moreover, a large wild population of fallow deer is known to be present in the area that has a strong impact on the vegetation (Figure 1). All sites have limited access to visitors due to security reasons (active quarry) and nature conservation restrictions (ex-quarry sites). Therefore, the area is a safe and quiet refugium for fallow deer, resulting in local densities of ≥20 deer per km^2.

2.2 | Experimental setup

In 2011, an exclosure experiment was set up at 10 different sites throughout a former quarry area. It comprised the following treatments (Figure 2): (a) a control without exclusion of animals, which was regularly grazed by herded sheep and wild fallow deer as described above; (b) a sheep exclosure, which was only temporarily enclosed for up to 5 days during the sheep grazing in May/June by a wooden fence of about 1 m height, leading to full access for wild fallow dear all year round; and (c) a total exclosure excluding fallow deer and sheep by a fence of about 2 m height. Effects of other animals such as rabbits or hares can be disregarded since they are not abundant in the area and have access to all treatments. Within each of the 30 site by treatment combinations, a permanently marked 3×3 m plot for vegetation sampling was established.

2.3 | Sampling and biomass analyses

Vegetation was sampled between mid-May and mid-June every 2 years since the setup of the experiment in 2011 until 2021. We recorded all vascular plants to species level and measured abundance by visual cover estimates following a modified Braun–Blanquet scale. We also visually estimated covers of litter, stones and open soil as well as covers of vegetation in general, woody species, Poaceae, Cyperaceae, Fabaceae, other herbs and bryophytes. By measuring at several parts of the plot, we recorded the average vegetation height, maximum vegetation height and maximum height of woody species. Green biomass and litter were sampled only in 2017, 2019 and 2021 within five frames of 0.1 m^2 per plot. The samples were dried at 70° for 24 h before weighing.

Our study did not require ethical approval. Fieldwork was carried out on the premises and with permission of the Dyckerhoff company and did not require further licences.

2.4 | Statistical analyses

In order to examine changes in species composition between the treatments, we extracted the following plant functional traits from the LEDA-Traitbase, an internet database of life-history traits of the Northwest European flora (Kleyer et al., 2008): leaf distribution, life-form, life cycle, age of first flowering, seed mass and seed bank type and, additionally, plant strategy types after Grime et al. (2007). For each of these traits, we calculated cover weighted means for each plot.

To test for treatment effects in the final study year, 2021, we applied linear mixed-effects models (R-package: NLME, Pinheiro et al., 2022) to each variable with treatment (control/sheep exclosure/total exclosure) as the explanatory variable. Since the treatment effect was nested in the site (10 sites with 3-fold connected plots), we added the site as random factor. We checked for normal distribution of the residuals and transformed the respective response variable if the assumption was not met. We used planned contrasts based on pre-experimental hypotheses to determine treatment effects: (a) control against both exclosure treatments (combined effect of sheep and fallow deer), (b) sheep exclosure against total exclosure (effect of fallow deer alone). We repeated the same procedure also for each of the other study years only for the four most relevant variables: species number per plot, litter cover, cover of woody species, and maximum height of woody species as well as for biomass and litter amount.

To assess the development of the treatment effects over time for the same four variables, we additionally calculated mixed-effects models including all study years (Appendix S2). For each response variable, we calculated a model using treatment in interaction with year as explanatory variable and site in interaction with treatment as random effect. Again, we assumed normality of the residuals and eventually transformed the response variable to achieve this.

Furthermore, we conducted an indicator species analysis to identify specific taxa for the treatments (Dufrêne & Legendre, 1997). All statistical analyses were done in in R 3.4.3 (R Core Team, 2017) except for the indicator species analysis, which was carried out in PC-ORD 6 (McCune & Mefford, 2011).

3 | RESULTS

3.1 | Structural changes

After 10 years of the experiment, substantial differences in vegetation structure occurred between treatments. These were most pronounced between the control and the total exclosure, while fallow deer foraging alone showed intermediate values.

