Global Ecology and Conservation 58 (2025) e03451

Contents lists available at ScienceDirect

Global Ecology and Conservation

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

Rare butterfly species vitally depend on soil disturbance by an ecosystem engineer in abandoned calcareous grasslands

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ARTICLE INFO

Keywords:
Biodiversity conservation
EU Habitats Directive
Marsh fritillary (*Euphydryas aurinia*)
Nickerl's fritillary (*Melitaea aurelia*)
Succession
Threatened insect
Wild boar (*Sus scrofa*)

ABSTRACT

Ecosystem engineers like wild boar (*Sus scrofa*) can reset successional processes in grasslands, creating open swards rich in bare ground and exhibiting a warm microclimate. However, studies on the effects of soil disturbance by wild boar (*Sus scrofa*) on butterfly species in calcareous grasslands are missing. Here, we analysed the effects of wild boar rooting in abandoned calcareous grasslands of the Hainich National Park, Germany, on two rare butterflies: marsh fritillary (*Euphydryas aurinia*) and Nickerl's fritillary (*Melitaea aurelia*). We sampled different environmental parameters as well as butterfly frequency and abundance in wild boar rootings and undisturbed calcareous grassland vegetation. Our study demonstrated that wild boar play a vital role as soil disturbing ecosystem engineers for the persistence of the butterfly species. They created early seral stages rich in bare ground, hence a warm microclimate, and host plants. The two fritillary species used almost exclusively (*E. aurinia*) or even solely (*M. aurelia*) rooting patches for reproduction. Overall, occurrence and abundance of the butterfly species were best explained by a (i) high host plant abundance/biomass and (ii) warm microclimate. Based on our study, high densities of wild boar and additionally wild herbivorous ungulates, which slow down the expansion of woody plants by browsing, should generally be promoted in the calcareous grasslands of the national park. However, overall, they cannot halt shrub encroachment and thus the continuous loss of calcareous grasslands. Accordingly, we recommend active grassland management, e.g. exhaustive shrub removal followed by large-scale grazing by cattle and horses with low stocking rates.

1. Introduction

Temperate, semi-natural grasslands rank among the most speciose ecosystems on our planet (Bonari et al., 2017; Feurdean et al., 2018; Fartmann, 2024). They hold the world record in small-scale plant species richness and are hotspots of insect diversity (Chytrý et al., 2015; Fartmann, 2024). For example, three fifths of the 436 native European butterfly species use calcareous grasslands as their main habitat (Van Swaay et al., 2006). For centuries, traditional land management has created and preserved such grasslands with

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https://doi.org/10.1016/j.gecco.2025.e03451
Received 28 October 2024; Received in revised form 14 January 2025; Accepted 20 January 2025
Available online 22 January 2025

their outstanding biodiversity (Pärtel et al., 2005; Bonari et al., 2017; Feurdean et al., 2018; Fartmann, 2024). However, with ongoing industrialisation of farming practise, especially after World War II, the area of semi-natural grasslands has severely declined. Two opposite, large-scale processes have been responsible for this development: (i) land use intensification and (ii) abandonment or afforestation (Squires et al., 2018; Fartmann, 2024). The former includes the conversion of nutrient-poor, semi-natural grasslands to improved grasslands or arable fields and has mainly occurred on productive soils (Löffler et al., 2023). By contrast, abandonment and afforestation has typically occurred on marginal land (Fumy et al., 2021). Due to their significance for biodiversity conservation and their greatly threatened status, many of the semi-natural grasslands, such as calcareous grasslands, are legally protected by the EU Habitats Directive (EC, 2013).

Ecosystem engineers are organisms that alter their environment so strongly that fundamental ecosystem processes are changed (Jones et al., 1994). In particular the effects of soil-disturbing ecosystem engineers, such as the European mole (*Talpa europaea*), wild boar (*Sus scrofa*) or the yellow meadow ant (*Lasius flavus*), on biodiversity have only recently been studied more intensively in Central European grasslands. These ecosystem engineers have been shown to reset successional processes in grasslands, leading to open swards rich in bare ground (Treiber, 1997; Dauber et al., 2006; Streitberger et al., 2014, 2017; Streitberger and Fartmann, 2016; Horcicková et al., 2019; Cabon et al., 2022). As a result, less competitive plant species, overall plant species richness and animal species that require warm early-successional stages are favoured.

Particularly, wild boar may have strong effects on the composition of plant and animal communities in grasslands since the areas disturbed by them can be relatively large (Horcicková et al., 2019; Ferretti et al., 2021; Labadessa and Ancillotto, 2023). During winter, when above-ground diet is very limited for wild boar, they search for food by digging the soil up to a depth of 15 cm (Simon and Goebel, 1999; Welander, 2000). Among animals, butterfly, grasshopper and reptile species have been reported to benefit from wild boar rooting (de Schaetzen et al., 2018; Cabon et al., 2022; Labadessa and Ancillotto, 2023). So far, however, studies on the effects of soil disturbance by wild boar on butterfly species in calcareous grasslands were missing.

