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Effects of wild boar (*Sus scrofa*) rooting on abandoned calcareous grassland in Hainich National Park, Germany

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ABSTRACT

Calcareous grasslands are semi-natural biodiverse ecosystems that hold high conservation value, but are threatened throughout Europe. Abandoned calcareous grasslands become afforested unless succession is reset. We tested the idea that wild boar (*Sus scrofa*) rooting activity could serve as a means to reset succession and thereby maintain characteristic herbaceous plant diversity in calcareous grasslands. We compared vascular plant abundance and environmental parameters between plots rooted by wild boar and undisturbed plots in unmanaged calcareous grasslands in Hainich National Park, Germany. We found that rooted plots had lower grass cover and higher herb cover, and a significantly higher species richness, Shannon diversity index and evenness. Indicator species analysis differentiated 23 species for rooted plots, and 8 for undisturbed plots. Of 17 characteristic species for calcareous grasslands, two were significant indicators in rooted plots, and one in undisturbed plots, while 14 did not differentiate between the treatments. Our findings suggest that wild boar rooting activity in Hainich National Park may maintain characteristic calcareous grassland vegetation, by resetting early grassland succession and enhancing heterogeneity, which in turn helps sustaining biodiversity.

1. Introduction

Calcareous grasslands (LRT 6210, Semi-natural dry grasslands and scrubland facies, *Festuco-Brometea*) rank among the most

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species-rich habitats in the world and were once widespread in Europe, covering large areas (van Swaay, 2002; Veen et al., 2009). Yet in the 20th century, they experienced a steep decline, largely attributed to agricultural intensification, afforestation, and the abandonment of shepherding induced by a devaluation of wool (Poschlod and WallisDeVries, 2002). Many calcareous grasslands, especially those in lowland areas, are thought to depend on human activities such as haymaking and shepherding (Fartmann, 2024; Grass et al., 2021; Leuschner and Ellenberg, 2017; Squires et al., 2021). Nowadays, many remaining calcareous grasslands are small and isolated from neighbouring grasslands, resulting in a significant loss of plant and insect diversity (Batáry et al., 2021; Olsen et al., 2018; Poniatowski et al., 2018; Steffan-Dewenter and Tscharntke, 2002; Zschokke et al., 2000). On top of that, atmospheric nitrogen deposition has negatively affected characteristic vegetation (Bauer and Albrecht, 2020; Diekmann et al., 2014). There is a critical need for management practices in order to conserve and restore calcareous grasslands (Poniatowski et al., 2020).

The management of calcareous grasslands varies across countries in Europe. Germany stands out with the core vision of national parks to leave nature to take care of itself; 'Natur Natur sein lassen' (Rommelfanger, 2023), a strategy that emphasises undisturbed natural processes (except wildlife management), also referred to as 'rewilding'. This is in contrast with many other European countries, such as the Netherlands, where the management of the remaining calcareous grasslands largely consists of mowing and shrub removal, requiring substantial effort and costs (WallisDeVries et al., 2002). However, there is debate about the German policy, which some believe to threaten semi-natural systems such as calcareous grasslands (Rommelfanger, 2023; Rupprecht et al., 2022). Concerns are that without mowing, livestock grazing, or other disturbance, these grasslands will eventually grow into forests, as a process of succession, resulting in a loss of characteristic species (Dekoninck et al., 2007; Dovčiak et al., 2008). Although mowing and grazing can effectively reset shrub encroachment, it can lead to a loss of landscape heterogeneity, which may reduce biodiversity (Bauer and Albrecht, 2020; Lepš, 2014; Ottaviani et al., 2011; Tälle et al., 2016). Therefore, there persists uncertainty to the question of how calcareous grasslands should be maintained.

It has been argued that large mammals can also maintain grassland vegetation and increase habitat heterogeneity, thereby preventing grassland succession (Jones et al., 1997). In European calcareous grasslands, extant allogenic ecosystem engineers include wild ungulates, for example wild boar (*Sus scrofa*), red deer (*Cervus elaphus*), and insects like the yellow meadow ant (*Lasius flavus*) (Barrios-Garcia and Ballari, 2012; Mohr et al., 2005; Streitberger et al., 2017). Especially wild boar may have a high impact on the plant community composition through their rooting behaviour. Rooting involves ploughing the land to feed on invertebrates, plant roots, and fungi (Barrios-Garcia and Ballari, 2012; Baubet et al., 2003; Sandom et al., 2013). By rooting – predominantly during autumn and winter – wild boar reduce the cover of dominant grasses, and trigger recolonisation of low-competitive plants in spring, which resets the succession of early grassland vegetation (Everitt and Alaniz, 1980; Horčičková et al., 2019; Sandom et al., 2013). Thus, it is important to know how rooting wild boar affect the characteristic vegetation.

An extensive review on the ecological impact of wild boar by Barrios-Garcia and Ballari (2012) concluded that the impacts of wild boar were widely studied in introduced ranges but are relatively less studied in their native range. On the one hand, reported ecological effects of wild boar in grasslands are mostly negative (Genov et al., 2017), such as a decrease in species diversity (Hone, 2002). On the other hand, some recent studies in native calcareous grasslands have suggested positive impacts of rooting on plant species richness and hostplants of endangered butterflies (Horčičková et al., 2019; Labadessa and Ancillotto, 2023). Comprehensive vegetation surveys are however lacking to corroborate these theories and evaluate the direct and complete influence of rooting on characteristic plant life in native ranges. Consequently, it remains unclear which plant species are influenced by native wild boar in calcareous grasslands, and to what extent.