Compared to the control, both exclosure treatments exhibited significantly higher values of litter biomass, cover of litter, total cover, cover of woody species and vegetation height, as well as lower species numbers, lower cover of open soil and lower cover of Fabaceae. The 'deer alone' treatment had significantly lower values in litter biomass, cover of woody species, average vegetation height, maximum height and maximum height of woody species than the total exclosures (Table 1, Appendix S2). While green above-ground biomass was equally high in all three treatments, litter mass was two times higher ('deer alone') and three times higher (total exclosures) than in the control (Table 1, Figure S1).

Over time (Figure 3, Appendix S3), control plots foraged by both sheep and fallow deer were stable in all major vegetation parameters throughout the 10 years of the experiment. Contrary, a strongly divergent development between both exclosures and the control could already be observed after 2–4 years in species numbers, litter cover, cover of woody species and maximum height of woody species. Fallow deer significantly lowered maximum height of woody species already after 4 years, compared to total exclosure plots, and significantly lowered cover of woody species after 10 years.

3.2 | Changes in species composition

Our analysis also revealed clear differences in plant functional trait expression between treatments after 10 years. Once again, major differences occurred between the control foraged by both sheep and fallow deer and the two exclosure treatments (Table 1). In control plots, the percentages of ruderals, stress tolerators, rosette or semi-rosette plants, and short-lived (annual or bi-annual) plants were significantly higher than in the exclosures. The control plots also had a distinctly higher proportion of plant species that flower already in the first year and that build short- or long-term persistent seed bank. Competitors, non-rosette plants, perennials, species that flower

TABLE 1 Characteristics of treatments after 10 experimental years in 2021. Community weighted means ± standard errors of the raw data of all investigated parameters and plant functional traits. Treatments: control (a) = foraging by wild fallow deer and sheep, (b) = sheep exclosure with foraging only by wild fallow deer, (c) = total exclosure without foraging. Treatment effects were tested by linear mixed-effects models with treatment as explanatory variable and site as random factor (model outputs in Appendix S2). Significant effects as marked with *$p < 0.5$, **$p < 0.05$, ***$p < 0.005$ were determined by planned contrasts: A vs. BC: control against both exclosure treatments (combined effect of sheep and fallow deer), B vs. C: sheep exclosure against total exclosure (effect of fallow deer alone)