Calcareous grasslands are among the main habitats of the closely related marsh fritillary (*Euphydryas aurinia*) and Nickerl's fritillary (*Melitaea aurelia*) in Central Europe (Eichel and Fartmann, 2008; Bräu et al., 2013, Scherer and Fartmann, 2024). Due to strong population declines in the last century, they are considered endangered and near threatened, respectively, in Germany (Reinhardt and Bolz, 2011). *Euphydryas aurinia* is additionally protected by the EU Habitats Directive (EC, 2013). For both butterfly species, succession of calcareous grasslands is a major threat in the long run (Eichel and Fartmann, 2008; Bräu et al., 2013, Scherer and Fartmann, 2024). The litter layer prevents the germination of host plants; still present host plants become overgrown and shaded. In our study area, however, surprisingly, the calcareous grasslands in the southern part of the Hainich National Park (Central Germany: western Thuringia) still harbour strong populations of both butterfly species, although they have been abandoned for 30 years (own observation). The population of *E. aurinia* is probably even the largest in dry habitats across Germany. However, the study area does not only host large populations of the two butterfly species but also of wild boar and herbivorous ungulates (Klamm et al., 2020; Scherer et al., 2024). The current population density of wild boar is estimated to be up to 12 individuals per 100 ha (Klamm et al., 2020). Among the herbivorous ungulates, particularly red deer (*Cervus elaphus*) are known to browse woody plants intensively and, thus, to slow down the expansion of the woody plants in the calcareous grasslands (Scherer et al., 2024).

Here, we analysed the effects of wild boar rooting in abandoned calcareous grasslands of the Hainich National Park on environmental conditions and the two rare butterfly species *E. aurinia* and *M. aurelia*. We randomly selected 100 plots of 4 m^2 size, 50 in wild boar rootings and 50 in undisturbed calcareous grassland vegetation. Per plot we sampled different environmental parameters (mesoclimatic conditions, vegetation structure, host plant characteristics) as well as butterfly frequency and abundance. Moreover, we assessed those environmental parameters that determine the occurrence and density of the butterfly species. In particular, we hypothesized that rooting by wild boar:

(i) creates warm early-successional stages,
(ii) favours the establishment of host plants and
(iii) increases the frequency and abundance of both butterfly species.

Based on the findings of our study, we give recommendations for future management of the calcareous grasslands.

2. Material and methods

2.1. Study species

Marsh fritillary (*Euphydryas aurinia*) and Nickerl's fritillary (*Melitaea aurelia*) are closely related nymphalid butterflies of the Palaearctic region (Bräu et al., 2013; Scherer and Fartmann, 2024). The distribution range of *E. aurinia* extends from the British Isles to eastern Asia. By contrast, *M. aurelia* is less widespread and occurs from Central Europe (eastern France) up to Central Asia. Both species are univoltine and on the wings between May and July (Bräu et al., 2013). They colonize nutrient-poor grasslands, such as calcareous grasslands, and require a network of suitable habitat patches since they build metapopulations (Anthes et al., 2003a; Hula et al., 2004; Eichel and Fartmann, 2008; Ghidotti et al., 2018, Scherer and Fartmann, 2022, 2024). Locally they exhibit a high host-plant specificity and prefer luxuriant host plants rich in biomass within short swards for oviposition. In calcareous grasslands, small scabious (*Scabiosa columbaria*) is the main host plant of *E. aurinia* (Bräu et al., 2013). However, the less common field scabious (*Knautia arvensis*) and fuller's teasel (*Dipsacus fullonum*) may also be used for oviposition (Anthes and Nunner, 2006; own observation). By contrast, the host plant of *M. aurelia* is the hoary plantain (*Plantago media*) (Eichel and Fartmann, 2008; Bräu et al., 2013). In both fritillary species, the

females attach their eggs as batches of 50–400 eggs on the underside of the host plants' leaves (Anthes et al., 2003b; Eichel and Fartmann, 2008; Scherer and Fartmann, 2022). The larvae feed gregariously in a more or less dense web attached to their host plants until they hibernate within the forth instar in September. In spring, after hibernation, larvae of *E. aurinia* resume foraging gregariously and disperse solitarily when reaching the fifth instar. By contrast, larvae of *M. aurelia* already separate shortly before hibernation (Scherer and Fartmann, 2024). Pupation occurs in both species in the course of May in litter or vegetation.

2.2. Study area

The study area is located in the Hainich National Park in western Thuringia (Central Germany; 51°03' N, 10°42' E). The national park has a size of about 7.500 ha and an elevational range of the 330–425 m a.s.l. The climate is subcontinental, with an average annual temperature of 8.5 °C and an average annual precipitation of 600–800 mm (long-term average 1989–2018; Kronenberg et al., 2021). Due to shell limestone sediments, the soils are alkaline (Großmann, 2018). The study area has a size of 152 ha.