In this study, we aimed to test the idea that wild boar (*Sus scrofa*) rooting activity could serve as a means to reset succession and thereby maintain characteristic herbaceous plant diversity in calcareous grasslands. To do so, we compared vascular plant species abundance and environmental variables between plots rooted by wild boar and undisturbed plots in unmanaged calcareous grasslands in the Hainich National Park in Germany. The question was whether rooting by wild boar indeed maintains the species richness of characteristic calcareous grassland vascular plant species, by reducing dominant grasses and increasing bare soil (Fig. 1), and increases the general vascular plant species richness and diversity in the system. We tested the predictions that compared to unrooted patches, rooted patches in early summer – assumed to have been disturbed during the previous winter or earlier (cf. Tierney and Cushman, 2006) – would have (1) the same species richness of characteristic calcareous grassland vegetation (2) higher overall vascular plant species richness, diversity and evenness.

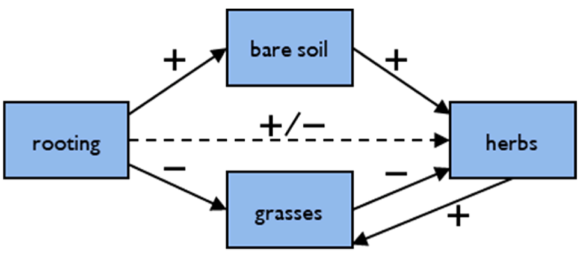

Fig. 1. Conceptual diagram of the environmental effects of rooting by wild boar (*Sus scrofa*). Arrows represent direct effects (solid) and both direct/indirect effects (dashed). The direct effect of rooting on herbs is negative, while the indirect effect is positive. Succession is shown as the positive arrow from herbs to grasses.

2. Methods

2.1. Study area

Hainich National Park (total area: 7.500 ha) is located in western Thuringia, central Germany (51°03'N/10°42'E), at 225–494 m above sea level. Shell limestone sediments characterise the shallow geological subsoil (Großmann, 2018). The national park predominantly consists of beech forests, but the southern part particularly contains semi-open calcareous grasslands (approx. total area 600 ha), which have minimal variation in soil type, depth, and aspect. The grasslands have a history of military use for decades, and were kept open by shepherding. In 1997, the grasslands became part of the national park, which marked the start of abandonment and no-intervention management. To date, the grasslands have nevertheless remained open, although shrub encroachment is evident (pers. obs.). The average atmospheric nitrogen deposition in Hainich National park is estimated at approximately 13 kg N/ha/yr, which is within the estimated nitrogen critical load value of 10–20 kg N/ha/yr for calcareous grasslands, as calculated by the European Monitoring and Evaluation Programme (Bobbink et al., 2022; EMEP, 2023).

The vegetation of calcareous grasslands belongs to the class *Festuco-Brometea*, which is typically dominated by grasses (e.g. *Brachypodium pinnatum*, *Bromus erectus*, *Helictotrichon pratense* and *Koeleria pyramidata*) and a wide variety of herbs (e.g. *Cirsium acaule*, *Ranunculus bulbosus*, *Sanguisorba minor and Thymus praecox*) (Ellenberg and Leuschner, 2010; Fartmann, 2004; Hennekens et al., 2001). These grasslands harbour many species of insects, such as threatened grasshopper species like wartbiter (*Decticus verrucivorus*) and butterflies like marsh fritillary (*Euphydryas aurinia*) and Nickerl's fritillary (*Melitaea aurelia*) (Fartmann, 2024; Poschlod and WallisDeVries, 2002; Wilson et al., 2012; Tuinder et al., 2025).

2.2. Sampling

We sampled 60 pairs of 2 × 2 m plots: one in a patch recently rooted by wild boar and one in adjacent vegetation without visible disturbance. Plot pairs were equally divided across three proximate subareas of calcareous grassland in unmanaged areas of the national park (Fig. A1). Plot selection was done on-site: rooted plots were placed in furrowed patches with overturned soil and dead grass tussocks (Fig. A2). These patches appeared unevenly scattered throughout the study area, which is a common pattern in these calcareous grassland systems (Burrascano et al., 2015a; Horčičková et al., 2019). Rooted plots were installed only in patches with > 8 m^2 recent rooting activity. Control plots ranged 8–25 m away from rooted plots in NE–SE direction. To minimize variation in exposure, plots with an aspect exceeding 10° were excluded, as well as plots with any northern aspect.

Vegetation surveys took place between June 1 and July 3, 2023. Cover of every vascular plant species was estimated by levels of 5 %. We included the additional levels of 1 %, 2.5 %, 97.5 %, and 99 % to account for the inclusion of rare species and accurate estimation of dominant species (cf. Streitberger et al., 2017). Scientific nomenclature of vascular plants followed Müller et al. (2017). Red-listed species were classified based on both the national red list for Germany ("Rote Liste Zentrum," 2018) and the federal red list of Thuringia (Korsch and Westhus, 2010). Characteristic species of calcareous grasslands were according to Fartmann (2004). Substrate relationships and Ellenberg indicator values followed Database of European Vegetation (n.d) and vegetation alliances followed Hennekens et al. (2001), and Oberdorfer (2001).

A suite of parameters was measured in each plot, prior to plant sampling (Table 1). Total cover of herbs, grasses, litter, and bare soil, and vegetation height were measured following the methods in Streitberger et al. (2017). In addition, we measured total cover of stones and gravel, anthills, shrubs (0.5–2 m tall woody vegetation), local environment disturbance (the percentage of rooted area within 15 m around each plot), and pleurocarpous and acrocarpous mosses. Vegetation height was the average of five fixed locations

Table 1
Differences in vegetation and environmental variables between plots with and without rooting by wild boar (*Sus scrofa*) in Hainich National Park, Germany. Mean values ± SD of all numerical vegetation structure parameters for rooted and control samples. $N = 60$ per group. Comparison between groups by GLMM, accounting for pair ID as random effect, with proportional binomial distributions for covers and log-linked Gaussian distribution for vegetation height. Subarea was used as fixed factor if significant, indicated by †. P-values were adjusted by Bonferroni correction, where 'n.s.' = not significant and *** = $P < 0.001$.