	2021			Effect of	
	Control (A)	Sheep Exclosure (B)	Total Exclosure (C)	Sheep A vs. BC	Deer B vs. C
Species number					
Species number on 9 m^{-2}	35.1 ± 2.9	32.3 ± 2.0	29.6 ± 1.7	*	
Structural parameters					
Green biomass [g/m^{-2}]	140.6 ± 24.5	139.9 ± 20.0	131.8 ± 12.1		
Litter biomass [g/m^{-2}]	49.4 ± 10.1	91.5 ± 14.2	148.4 ± 36.1	***	*
Litter cover [%]	27.0 ± 7.4	65.0 ± 8.2	71.5 ± 6.5	***	
Stones [%]	8.7 ± 4.6	8.2 ± 5.1	3.8 ± 2.9		
Open soil [%]	5.7 ± 1.9	3.0 ± 1.5	1.0 ± 0.6	**	
Vegetation cover [%]					
Cover total	84.1 ± 5.3	89.5 ± 4.4	94.1 ± 3.0	**	
Woody species	1.2 ± 0.7	22.2 ± 10.1	43.5 ± 12.7	***	*
Poaceae	35.0 ± 6.1	42.5 ± 6.6	31.5 ± 6.3		
Cyperaceae	3.0 ± 0.7	1.8 ± 0.4	3.8 ± 1.4		
Fabaceae	10.4 ± 3.4	4.6 ± 2.9	6.6 ± 2.4	**	
Herbs	40.0 ± 6.1	31.5 ± 6.0	30.5 ± 7.2		
Bryophytes	65.0 ± 7.7	68.5 ± 7.4	70.5 ± 7.8		
Vegetation height [cm]					
Average height	26.6 ± 5.1	47.0 ± 9.9	101.5 ± 37.3	***	**
Max. height	111.3 ± 10.9	141.0 ± 25.6	239.0 ± 50.1	**	**
Max. height woody species	15.5 ± 6.7	78.2 ± 33.0	216.3 ± 57.8	***	**
Strategy type [% of group]					
Competitors	52.3 ± 2.9	60.4 ± 5.8	72.6 ± 6.4	**	*
Stress tolerators	31.5 ± 2.1	31.0 ± 3.8	21.1 ± 4.5	*	**
Ruderals	15.8 ± 1.8	8.2 ± 2.8	6.0 ± 2.5	***	
Leaf distribution [% of group]					
Non-rosette	29.4 ± 4.1	44.0 ± 9.0	60.4 ± 9.3	*	
Semi-rosette	48.2 ± 2.5	45.6 ± 8.6	31.7 ± 6.6	*	
Rosette	22.5 ± 5.2	10.4 ± 6.0	7.8 ± 5.4	***	
Life cycle [% of group]					
Annual	2.2 ± 0.8	1.1 ± 0.5	0.5 ± 0.3	**	
Bi- or polyannual	4.1 ± 0.7	2.2 ± 0.9	1.9 ± 0.8	***	
Perennial	93.3 ± 1.3	96.3 ± 1.1	97.6 ± 1.0	***	*
Age of first flowering [% of group]					
Within 1 year	46.8 ± 3.2	28.1 ± 4.6	21.1 ± 6.2	***	
Between 1 and 5 years	50.9 ± 2.4	66.3 ± 3.5	67.1 ± 6.9	**	
over 5 years	2.0 ± 1.6	5.5 ± 3.9	11.8 ± 6.8	*	
Seed bank type [% of group]					
Transient	74.0 ± 1.3	78.6 ± 3.1	80.1 ± 2.7	*	
Short-term persistent	9.3 ± 0.6	7.1 ± 1.0	6.7 ± 0.7	**	
Long-term persistent	3.0 ± 0.4	2.0 ± 0.5	2.2 ± 0.5	*	
Seed mass [mg]	6.5 ± 4.5	17.9 ± 12.5	50.1 ± 21.1	**	**