Most of the national park is covered by deciduous forests dominated by beech. However, the southern part, including the study area, still contains large remnants of calcareous grasslands, originating from centuries of former large-scale sheep grazing (Großmann, 2018). Of the total 827 ha of calcareous grasslands, 517 ha are situated in the southern part. Low-intensity land use has strongly declined across the region during the last century, and large parts of the present national park have been afforested. However, the calcareous grasslands in the south of the national park have persisted due to military management and training activities. Since 1930, the Wehrmacht and later on the Soviet Army kept the area open through large-scale sheep grazing, clear-cutting and military activities until the early 1990s. Since the establishment of the national park in 1997, anthropogenic influence has ceased. Today, after nearly 30 years of abandonment, the grasslands are characterised by shrub encroachment. Nevertheless, some of the grassland patches, especially on south-facing slopes, have surprisingly remained largely open. The reasons for the slow succession are the shallow dry soils and the strong effects of browsing wild ungulates (Scherer et al., 2024). Fallow deer (*Dama dama*), red deer (*Cervus elaphus*) and roe deer

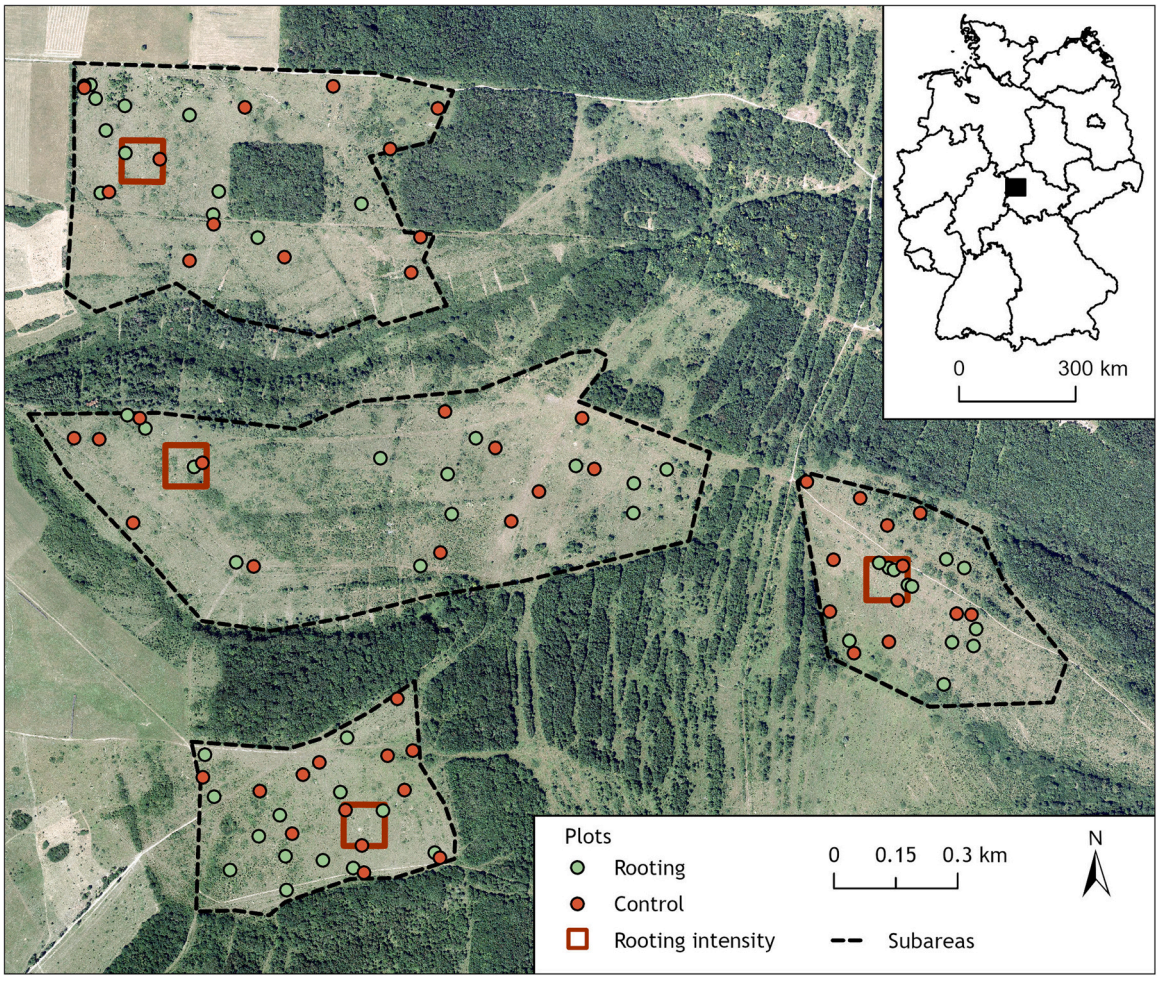

Fig. 1. The study area within the strictly protected zone (core zone) of the Hainich National Park in western Thuringia (Central Germany; inlay). Displayed are the locations of the four subareas with the three different types of plots.

(*Capreolus capreolus*) exhibit high abundances in the study area. Particularly, red deer are known to browse woody plants intensively and, thus, suppress the expansion of the most frequent wood plants in the calcareous grasslands: blackthorn (*Prunus spinosa*) and hawthorn (*Crataegus* spp.). Overall, the calcareous grasslands still host strong populations of *E. aurinia* and *M. aurelia* (own observation). Those of *E. aurinia* are probably even the largest in dry habitats within Germany.