Parameter	Rooted	Control	P
Horizontal cover (%)			
Bare soil	38.9 ± 15.3	1.5 ± 2.1	***
Rocks, gravel	3.6 ± 2.4	0.0 ± 0.2	***
Litter †	3.9 ± 4.0	85.8 ± 16.1	***
Anthills	1.8 ± 4.1	7.6 ± 10.8	***
Lichens	0.1 ± 0.6	0.0 ± 0.1	n.s.
Pleurocarpous moss †	1.1 ± 2.2	77.8 ± 16.2	***
Acrocarpous moss	0.1 ± 0.6	0.1 ± 0.3	n.s.
Grasses	25.4 ± 15.3	92.7 ± 6.2	***
Herbs	57.8 ± 14.4	45.2 ± 17.0	***
Shrubs (0.5 – 2 m)	1.4 ± 3.3	3.5 ± 8.6	***
Local environment disturbance	33.8 ± 24.0	18.0 ± 19.0	***
Vertical features (cm)			
Vegetation height	12.1 ± 6.5	28.2 ± 9.6	***

within the plot.

2.3. Data analysis

All analyses and visualizations were done in R 4.3.1 (R Development Core Team, 2023). To test for differences in cover and height, we fitted generalised linear mixed-effects models (GLMM) using the function glmer from the package lme4 (Bates et al., 2015), with pair ID as random effect, and with a log-linked Gaussian distribution for height and proportional binomial distributions for cover data (cf. Kettermann and Fartmann, 2023). Subarea was used as fixed effect if significant. Twelvefold Bonferroni correction was applied to account for multiple testing, using the function p.adjust.

To test for a difference in species richness, we used a GLMM with pair ID as random factor and a Poisson distribution. To determine which underlying factors best explained the differences, we also fitted multivariate GLMMs with cover and height (cf. Löffler et al., 2023). In case of high correlation between parameters (Spearman rank correlation $|r_s| > 0.7$, Table A1), only the parameter with the highest ecological relevance was used. Variance inflation factors were < 5. Models were generated using the function dredge from the R package MuMIn (Barton, 2021). The best-fitting models (< 3 ΔAIC from the lowest AIC model) were conditionally averaged. Acrocarpous moss and lichens were excluded from further analysis due to a low occurrence (< 4 %) in the dataset.

To test for differences in species composition, we performed an indicator species analysis (ISA), with the R package indicspecies (Dufrêne and Legendre, 1997), as in similar studies (Burrascano et al., 2015a; Streitberger et al., 2017), using the indval function with 999 permutations. To test for differences in species diversity and evenness, we calculated Shannon indices (H') with the function diversity from the R package vegan (Oksanen et al., 2022), and compared them with Gaussian GLMMs, as above. Furthermore, we used NMDS to test for differences in community composition in relation to environmental conditions, using vegan with a Bray-Curtis dissimilarity index. For all ordinations, we used species with an occurrence of > 3. All parameters were scaled and fit using the function envfit with 1000 permutations.

3. Results

A total of 155 vascular plant species were found. These included three red-listed species: *Euphorbia platyphyllos* (threatened in Germany, found on rooted plots), *Betonica officinalis* (threatened in Thuringia, found on rooted plots), and *Lathyrus nissolia* (threatened in Germany and highly threatened in Thuringia, found on rooted and control plots). Rooted plots had a significantly higher species richness (range 13–48 species) than did control plots (range 18–39; GLMM: $Z = 4.885$, $P < 0.001$; Fig. 2a), as well as a significantly higher Shannon index (GLMM: $T = 20.97$, $P < 0.001$; Fig. 2b) and a higher evenness (GLMM: $T = 24.19$, $P < 0.01$; Fig. 2c). Community composition of both rooted and control treatments largely overlapped with the calcareous grassland class *Festuco-Brometea* and together included 17 characteristic species (e.g. *Brachypodium pinnatum, Koeleria pyramidata, Ononis repens, Pimpinella saxifraga, Sanguisorba minor, Salvia pratensis, Scabiosa columbaria, and Thymus praecox*). *Brachypodium pinnatum* was present in all plots.

Altogether 31 species differentiated significantly for one of the treatments: 23 differentiated for the rooted plots and 8 differentiated for the control plots (ISA; Table 2). For rooted plots, these included one characteristic calcareous grassland species (*Ranunculus bulbosus*), for control plots another two (*Helictotrichon pratense* and *Polygala comosa*). We found 32 annuals, including 19 arable weeds and one perennial arable weed (*Allium vineale* s. str). Eight of the 23 rooted-indicator species were annuals, and 8 were arable weeds (of which 6 species were both). Indicator species for control plots had two annual species, of which one was also an arable weed (*Vicia hirsuta*).

Furthermore, the differentiating species for rooted plots included pioneer species (e.g. *Anagallis arvensis, Acinos arvensis, Euphorbia exigua* and *Papaver dubium* subsp. *lecoquii*), and indications of other vegetation communities, such as *Molinio-Arrhenatheretea* (nutrient-

Fig. 2. Differences in plant species richness (a), Shannon index (b), and evenness (c) between plots with and without rooting by wild boar (*Sus scrofa*) in the Hainich National Park, Germany. Comparisons were made using a Poisson-distributed GLMM for (a) ($Z = 4.885$, $P < 0.001$) and log-linked Gaussian-distributed GLMM for (b) ($T = 20.97$, $P < 0.001$) and (c) ($T = 24.19$, $P < 0.01$), with pair ID as a random effect. Error bars show SD.