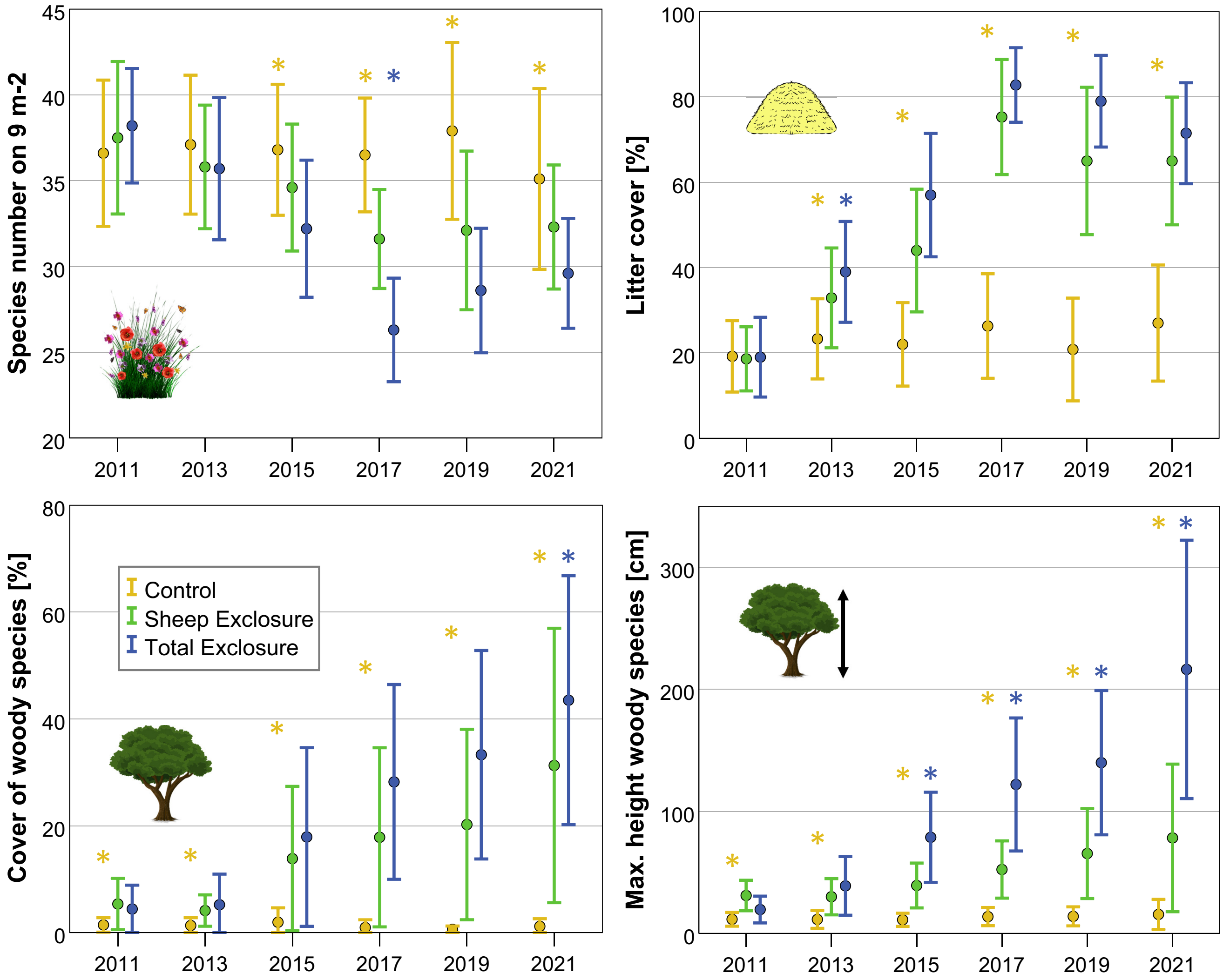

FIGURE 3 Changes of important treatment characteristics over time (2011–2021). Grouped means of the raw data of plant species number per plot, litter cover, cover of woody species, and maximum height of woody species. Error bars indicate 90% confidence intervals. We calculated mixed-effects models with site as random factor separately for each year. Differences between treatments were tested by planned contrasts: A vs. BC: control against both exclosure treatments (combined effect of sheep and fallow deer, marked with yellow star), B vs. C: sheep exclosure against total exclosure (effect of fallow deer, marked with blue star). Additional models investigating the development over time are available in Appendix S3.

after up to 5 years or later and species with transient seed banks, which persist in the soil for less than 1 year were less represented compared to the exclosures. The seed mass was distinctly lower than in exclosure plots. Moreover, several species were found in higher abundance in the control plots (Table 2). Characteristically, these were small annuals such as *Trifolium dubium* and *Trifolium campestre*, other short-growing and prostrate species such as *Polygala vulgaris* as well as typical rosette-plants such as *Plantago lanceolata*.

The effects of fallow deer foraging alone compared to no foraging (total exclosure) were generally minor compared to vegetation changes between control and exclosures described above: Fallow deer foraging compared to total exclosures only significantly reduced the proportion of competitive and perennial species as well as the seed mass and increased the proportion of stress tolerating species. No significant indicator species could be found for fallow deer forging alone (Table 2). However, the shrub species *Rosa canina* and *Cornus sanguinea* were identified as indicators for the total exclosures.

4 | DISCUSSION

4.1 | Effects of fallow deer on vegetation structure and plant species richness

Our exclosure study is a renewed proof for the crucial role of ungulate foraging for preserving the threatened habitat type of semi-natural calcareous grasslands (see e.g. Jacquemyn et al., 2011). In contrast to the combined effect of sheep and fallow dear foraging, the influence of wild fallow deer on vegetation alone was unexpectedly weak in