2.3. Sampling design

2.3.1. Plot selection

The study area consisted of four patches of calcareous grasslands (17–63 ha) separated by at least 50 m of woodland. These four patches (hereinafter referred to as subareas) contained the strongest populations of *E. aurinia* in the national park and were intensively rooted by wild boar to an equal degree (own observation). All plots were equally divided across the four subareas, excluding areas dominated by shrubs or trees (Fig. 1). Because rooting behaviour is not completely random, some areas might be rooted more often, e.g. locations close to hideouts like larger shrub encroachments, areas with high concentrations of specific food sources or already rooted areas (Horcicková et al., 2019). To reduce bias by oversampling areas with a high concentration of rootings and because we did not find larger unrooted areas, we decided to conduct a randomized sampling approach. We randomly selected 100 plots of 4 m^2 (2 m × 2 m) size, 50 in wild boar rootings (hereinafter referred to as rooting plots) and 50 in undisturbed calcareous grassland vegetation (hereinafter referred to as control plots) (Fig. 1). Although rootings were often larger, we chose these measures to standardize the irregular shape of the rootings. Locations of these plots were chosen using a digital raster layer with numerated 20 m × 20 m grid cells across the four subareas, created in ArcGIS Pro 3. We randomly selected 50 grid cells per plot type with a minimum number of at least 12 plots per type in each subarea. Random selection was repeated if the selected grid cell only contained shrubs or trees. Control plots were established at the centre of the selected grid cells. To select rooting plots, the nearest wild boar rooting of at least 4 m^2 size to the centre of the selected grid cell was chosen. Moreover, it was always located in the centre of the respective rooting.

To assess wild boar rooting intensity, we additionally established four randomly selected 100 m × 100 m (1 ha) plots (hereinafter referred to as rooting intensity plots), one in each subarea. To select plots, we used the same method as described above with numerated 100 m × 100 m grid cells. Each plot had to contain at least one rooting and one control plot, otherwise random selection was repeated.

2.3.2. Sampling of butterflies and environmental conditions

All sampling was done in 2022. During July and August, all rooting and control plots were systematically searched for egg batches or larval webs (hereinafter we only refer to larval webs for reasons of simplicity) of *E. aurinia* and *M. aurelia* and their numbers were counted. Moreover, per plot, we recorded the used host plant and the number of webs.

After butterfly sampling, we recorded several environmental parameters for all rooting and control plots. For rooting and control plots, we measured daily sunshine duration with the help of a horizontoscope (Scherer et al., 2021) as well as aspect and slope using a compass with an inclinometer. The two latter parameters were used to calculate the heat load index (McCune and Keon, 2002). We estimated the cover of bare ground, mosses, litter, grasses, herbs and shrubs within each plot. The heights of the herbaceous and shrub layer were measured using a folding rule at three randomly chosen points within the plot and averaged for further analysis. We counted the number and estimated the cover of available host plants (*D. fullonum*, *K. arvensis P. media* and *S. columbaria*) separately for each species. Additionally, for the two main host plants, *S. columbaria* and *P. media*, we counted the number of leaves and measured the diameter of the rosette of three randomly chosen plants per plot as a proxy for their biomass. For further analysis, the values for the number of leaves and diameter of the three plants were averaged.

Per rooting intensity plot, we mapped all rootings on the basis of high resolution aerial photographs (1: 300) in the field. Later we digitized them using ArcGIS Pro 3 and calculated their number and size.

2.4. Statistical analysis

All statistical analyses were performed using R 4.3.2 (R Development Core Team, 2023). To assess significant differences in environmental conditions as well as in larval web frequency and abundance between rooting and control plots, we used pairwise comparisons conducted by generalized linear mixed-effect models (GLMMs). For different data types we used the following error structures: count data – Poisson; interval scaled data – gamma; percentage data – binomial. To account for possible spatial autocorrelation, we used subarea as a random factor.

To assess the environmental parameters that determine larval web frequency and abundance, we fitted multivariable GLMMs with binomial (frequency) and Poisson (abundance) error structure, respectively. Since *E. aurinia* occurred in both rooting and control plots, we calculated models over all 100 plots (= full models) and solely for the 50 rooting plots (= rooting models). By contrast, *M. aurelia* was only present in rooting plots. Accordingly, we only performed rooting models for this species. Before the analyses, we conducted several tests to increase model robustness and transformed or excluded some variables. To reduce model overfitting, we checked all predictors for intercorrelations using Spearman's rank correlation (r_S). The number of host plants (abundance) was always strongly intercorrelated with the cover of host plants ($r_S > 0.9$, $P < 0.005$). Since the abundance was precisely counted while cover was estimated, we excluded the latter. To account for host plant biomass, we merged host plant diameter and leaf count into a new variable called "biomass" via principal component analysis (PCA). Intercorrelations between both variables were high in both plant species (*S. columbaria*: $r_S = 0.8$, $P < 0.005$ *P. media*: $r_S = 0.9$, $P < 0.005$). To further prevent multicollinearity, we calculated the variance

inflation factor (VIFs) for all selected variables. For all remaining variables, the VIF was below 10; accordingly, no variables were removed. To further increase model robustness, we limited the number of introduced variables per model by n/10 and added subarea as a random factor. All predictor variables were scaled prior to the calculations to ensure the comparability of the model coefficients. When conducting the GLMMs, we used model averaging based on an information-theoretic approach using the 'dredge' function (R package MuMIn; Barton, 2023) to identify the most important predictors (Burnham and Anderson, 2004; Grueber et al., 2011). To allow all remaining variables within model selection, we introduced the correlation matrix into the models. If variables were intercorrelated ($|r_S| > 0.6$), only one of the intercorrelated predictors was allowed within each model. For the binomial rooting model of *E. aurinia*, complete separation impeded the models due the interaction of some variables perfectly predicting the outcome. We solved the problem by conducting two separate models, one containing all host plant parameters (= host plant model) and the other one containing the other environmental parameters (= mesoclimate/vegetation structure model) (Table A1). Afterwards, we performed a synthesis model containing only the significant parameters of the two prior models. Overall, the number of predictor variables used in the models varied between 12 and 14 (Table A2). The resulting averaged models only included the top-ranked models with ΔAICC < 3 (Grueber et al., 2011). Finally, the explanatory power of the models (depicted as a span for averaged models) was assessed by calculating marginal (variance explained by fixed effects; R^2_m) and conditional R^2 (variance explained by both fixed and random effects; R^2c) (Nakagawa et al., 2017).