Table 2
Plant species differentiating between plots with and without rooting by wild boar (*Sus scrofa*) in the Hainich National Park, Germany. Species were sorted by decreasing indicator value. *IV* = indicator value, *ra* = relative abundance (the probability that the site where this species is found belongs to the assigned site group), *rf* = relative frequency (the probability of finding this species in the assigned site group). *N* = 60 per group. * *P* < 0.05, ** *P* < 0.01, *** *P* < 0.001.

Species		ROOTED			CONTROL		
	P	IV	ra	rf	IV	ra	rf
Daucus carota	***	87	75	100	.	.	.
Plantago lanceolata	***	85	79	92	.	.	.
Ranunculus bulbosus	***	77	86	68	.	.	.
Trifolium medium	***	74	81	68	.	.	.
Euphorbia exigua	***	67	100	45	.	.	.
Picris hieracioides s. l.	***	65	80	53	.	.	.
Acinos arvensis	***	62	89	43	.	.	.
Allium vineale s. str.	***	60	91	40	.	.	.
Lepidium campestre	***	54	97	30	.	.	.
Cirsium arvense	**	50	84	30	.	.	.
Ajuga genevensis	***	50	100	25	.	.	.
Anthemis tinctoria	***	47	100	22	.	.	.
Anagallis arvensis	**	43	93	20	.	.	.
Trifolium pratense	**	43	85	22	.	.	.
Elymus repens s. str.	**	41	100	17	.	.	.
Valerianella locusta	**	41	100	17	.	.	.
Hieracium pilosella	*	39	83	18	.	.	.
Euphorbia platyphyllos	*	34	100	12	.	.	.
Linaria vulgaris	*	34	100	12	.	.	.
Bromus commutatus	*	32	100	10	.	.	.
Cirsium vulgare	*	32	100	10	.	.	.
Dipsacus fullonum	*	32	100	10	.	.	.
Papaver dubium subsp. *lecoquii*	***	29	100	8	.	.	.
Carex flacca	***	.	.	.	71	78	65
Helictotrichon pratense	***	.	.	.	67	79	57
Vicia hirsuta	***	.	.	.	65	90	47
Rosa canina agg.	**	.	.	.	52	82	33
Primula veris	**	.	.	.	48	81	28
Astragalus glycyphyllos	*	.	.	.	46	79	27
Polygala comosa	*	.	.	.	42	81	22
Vicia angustifolia	**	.	.	.	41	90	18

poor mesic grasslands, species *Plantago lanceolata, Trifolium pratense* and *Valerianella locusta*), the alliance *Dauco-Melilotion* (class *Artemisietea vulgaris,* recently disturbed nutrient-rich soils, species *Anthemis tinctoria, Daucus carota, Dipsacus fullonum, and Elymus repens*), the alliance *Fumario-Euphorbion* (class *Stellarietea mediae,* pioneer communities, species *Allium vinneale, Anagallis arvensis, Cirsium arvense, Euphorbia exigua and Plantago lanceolata*), and the alliance *Sedo-Cerastion* (class *Koelerio-Corynephoretea,* dry grasslands, species *Allium vineale, Plantago lanceolata,* and *Valerianella locusta*). Altogether 18 species were associated with a eutrophic or mesotrophic nutrient relationship, as opposed to four out of eight for the control plots (Table 3). All control differentiating species were

Table 3
Proportion of indicator species (see Table 2) and their environmental relationships. There were 23 indicator species for plots disturbed by wild boar ("ROOTED", *N* = 60) and 8 for undisturbed plots ("CONTROL", *N* = 60).

Relationship	Rooted (23 spp.)	Control (8 spp.)
Reaction		
Alkaline	0.61	0.88
Slightly acidic to near-neutral	0.35	0.00
NA	0.04	0.12
Nutrients		
Dystrophic	0.04	0.00
Oligotrophic	0.13	0.50
Mesotrophic	0.35	0.38
Eutrophic	0.43	0.12
NA	0.04	0.00
Humidity		
Dry	0.52	0.62
Mesic	0.43	0.25
NA	0.04	0.12
Salinity		
Non-saline	0.91	0.88
Slightly saline or brackish	0.09	0.12

associated with an alkaline substrate-reaction relationship, but for rooted differentiating species, 8 of the 23 species were associated with a slightly acidic to near-neutral relationship. The substrate humidity and salinity relationships of the differentiating species did not differ between the rooted and unrooted plots.

Species richness increased with the overall proportion of bare soil (GLMM; Fig. 3), but declined with the proportion of bare soil in the rooted plots (Table A2). Compared to control plots, rooted plots had significantly higher covers of bare soil, rocks, and herbs, yet significantly lower covers of litter, anthills, pleurocarpous moss, grasses, shrubs and a shorter turf (GLMM; Table 1).

NMDS showed distinct clusters for rooted and control plots (Fig. 4a), which were associated with the differentiating vascular plant species (Fig. 4b). The differentiating species for rooted plots were associated with a short height, and low covers of grasses, anthills, litter, and pleurocarpous moss, but a high cover of bare soil and stones and gravel (for detailed results, see Table A3). Annual arable species were scattered throughout the ordination (Fig. A3).

4. Discussion

Our results suggest that rooting by wild boar plays a vital role in maintaining characteristic calcareous grassland vegetation. Altogether 17 characteristic calcareous grassland species were found, and most of these occurred both in rooted and control plots. Furthermore, species richness was higher in rooted plots than in control plots, in agreement with prediction 2. This is in line with previous grassland studies that positively correlate plant biodiversity with disturbance of native wild mammals (Horčičková et al., 2019; Schütz et al., 2003). In fact, natural disturbances such as wild boar rooting may be key to maintaining complexity of natural ecosystems (Bengtsson et al., 2003; Kulakowski et al., 2017; Perino et al., 2019), and the variation in frequency, distribution and size of rooted patches may especially add to species diversity and landscape heterogeneity (Burrascano et al., 2015a; Cortés-Avizanda et al., 2012; Horčičková et al., 2019; Welander, 2000). Species diversity and evenness were also higher in rooted plots. Control plots had a high dominance of a few grass species, such as *Brachypodium pinnatum* and *Festuca rupicola*, emphasising the idea that disturbance triggers the recruitment of – less-competitive – herb species (Sousa, 1984).