	IV	Control N = 10 f | a	Sheep Exclosure N = 10 f | a	Total Exclosure N = 10 f | a	p-value
Festuca rubra	67.3	100 | 67	50 | 25	40 | 8	0.001
Trifolium pratense	50.0	50 | 100	0 | 0	0 | 0	0.007
Trifolium dubium	40.0	40 | 100	0 | 0	0 | 0	0.021
Lotus corniculatus	53.8	90 | 60	70 | 15	60 | 25	0.023
Trifolium campestre	40.0	40 | 100	0 | 0	0 | 0	0.024
Plantago lanceolata	58.0	70 | 83	20 | 5	50 | 12	0.026
Polygala vulgaris	51.2	70 | 73	50 | 14	30 | 12	0.028
Poa pratensis	39.0	40 | 98	10 | 2	0 | 0	0.046
Cornus sanguinea	49.2	10 | 0	20 | 1	50 | 98	0.019
Rosa canina	39.9	10 | 0	20 | 0	40 | 100	0.054

TABLE 2 Indicator species analysis (Dufrêne & Legendre, 1997) calculated with data from 2021. It shows maximum indicator values (IV) for the shaded treatment (control = foraging by wild fallow deer and sheep, sheep exclosure = foraging only by wild fallow deer, total exclosure = no foraging). f = relative frequency [%] represents the species' proportion of occurrences in the respective treatment, and a = relative abundance [%] represents the proportion of its total cover. *p*-values result from Monte Carlo tests of significance of observed maximum indicator values. All species with a *p*-value < 0.05 are depicted

our experiment. Fallow deer only partially diminished successional processes: They reduced litter biomass, cover of woody species, maximum height of woody species and vegetation height in general significantly, but hardly had an effect on litter cover.

During the 10 years of the experiment, species numbers declined in solely deer-foraged plots, albeit weaker than in completely exclosed sites. Only the plots with additional sheep grazing maintained the level of species richness as in the starting year 2011, especially concerning typical plants of calcareous grasslands. Many studies have found a decline in species numbers after cessation of grazing in semi-natural dry grasslands (e.g. Rupprecht et al., 2016; Wehn et al., 2017). We attribute the observed changes in species richness in fenced plots to the processes typical of early stages of succession such as litter accumulation and shrub encroachment, which are clearly reflected in several structural vegetation parameters. Therefore, we expect a further decline of calcareous grassland species in the exclosures in the future.

In both exclosure treatments, we observed a strongly increased accumulation of litter. Although fallow deer foraging alone led to a decrease in litter biomass, the difference in litter cover between the sheep exclosure plots and the total exclosure plots was relatively small, indicating that fallow deer had only a minor effect on the accumulation of dead plant material. Litter accumulation is an important primary consequence of abandonment (Valkó et al., 2018). Semi-natural grasslands are dependent on frequent removal of plant material to allow light penetration to the soil surface and the lower vegetation layers to create specific microclimatic conditions, which are usually warmer and dryer than under a closed canopy. Moreover, many small growing target species of nutrient-poor calcareous grasslands can only survive permanently when light reaches the soil surface.

A thick litter layer can act as a seed trap by preventing the emergence and establishment of light-demanding seeds, which is especially true for annual and bi-annual grassland species that crucially depend on regular regeneration by seeds (Ruprecht & Szabó, 2012; Valkó et al., 2018). An accumulation of litter also reduces the proportion of open soil, which serves as an important niche for the regeneration of dry grassland species. We observed an almost complete disappearance of open soil patches in both exclosures, indicating that fallow deer were apparently not effective in preventing litter accumulation.

Another sign of successional processes induced by the exclosures is the encroachment of competitive woody species such as trees, shrubs and climbing lianas (Figure 2). Semi-natural grasslands are dependent on frequent removal of such woody species (Valkó et al., 2018). In our study, fallow deer were apparently able to reduce tree and shrub growth to a lower height (Figure 2) and to reduce their cover, but the effect was small compared to control plots. Because of the comparably small amount of woody parts in their diet, the influence of fallow deer on tree species is generally assumed to be smaller than in other deer species such as roe or red deer (Spitzer et al., 2020): In the growing season, 60%–95% of fallow deer diet consists of grasses, which can be reduced to 20% in winter. Fallow deer selectively choose the more energy-rich parts of woody plants like fresh shoots and buds. They are, however, not dependent on woody plants as food source.