To visualize environmental differences between rooting and control plots, we applied non-metric multidimensional scaling (NMDS; R package vegan; Oksanen et al., 2022). We fitted the data according to their environmental parameters using the Bray-Curtis distance as a distance measure and a maximum number of 100 random starts.

3. Results

3.1. Environmental conditions

The rooting intensity plots of 1 ha size contained 24–45 rootings, which covered 14–18 % of the total plot area. The mean size (± SE) of the rootings was 51 ± 5 m² (range: 2–450 m²).

Table 1.
Mesoclimatic conditions, vegetation structure and host plant parameters in rooting ($n = 50$) and control plots ($n = 50$). Pairwise comparisons were conducted by GLMMs using subarea as a random factor. For different data types we used the following error structures: count data – Poisson, interval scaled data – gamma, percentage data – binomial. Pl. = plants. *$P < 0.05$, **$P < 0.01$, ***$P < 0.001$; n.s., not significant.

Parameter	Rooting		Control		*P*
	Mean ± SE	Range	Mean ± SE	Range	
Mesoclimate					
Sunshine duration (h)	13.8 ± 0.2	10–15	14.0 ± 0.3	8–15	n.s.
Heat load index	0.87 ± 0.01	0.71–0.93	0.85 ± 0.01	0.68–0.91	*
Vegetation structure					
Cover (%)					
Bare ground	41.7 ± 3.3	5–90	1.9 ± 0.4	0–10	***
Mosses	0.5 ± 0.3	0–10	51.8 ± 5.1	0–100	***
Litter	21.4 ± 1.9	5–75	71.3 ± 2.1	30–100	***
Grasses	38.5 ± 2.9	5–80	78.0 ± 2.5	15–100	***
Herbs	43.5 ± 2.3	15–80	36.4 ± 2.3	10–75	*
Shrubs	15.7 ± 2.5	0–70	18.5 ± 3.4	0–80	n.s.
Height (cm)					
Herbaceous layer	43.1 ± 1.7	15–66	51.2 ± 2.5	13–110	**
Shrub layer	120.8 ± 21.1	50–400	99.1 ± 14.5	50–337	n.s.
Host plants					
Dipsacus fullonum					
Frequency (%)	22 ± 6.0	0/100	2 ± 2.0	0/100	**
Cover (%)	1.2 ± 0.5	0–20	0.2 ± 0.1	0–1	**
K. arvensis					
Frequency (%)	56 ± 7.0	0/100	32 ± 7.0	0/100	*
Cover (%)	7.8 ± 1.7	0–50	1.7 ± 0.5	0–10	***
Plantago media					
Frequency (%)	86 ± 5.0	0/100	12 ± 4.6	0/100	***
Abundance (pl./4 m²)	11.1 ± 1.5	0–53	0.3 ± 0.2	0–7	***
Cover (%)	8.5 ± 1.3	1–40	0.2 ± 0.1	1–2.5	**
Diameter (cm)	14.6 ± 0.4	9.6–19.3	12.8 ± 1.2	9.5–16.5	n.s.
No. leaves	8.6 ± 0.4	4–15.5	5.1 ± 0.6	3.3–7	***
Scabiosa columbaria					
Frequency (%)	82 ± 5.5	0/100	54 ± 7.1	0/100	*
Abundance (pl./4 m²)	10.6 ± 1.7	0–45	6.3 ± 1.2	0–32	**
Cover (%)	9.9 ± 1.4	1–40	3.8 ± 0.9	1–25	**
Diameter (cm)	13.7 ± 0.7	8–27.3	11.2 ± 0.8	2.8–28.0	*
No. leaves	9.5 ± 0.7	4–24.3	6.1 ± 0.5	3.3–14	***

Overall, rooting and control plots strongly differed in environmental conditions (Table 1). Although both plot types exhibited a similar sunshine duration, rooting plots had a higher heat load. Very striking was the difference in vegetation structure and host plant parameters. Rooting plots were characterised by earlier successional stages compared to control plots. They had shorter swards and a higher cover of bare ground and herbs, but a lower cover of grasses, litter and mosses. All four host plant species were more frequent and had a higher cover in rooting than in control plots. Moreover, in the host plants *P. media* and *S. columbaria,* abundance was higher and plants had more leaves. Additionally, plants of *S. columbaria* had larger rosettes in rooting plots than in control plots. By contrast, shrub cover and height as well as diameter of the *P. media* rosettes did not differ between the two plot types. The large differences in environmental conditions are also depicted by the NMDS, which showed a clear separation of both plot types on the first axis (Fig. 2).