As many as 23 species were indicators for rooted plots, suggesting that rooting also adds non-characteristic species to calcareous grasslands. Most were species associated with more eutrophic and slightly acidic soil conditions. Rooted patches can offer changed nutrient availability (Bueno et al., 2013; Groot Bruinderink and Hazebroek, 1996; Mohr et al., 2005). Wild boar may thus not only maintain and introduce calcareous grassland species, but also add species that are not typical to this unmanaged habitat. For instance, eight of these rooted-indicator species are locally considered arable weeds (e.g. *Anagallis arvensis*, *Euphorbia exigua*, *E. platyphyllos* and *Papaver dubium* spp. *lecoquii*). This phenomenon may be similar to findings in introduced ranges, where rooting was correlated with an increase in exotic species (e.g. Aplet et al., 1991; Siemann et al., 2009; Tierney and Cushman, 2006). Yet the introduction of arable species in the native range of wild boar is not necessarily negative, as they add ecological value and complexity to the system (Balfour and Ratnieks, 2022).

Bare soil appeared to be the main factor facilitating characteristic species (Fig. 4b). These low-competitive species, that were rarely found amidst the dominant vegetation in control plots, may require the clearance found in rooted plots for persistence in calcareous

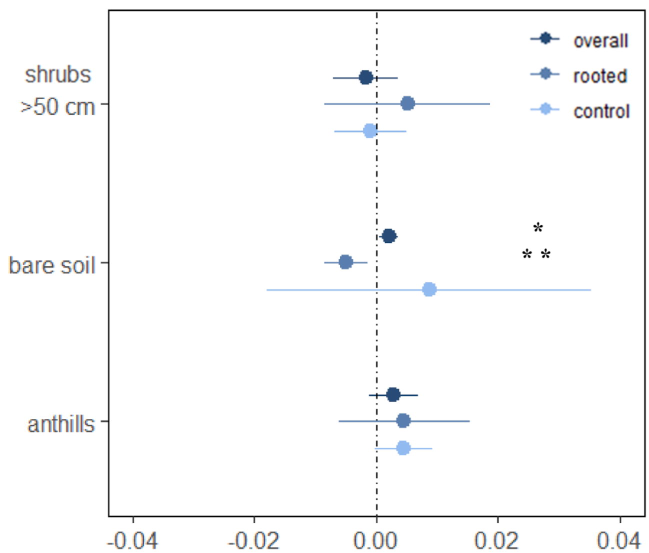

Fig. 3. Differences between plots with and without rooting by wild boar (*Sus scrofa*) in the Hainich National Park, Germany. Effect sizes are for the relationship of environmental parameters with the species richness. Models fitted by conditionally averaged GLMM (<3 AIC from best model), with Poisson family, accounting for pair ID as random effect. The overall model had $N = 120$, the rooted and control sub-models had $N = 60$. Horizontal bars represent the 95 % confidence interval. Parameters crossing the $y = 0$ line were not significant. * $P < 0.05$, ** $P < 0.01$. For detailed results, see Table A2.

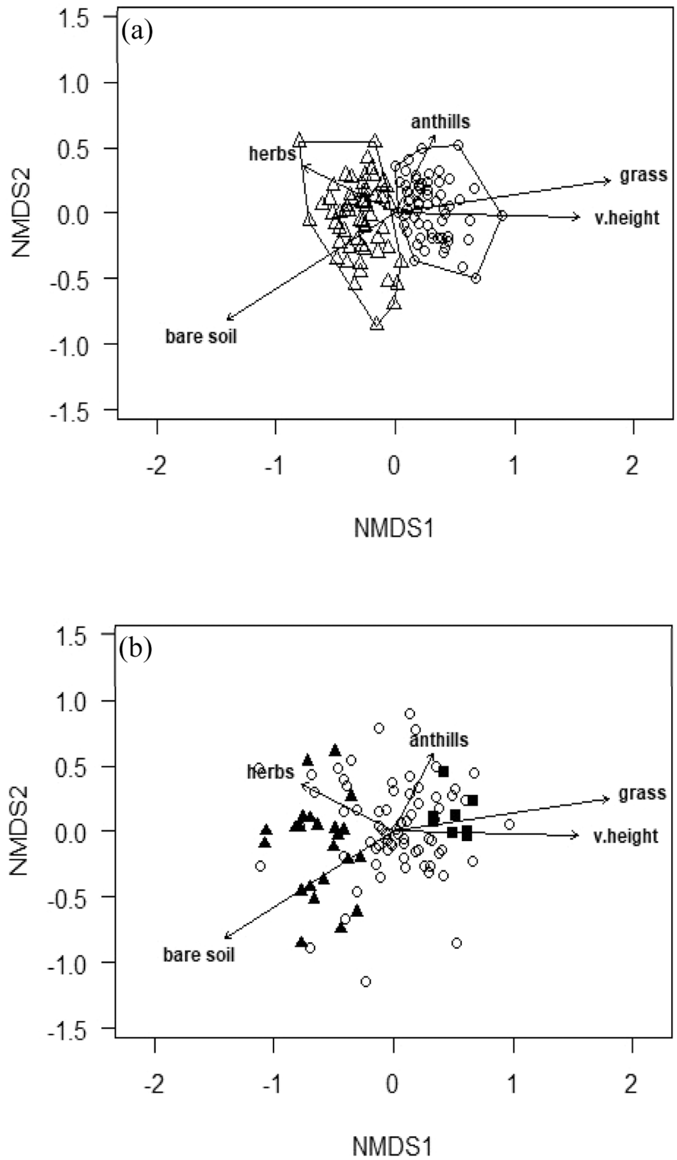

Fig. 4. NMDS ordination of plots with and without rooting by wild boar (*Sus scrofa*) in the Hainich National Park, Germany, for (a) sampling locations and (b) vascular plant species, with environmental parameter overlaid. The stress of the ordination was 0.197, with 3 dimensions. In (a), open triangles = rooted locations, and open circles = control locations. In (b), filled triangle = indicator species for rooted locations, filled square = indicator species for control locations, open circles = non-indicator species. Distinction was based on ISA (Table 2). v.height = vegetation height. Only significant environmental parameters were shown (at $P < 0.05$, based on 1000 permutations). In case of overlapping arrows, the most ecologically explanatory parameter was shown (for detailed results, see Table A3). Only species with an occurrence of > 3 were used.