4.2 | Changes in species composition

The observed successional processes led not only to a decline in plant species richness after exclusion of ungulate foraging, but also to significant shifts in species composition. Several plant species could clearly be linked to the exclosure treatments because they disappeared almost completely in plots foraged only by fallow deer or without foraging at all. Among them were many short-growing species such as *Polygala vulgaris*, *Trifolium campestre* and *T. dubium*, which are poor competitors in dense vegetation. These species mainly follow a ruderal or opportunistic strategy, which means that they are able to grow under continuous disturbances (Grime et al., 2007).

Among them were also some rare and endangered orchid species such as *Ophrys apifera* or *Anacamptis pyramidalis* and other target species typical of semi-dry calcareous grasslands that are protected under the EU Habitats Directive (Ssymank et al., 1998).

Most of the plant species more abundantly found in the control plots show clear adaptations to avoid biomass losses through larger herbivores; for example, by prostrate growth forms pressed closely to the ground, bitter taste, ethereal oils, toxic contents or mechanical defence mechanisms such as thorns or exceptionally hairy leaves (Bunzel-Drüke et al., 2008; Díaz et al., 2007). Moreover, members of the Fabaceous family are supported here which might be due to their ability to fix air-borne nitrogen leading to a competitive advantage under nutrient poorer conditions. In contrast, both exclosure treatments were characterized by less target species for calcareous grasslands. We found only two woody species but not a single herb indicator species of exclosure treatments. The foraging effect of the fallow deer reducing competitive and perennial species to some extent, is apparently not strong enough to maintain target species. Other studies have shown that foraging by wild deer clearly promoted clonal, prostrate and non-palatable species (Hegland & Rydgren, 2016; Riesch et al., 2020; Schütz et al., 2003).

4.3 | Potential reasons for the minor effect of fallow deer on vegetation structure and composition

We ascribe the weak measurable effect of wild fallow deer on important successional drivers such as litter accumulation and woody species encroachment to two main reasons: Firstly, the animals are not constrained to the habitat. When food quality diminishes, they can easily choose more productive sites for foraging. The investigated quarry is situated in a fragmented cultural landscape with, mostly small, patches of grassland of high conservation value. The study area itself is mostly surrounded by forest, but there are extensive neighbouring agricultural areas providing fodder of high nutritional value such as fertilized meadows and cereal fields. Especially in the winter months, when food sources are limited, fallow deer are apparently not forced to forage on low-quality fodder such as standing old plant material or shrubs and trees, but are able to move to better-quality foraging habitats of the agricultural landscape, as also reported by Spitzer et al. (2020).

Our findings are in line with the forage maturation hypothesis, which could often be supported in studies on cervids (Debeffe et al., 2017; Riesch et al., 2019). This hypothesis states that deer strongly prefer early phenological stages for foraging because of better digestibility and higher nutritious value. Freshly mown or grazed grassland contains more crude protein, which is preferred by deer, and less fibre components, which are avoided (Riesch et al., 2019). In our experiment, the grasslands harbouring the exclosures are regularly grazed by sheep, except for the fenced plots. Sheep grazing improves the quality of the biomass (Kleinebecker et al., 2011). If enough well-maintained grassland is available in the area, fallow deer will not choose ungrazed spots with phenologically older plant material of comparably lower forage quality. Some authors suggest mowing certain parts of a conservation area to increase fodder quality and thereby increase attractiveness to wild deer (Riesch et al., 2019). But in a fertile and heterogenous landscape matrix, as in our study, this approach seems to be inefficient. However, with our experiment, we cannot detect synergistic effects of combined sheep and deer foraging, because it did not include a solely sheep-grazed treatment.

As a second reason for the small effect of fallow deer, we assume the population density was, despite obvious signs of heavy browsing (Figure 1), apparently not large enough to have a distinct effect on the herbaceous vegetation. We assume that a further increased fallow deer population could potentially show more intense effects. However, lowering the hunting pressure is not a feasible option in the studied cultural landscape due to conflicting interests, especially with foresters aiming at natural regeneration of major tree species. Other studies have shown that population density is often only weakly correlated with influence on vegetation (Moore et al., 2015). More important is the spatial distribution of preferred foraging habitats, the proximity to closed vegetation types offering protection and especially the hunting regime (Coppes et al., 2017; Lone et al., 2015; Westekemper et al., 2018). In our case, it is obvious from field observations that the fallow deer prefer to forage in the quarry only during the daytime because it has strongly restricted public access and is therefore more protected from human disturbance than the surrounding cultural landscape. In the night, however, the animals are free to forage in more attractive habitats outside (Gaynor et al., 2018).