3.2. Response of butterfly species to wild boar rooting

Overall, we detected 68 larval webs of *E. aurinia* and 44 of *M. aurelia* in the 100 plots. More than four fifths (81 %) of the *E. aurinia* webs were found on *S. columbaria*. The remaining webs were located on *D. fullonum* (10 %) and *K. arvensis* (9 %). All webs of *M. aurelia* were observed on *P. media*. Both butterfly species positively responded to the rooting activity of the wild boar. They had a much higher frequency and abundance in rooting than in control plots (Fig. 3). *Euphydryas aurinia* was present on 52 % of the rooting plots, but occurred only on 8 % of the control plots. On average (±SE), 1.3 ± 0.2 larval webs were found per rooting plot of 4 m^2 size, which was a 13 times higher abundance than on control plots (0.1 ± 0.1). By contrast, *M. aurelia* even occurred only in rooting plots. There it had a frequency of 42 % and a mean (±SE) abundance of 0.9 ± 0.2 webs/4 m^2.

The abundance and biomass, respectively, of *S. columbaria* and *P. media*, the two main host plant species, were the most important driver of butterfly frequency and abundance (Fig. 4, Tables A3 and A4). Frequency and abundance of *E. aurinia* increased with the abundance of *S. columbaria* across all and rooting plots; those of *M. aurelia* increased with the biomass of *P. media* in the rooting plots. Moreover, the abundance of the two further host plant species, *D. fullonum* and *Knautia arvensis*, fostered the frequency of *E. aurinia* across all plots. In *E. aurinia*, vegetation structure additionally affected the frequency and abundance. Across all plots, cover of mosses and vegetation height (only abundance model) had negative effects. Moreover, cover of shrubs fostered *E. aurinia* abundance in all and rooting plots. Overall, the explanatory power of all models was high (R^2_m = 0.49–0.80, R^2_c = 0.49–0.84).

4. Discussion

Long-term abandonment of semi-natural grasslands is known to result in litter accumulation and encroachment of some competitive grass and moss species, which overall results in species-poor plant and insect communities (Ellenberg and Leuschner, 2010; Streitberger et al., 2017; Schüle et al., 2023; Fartmann, 2024). However, successional speed varies depending on the productivity of the soils. Although all four studied subareas were characterised by a low successional speed due to shallow soils and mostly south-facing slopes, which cause high heat load, the negative effects of abandonment were clearly visible in the control plots. They had a high cover of litter, mosses and grasses, but a very low cover of the host plants of the two butterfly species (mean cover: always < 4 %).

Population estimates for wild boar using non-invasive genetic methods in 2018 indicate a population of approximately 12 individuals per 100 ha. (Klamm et al., 2020). Although wild boar density can be subject to significant annual fluctuations, a similar population density is assumed at the time of these studies. As a result, a proportion of 14–18 % of rooted areas within the calcareous grasslands was recorded in our study. Wild boar are considered ecosystem engineers that can alter ecosystem processes through changing their physical environment (Jones et al., 1994; Simon and Goebel, 1999). By digging the soil while searching for food, they can reset successional processes leading to open swards rich in bare ground (Treiber, 1997; Sandom et al., 2013; Sims et al., 2014;

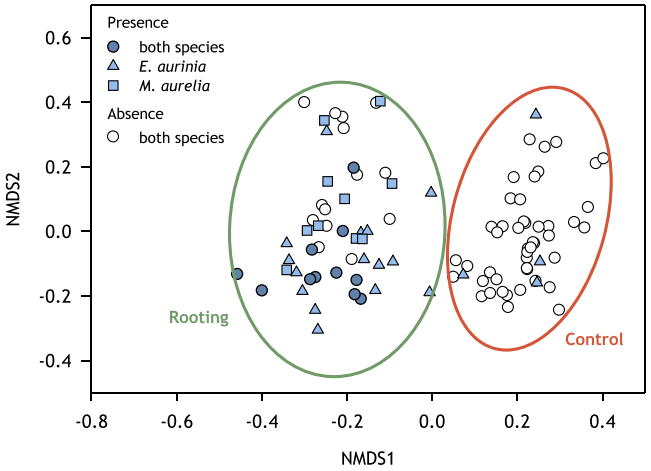

Fig. 2. NMDS of control (n = 50) and rooting plots (n = 50) based on environmental parameters.