grassland. NMDS showed that wild boar rooting and its indicator species are correlated with high bare soil cover, which is in line with other studies (e.g. Welander 2000, for review).

Rooted plots differed from control plots by a higher cover of bare soil, stones and gravel, and herbs, shorter vegetation, and lower covers of grasses, litter, pleurocarpous mosses, shrubs, and anthills. Our GLMMs revealed a slight positive overall effect of bare soil on species richness, suggesting that rooting can benefit plant diversity. Nevertheless, this effect was negative within rooted plots (Fig. 3), possibly indicating that a disturbance threshold was exceeded in some plots (Connell, 1978). The GLMMs, however, had low fit, and variation of bare soil cover in rooted plots may reflect differences in the time since disturbance (Fig. A4). In contrast, bare soil in control plots was found only on anthills, which were typically covered with *Brachypodium pinnatum*, *Thymus praecox* and *Thymus pulegioides*. These species are known indicator species of anthills associated with the yellow meadow ant (*Lasius flavus*) (Streitberger et al., 2017). Ants, like wild boar, are allogenic ecosystem engineers. They affect the plant community differently (King, 2021), and may contribute to unique biodiversity and also influence early grassland succession in calcareous grasslands.

According to grassland succession studies, early stages are characterised by annual herbs, followed up by an increase in perennial herbs, to be ultimately taken over by grasses and shrubs (Čarni et al., 2020; Collins and Adams, 1983; Pickett et al., 2001). Rooted plots in our study can be seen as an early stage in succession, and control plots as a late stage. This supports the idea that wild boar reset succession in calcareous grasslands, and may help sustain biodiversity in calcareous grasslands by promoting early successional plants in rooted plots, which are a food source for other wildlife (Everitt and Alaniz, 1980).

Succession in calcareous grasslands can also be reset by mowing or grazing, as in various European calcareous grasslands (Barbaro et al., 2001; Jacquemyn et al., 2011; Milberg and Tälle, 2023; Tälle et al., 2016). Long-term mowing effectively inhibits shrubs encroachment, and the removal of biomass from the system by hay collection helps to conserve the low-nutrient state of calcareous grasslands. This may be particularly important in regions with high levels of atmospheric deposition. Maintaining this low-nutrient state is essential for preserving biodiversity in many (managed) grassland systems (Al-Mufti et al., 1977; Klimek et al., 2006). However, mowing may result in homogenous vegetation and a selection for early flowering species, species with low rosettes (Jacquemyn et al., 2011; Lepš, 2014; Ottaviani et al., 2011), and reduce insect populations (Barber et al., 2022; Tanis et al., 2020, Schwarz et al., 2023). Grazing is regarded as more beneficial for biodiversity than mowing (Barber et al., 2022; Fartmann, 2024; Oates, 1995; Tälle et al., 2016), but a vegetation shift towards unpalatable or arable crops may occur (Ottaviani et al., 2011; Zhang et al., 2022). With both mowing and grazing, costs are an increasing concern (Tälle et al., 2016). What sets wild boar rooting apart from mowing and grazing is the sporadic turnover of soil and the creation of open patches. These factors have been shown to facilitate indicator species and enhance landscape heterogeneity. However, some species, such as those having bulbs and fleshy fruits, may be more sensitive to rooting than others, although they could also benefit from wild boar for seed dispersal (Cuevas et al., 2010; Kotanen, 1995; Massei and Genov, 2004).

Plot selection limitations were evident in this study, with bare soil being part of the criteria, the minimum patch size of 8 m^2 (patches are often < 4 m^2, see Horčičková et al. (2019) and Welander (2000)), the lack of randomness, and uncertain time since disturbance. Although we assume identical baseline conditions in rooted and control plots, we cannot exclude the possibility that habitat selection by wild boar may have influenced our results. Similar studies also faced complexities in plot selection (e.g. Burrascano et al., 2015b; Fagiani et al., 2014; Labadessa and Ancillotto, 2023). Some tried to overcome this by comparing areas with low and high rooting intensity, posing difficulties for replication and comparison between studies, others by simulating rooting (Horčičková et al., 2019; Mohr et al., 2005). Enclosure experiments may be attempted to single out effects of wild boar rooting (Burrascano et al., 2015b). Determining the age of a rooting (see Cabon et al., 2022; Tierney and Cushman, 2006) may be challenging due to patch dynamics: patches are often revisited and partially rooted again in subsequent years (Bankovich et al., 2016).

Our study area was an unmanaged wild zone, which can be seen as a form of rewilding (Pereira and Navarro, 2015). Although rewilding projects indicate that large herbivores can maintain semi-open grasslands (Guyton et al., 2020), human interventions sometimes remain necessary (Rupprecht et al., 2022). One option for maintaining open and diverse calcareous grassland ecosystems could be to incorporate a mixture of undisturbed wild zones with the presence of naturally occurring ecosystem engineers and herbivores (wild boar, red deer, roe deer) and areas managed by mowing and grazing by livestock or domestic ungulates (cattle, horse), as is currently practised in some areas of Hainich National Park. To enable wild boars to fulfil their role as ecosystem engineers, we recommend to allow substantial rooting in open, calcareous grassland ecosystems of high conservation importance (Scherer et al., 2025). However, their high fecundity rates may lead to excessive population growth (Bieber and Ruf, 2005), potentially surpassing a disturbance threshold (Connell, 1978), with possible negative effects on vegetation (Barrios-Garcia and Ballari, 2012). Therefore, management could benefit from population modelling studies, though various ecosystem processes may complicate precise determination of an optimum population size (Fox, 2013).