Most studies on the effect of deer foraging on vegetation focus on forests habitats, specifically forest damages. Several of these studies have shown that deer foraging generally led to a richer understory vegetation in forest habitats (e.g. Boulanger et al., 2018; Hegland & Rydgren, 2016). The observed positive effect on species richness of herbaceous forest vegetation relies on wild ungulates foraging mainly on woody species, which favours light-demanding herbaceous species in the understory. On the contrary, many studies from North America have shown that overly abundant deer may lead to negative effects on forest understories due to high foraging pressure (e.g. Côté et al., 2004; Goetsch et al., 2011,). However, there is hardly any published evidence for deer effects on vegetation composition and species richness in open habitats (Riesch et al., 2019, 2020; Schütz et al., 2003). Compared to our study, Riesch et al. (2020) observed a much stronger impact of deer on vegetation, possibly due to higher deer population densities, much larger extent of the study area and a different deer species (Red deer). Another difference might be that their hunting management focuses on protecting forest regeneration by offering open grassland without hunting to the deer. Red deer have been the focus of studies much more frequently than fallow deer. We see a strong need to further investigate impacts of wild ungulates on vegetation and discover possible benefits for nature conservation. Such ideas have been discussed recently in different scenarios under the aspect of rewilding (e.g.

du Toit & Pettorelli, 2019; Pereira & Navarro, 2015). However, there is still a severe deficit of empirical studies supporting these theoretical considerations.

5 | CONCLUSIONS

Our experiments clearly demonstrated that fallow deer browsing holds the potential to slow down woody species encroachment in calcareous grasslands. However, we also showed that fallow deer browsing alone was not able to prevent litter accumulation, which proved to be the main factor of species richness decline and shifts in species and trait composition in our study. Our results strongly suggest that even high densities of wild free-ranging fallow deer are not able to maintain species-rich calcareous grassland, at least in a heterogenous and intensively used cultural landscape. How long fallow deer foraging may preserve calcareous grasslands from complete shrub encroachment remains an open question and lies beyond the runtime of our experiment.

In contrast to our findings, there are recent examples of nutrient-poor open habitats such as heath and grasslands that have been maintained exclusively by extensive year-round grazing (Köhler et al., 2016; Rupprecht et al., 2016). However, instead of relying on wild ungulates already present in the landscape, these projects include breeds of extinct European large herbivores such as horses and cattle, that are kept in rather large, but fenced and, therefore, spatially restricted areas. These large grazers seem to be mandatory to prevent litter accumulation, while wild fallow deer may significantly contribute to the suppression of woody species. Therefore, a combination of different herbivore species with complementary traits might be most beneficial to open habitat conservation (e.g. Putfarken et al., 2008). Based on our results, and in contradiction to our initial hypothesis, we argue that rewilding projects completely relying on fallow deer browsing will rapidly lead to the degradation of calcareous grasslands, at least in a landscape context where more attractive forage sources are available and hunting serves other goals. However, more knowledge on the impacts of wild deer populations on open grassland vegetation in Central Europe is urgently needed, especially with respect to interactions with "semi-domestic" large herbivores such as horses or cattle in the course of trophic rewilding (du Toit & Pettorelli, 2019; Pereira & Navarro, 2015).

AUTHORS' CONTRIBUTIONS

N.H. and B.J. conceived the ideas and designed methodology; D.R. and B.J. collected the data; D.R. analysed the data; D.R. and N.H. led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

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CONFLICT OF INTEREST

The authors have no conflict of interest to declare.

DATA AVAILABILITY STATEMENT

Data available via the Dryad Digital Repository https://doi.org/10.5061/dryad.j3tx95xhx (Rupprecht et al., 2022).

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