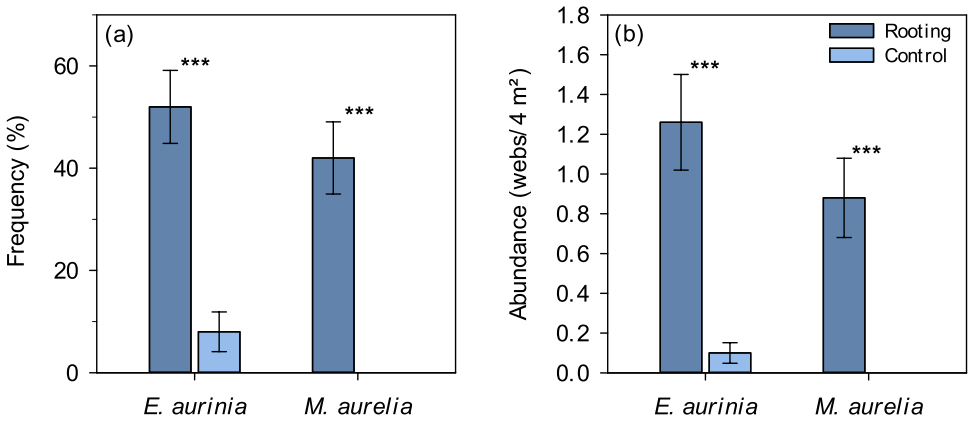

Fig. 3. Frequency (a) and abundance (b) of larval webs of *E. aurinia* and *M. aurelia* in control ($n = 50$) and rooting plots ($n = 50$). Pairwise comparisons were conducted by GLMMs using subarea as a random factor. For percentage data (frequency) a binomial and for count data (abundance) a Poisson error structure was used. ***$P < 0.001$.

Burrascano et al., 2015; Horcicková et al., 2019). As a result, competitive plant species become suppressed and the establishment of less-competitive ones (e.g. pioneer or annual species) and overall plant species richness are favoured. In line with this, the rooting plots were characterised by short, open swards rich in bare ground and a high cover of herbs. Moreover, the rooting activity of the wild boar had strongly favoured the establishment and vitality of all four host plant species. They had a much higher frequency and cover in rooting than in control plots. Abundance, rosette diameter and number of leaves, which were only sampled in *S. columbaria* and *P. media*, were also higher (except rosette diameter in *P. media*).

For both butterfly species, the most important parameters defining habitat quality are host plant abundance and biomass (Eichel and Fartmann, 2008; Botham et al., 2011; Brunbjerg et al., 2017). To avoid food shortage among the gregariously feeding caterpillars, the adult females prefer luxuriant host plants in microhabitats of high host plant abundance for oviposition (Anthes et al., 2003a; Eichel and Fartmann, 2008; Scherer and Fartmann, 2022). Our study confirmed the prime importance of sufficient food for the caterpillars of both fritillary species. In *E. aurinia*, the abundance of *S. columbaria* was the key driver of occurrence and abundance (all and rooting plots). In *M. aurelia*, the same was true for the biomass of *P. media* (rooting plots). Regarding all plots, interestingly, the frequency of *E. aurinia* was also favoured by the abundance of two further host plant species, *D. fullonum* and *K. arvensis*. Both plant species were less widespread and more rarely used as a host plant by *E. aurinia* in the study area. At most 10 % of the webs were found on each of the two host plant species. These findings reveal at least a certain degree of flexibility in host plant selection of *E. aurinia* in our study area. Similar observations have been made in other parts of its distribution range (Anthes et al., 2003b; Anthes and Nunner, 2006; Scherer and Fartmann, 2022).

Butterfly, grasshopper and reptile species have been reported to benefit from the warm microclimatic conditions created by wild boar rooting (de Schaetzen et al., 2018; Cabon et al., 2022; Labadessa and Ancillotto, 2023). The butterfly species studied here, *E. aurinia* and *M. aurelia*, are also known to require warm microhabitats for successful development of the immature stages (Eichel and Fartmann, 2008; Pielech et al., 2017; Scherer and Fartmann, 2022). For reproduction, they mainly (*E. aurinia*) or even only (*M. aurelia*) used the rooting plots. They were present in 52 % and 42 %, respectively, of the plots. Overall, rooting plots were characterised by a high sunshine duration and heat load as well as a very high cover of bare ground (mean: 42 %). Accordingly, they provided very warm microclimatic conditions during sunny days (Stoutjesdijk, Barkmann, 2014), which explains, besides the high abundance/biomass of host plants, why they were so relevant for the two butterfly species. The detected vegetation structure preferences also underpin the strong dependence on earlier successional stages providing a warm microclimate. The cover of mosses had a negative effect on the frequency and abundance of *E. aurinia* across all plots. Moreover, shorter swards (all plots) and a higher cover of shrubs (all and rooting plots) favoured the abundance of *E. aurinia.* In calcareous grasslands, a higher cover of mosses is typical of taller and denser swards exhibiting a moister and cooler microclimate (Ellenberg and Leuschner, 2010; Stoutjesdijk, Barkmann, 2014; Streitberger et al., 2017). In the studied plots, usually shrubs had a low cover (mean: < 19 %) and were small (height< 1 m) (own observation). Nevertheless, they may favour heat accumulation on their southern sides in the otherwise open swards (cf. Stoutjesdijk, Barkmann, 2014) and could also play an important role in male mate-locating behaviours (Konvicka et al., 2023). By contrast, within the rooting plots, the cover of litter had positive effects on the occurrence of *E. aurinia*. Accordingly, the earliest successional stages in the rooting plots seemed to be avoided. Here, at least some litter may prevent the soil from excessive drying up and heat accumulation, and, hence, from heat stress for host plants and larvae during very hot summer days (cf. Bräu et al., 2013; Shi et al., 2022).