In conclusion, our results suggest that wild boar can indeed contribute to the conservation of calcareous grasslands and their characteristic vegetation. By rooting, wild boar clear dominant grasses and increase the cover of bare soil, creating opportunities for low-competitive and more nutritious species. This process helps to maintain characteristic calcareous grassland vegetation and, in our study, even facilitated the recruitment of a plant species that is characteristic for calcareous grasslands. Rooting positively correlated with a higher species richness, diversity, and evenness. From a grassland and biodiversity conservation perspective, allowing wild boar populations to roam undisturbed and freely in calcareous grasslands can provide clear ecological benefits. However, additional interventions may be required to maintain the openness of these biodiverse ecosystems. Moreover, populations should be monitored, as excessive growth could pose a risk of over-disturbance.

Ethics

Not applicable: This manuscript does not include human or animal research.

CRediT authorship contribution statement

Bob O. van Leeuwen: Conceptualisation, Methodology, Formal analysis, Investigation, Data curation, Writing – Original draft, Visualisation, Project administration, Writing – Review & editing. **Quiniver Tuinder:** Conceptualisation, Methodology, Investigation, Writing – Review & editing. **Thomas Fartmann:** Conceptualisation, Writing – Review & editing, Supervision. **Gwydion Scherer:** Writing – Review & editing, Supervision. **Alisa Klamm:** Writing – Review & editing, Funding acquisition. **Madlen Schellenberg:** Funding acquisition. **Philippine Vergeer:** Writing – Review & editing, Supervision. **Patrick A. Jansen:** Methodology, Writing – Review & editing, Supervision.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper

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Appendix

Fig A1. Map showing the location of pairs of plots with and without rooting by wild boar (*Sus scrofa*) in the Hainich National Park, Germany. Sampling locations were equally divided over three subareas of calcareous grassland, marked yellow and identified with white numbers. Each white dot represents a rooting-control pair (the rooted plot is shown). There were 20 pairs per subarea, summing up to $N = 60$ per treatment ($N = 120$ total)

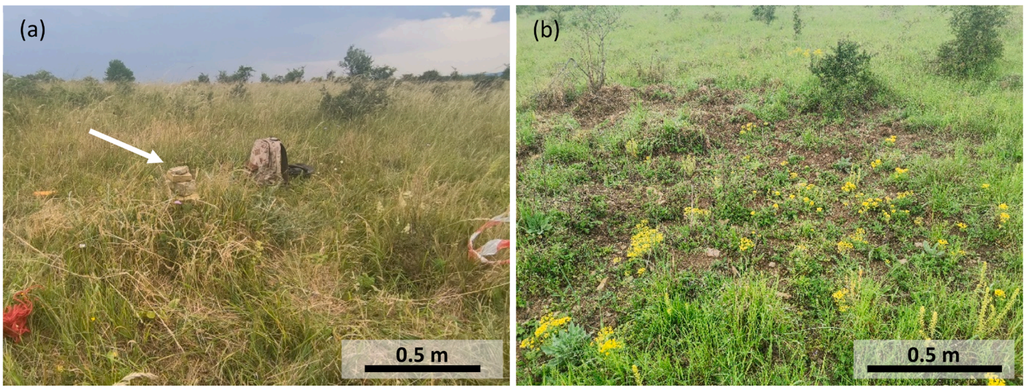

Fig. A2. Photographs showing plots (a) without (control) and (b) with rooting by wild boar (*Sus scrofa*) in the Hainich National Park, Germany. The white arrow marks the centre of the control plot

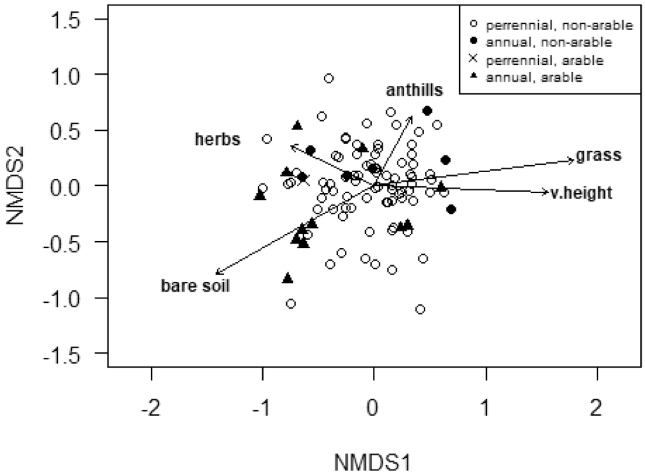

Fig. A3. NMDS ordination of plant species in the Hainich National Park, Germany, showing annual and arable species with parameter overlaid. The stress of the ordination was 0.197, with 3 dimensions. 'v.height' = vegetation height. Only significant environmental parameters were shown (at $P < 0.05$, based on 1000 permutations). In case of overlapping arrows, the ecologically comprehendable parameter was shown (for detailed results, see Table A3). Only species with an occurrence of > 3 are shown

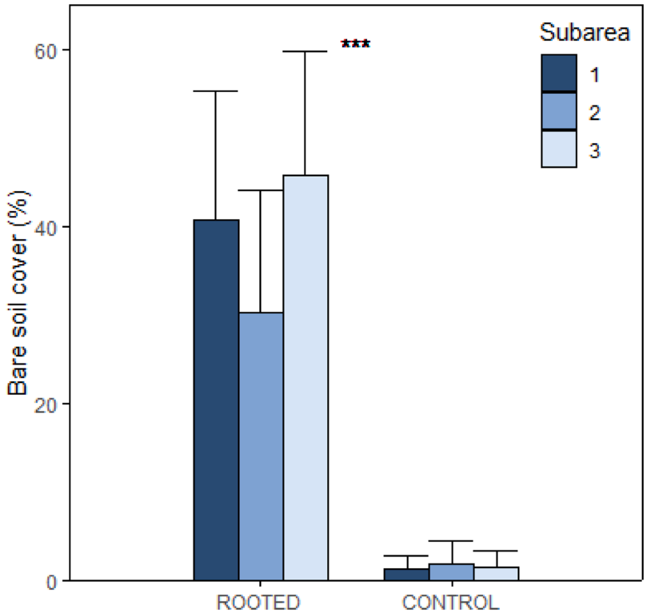

Fig. A4. Differences in bare soil cover between plots with and without rooting by wild boar (*Sus scrofa*) in the Hainich National Park, Germany. Comparison by GLMM ($Z = 29.75$, $P < 0.001$) with a proportional binomial distribution, accounting for pair ID as random effect. Subarea was not significant. Error bars show SD

Table A1

Correlation matrix of parameters measured in the Hainich National Park, Germany, by Spearman rank correlation. Strong correlation (>0.7 & <−0.7) is indicated with parentheses

Parameter	1	2	3	4	5	6	7	8	9	10	11	12
1. Vegetation height	1											
2. Local env. disturbance	−.28	1										
3. Bare soil	(−.72)	.32	1									
4. Stones and gravel	(−.74)	.31	(.84)	1								
5. Litter	(.75)	−.38	(−.83)	(−.82)	1							
6. Anthills	.20	−.33	−.17	−.31	.21	1						
7. Lichens	−.10	.03	−.07	−.05	−.01	.06	1					

(continued on next page)

Table A1 (*continued*)

Parameter	1	2	3	4	5	6	7	8	9	10	11	12
8. Pleurocarpous moss	(.70)	−.41	(−.84)	(−.85)	(.85)	.33	−.03	1				
9. Acrocarpous moss	−.13	−.03	−.02	−.05	−.02	.17	.35	.02	1			
10. Grasses	(.78)	−.35	(−.81)	(−.87)	(.88)	.22	−.08	(.79)	−.06	1		
11. Herbs	−.24	.04	.16	.31	−.25	−.03	.03	−.26	−.01	−.29	1	
12. Shrubs > 50 cm	.17	.03	−.02	−.03	−.04	.02	.02	−.05	−.04	−.05	−.16	1

Table A2
Detailed results of the GLMM analyses investigating the relationship between the species richness and environmental parameters, in Hainich National Park, Germany, for plots with and without rooting by wild boar (*Sus scrofa*), with Poisson family and random factor plot ID. Conditional averaging models were used (< 3 AIC from best model). OVERALL = overall model ($N = 120$), ROOTED = Wild boar-rooted sub-model ($N = 60$), CONTROL = control sub-model ($N = 60$). R^2m/R^2c shows marginal and conditional (delta) R-squared values of the full models. Statistical significances are indicated as 'n.s' not significant, * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$

Parameter	OVERALL				ROOTED				CONTROL			
	Est.	SE	Z	P	Est.	SE	Z	P	Est.	SE	Z	P
(Intercept)	3.363	0.029	117.3	***	3.685	0.062	57.78	***	3.301	0.033	99.01	***
Bare soil	0.002	0.001	2.521	*	− 0.005	0.002	3.368	***	0.009	0.013	0.667	n.s.
Anthills	0.003	0.002	1.483	n.s.	0.005	0.005	0.872	n.s.	0.004	0.002	1.865	n.s.
Shrubs > 50 cm	− 0.002	0.003	0.704	n.s.	0.005	0.007	0.733	n.s.	− 0.001	0.003	0.292	n.s.
R^2m / R^2c (full model) =	0.07 / 0.07				0.19 / 0.19				0.06 / 0.06			

Table A3
Detailed results of the NMDS fit. Environmental parameters were scaled. Statistical significances are indicated as 'n.s.' not significant, *** $P < 0.001$

Parameter	NMDS 1	NMDS 2	R^2	P
Vegetation height	1.000	0.017	0.5665	***
Bare soil	− 0.867	0.498	0.6352	***
Stones and Gravel	− 0.947	0.322	0.5291	***
Litter	0.983	− 0.181	0.7278	***
Anthills	0.479	− 0.878	0.1112	***
Pleurocarpous moss	0.975	− 0.221	0.7136	***
Grasses	0.991	− 0.137	0.7909	***
Herbs	− 0.905	− 0.426	0.1738	***
Shrubs > 50 cm	0.976	− 0.219	0.0419	n.s.

Data availability

Data will be made available on request.

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Glossary

Calcareous grassland: Semi-natural (semi-)dry grasslands, LRT 6210, with calcareous, thin, well-draining, lime-rich, nutrient-poor soils.

Ecosystem engineer: An organism that physically modifies, maintains, or creates habitat, excluding trophic interaction and resource competition (Jones et al., 1997). Allogenic ecosystem engineer indicates that the engineering comes forth from the organism's behaviour, not its body structure.

Landscape heterogeneity: the diversity of features in a landscape, such as vegetation or anthills

Rewilding: the passive management of ecological succession with the goal of restoring natural ecosystem processes and reducing human control of landscapes, which may require initial interventions (Pereira and Navarro, 2015)

Rooting: foraging behaviour exhibited by wild boar whereby the soil is disturbed, also called grubbing

Succession: the replacement of characteristic vegetation over time