In conclusion, in calcareous grasslands characterized by long-term abandoned, wild boar as soil disturbing ecosystem engineers reset succession. They created early seral stages rich in bare ground, hence a warm microclimate, shorter swards and herbs, but with a lower cover of grasses, litter and mosses. The two fritillary species used almost exclusively (*E. aurinia*) or even solely (*M. aurelia*) wild boar rootings for reproduction. Overall, occurrence and abundance of the butterfly species were best explained by a (i) high host plant abundance/biomass and (ii) warm microclimate. Consequently, our study demonstrated that wild boar play a vital role as soil disturbing ecosystem engineers for the persistence of two rare butterfly species in abandoned calcareous grasslands. However, as depicted

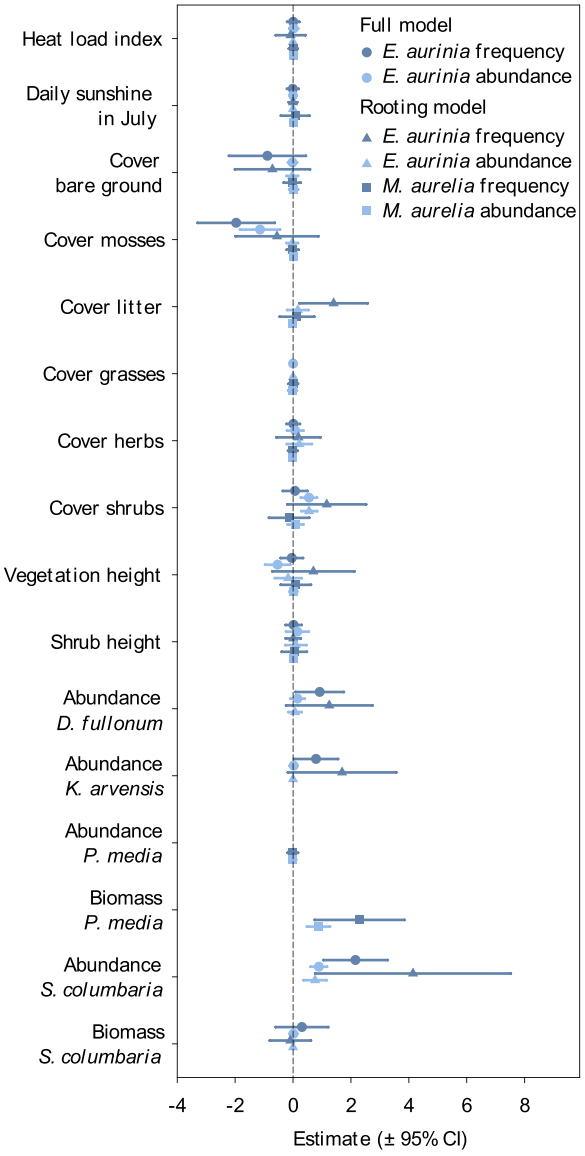

Fig. 4. Estimates (±95 % CI) of environmental predictors of the frequency (presence/absence) and abundance of *E. aurinia* and *M. aurelia* in all plots (full model: rooting [$n = 50$] and control plots [$n = 50$]) and rooting plots (rooting model, $n = 50$), respectively. Confidence intervals of significant predictors ($P < 0.05$) do not cross x = 0. For further details see Tables A3 and A4.

by Schröer et al. (2024), shrub encroachment increased drastically during the last three decades. Thus, we appeal for urgent action to promote the legally protected calcareous grasslands and thereby the two rare butterfly species. Because our study only covers one year, we propose a long-term monitoring for all species included in this study. Monitoring should include microhabitat assessments of *E. aurinia* and *M. aurelia* as well as population monitoring of wild boar and their rooting behaviour. This is important to derive patterns and to monitor possible tipping points of the populations of the two butterflies in the constantly deteriorating calcareous grasslands.

5. Implications for conservation

After 30 years of abandonment, the intensive rooting activity of the wild boar has been identified as the key for the still strong populations of *E. aurinia* and *M. aurelia* in the calcareous grasslands of the Hainich National Park. Herbivorous wild ungulates also occur in high abundance in the study area. Among them in particular red deer suppress the expansion of woody plants by browsing and, thus, slows down succession (e.g. Tschöpe et al., 2011; de Schaetzen et al., 2018; Pápay et al., 2020). Accordingly, to promote natural dynamics and to keep anthropogenic influence small in the national park, high densities of wild ungulates in the calcareous grasslands should generally be promoted. However, overall, they cannot halt shrub encroachment and thus the continuous loss of calcareous grasslands (Pápay et al., 2020; Schröer et al., 2024). Accordingly, active grassland management is also required. Therefore,

we recommend initial exhaustive shrub removal (Poniatowski et al., 2020). However, some scattered shrubs or small groups of them should be preserved, since they act as important habitat structures for many threatened species of grassland birds (Fartmann et al., 2022), of which are still some present in the study area (Handschuh and Klamm, 2022). Opposed to *M. aurelia*, *E. aurinia* is less tolerant to mowing and sheep grazing in calcareous grasslands (Ulrich, 2004; Anthes and Nunner, 2006). For that reason, we advise year-round, large-scale grazing by cattle and horses with very low stocking rates to secure the persistence of probably the largest population of *E. aurinia* in dry habitats in Germany in the long run.

Ethics statement

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

Funding information

This study was funded by the Hainich National Park.

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.

Acknowledgements

We are grateful to Manfred Großmann, former head of the Hainich National Park, for insights into the history of the national park. We are particularly thankful to Alisa Klamm, Madlen Schellenberg and Andreas Henkel, Department for Nature Conservation and Research, for their help in coordinating the study and valuable comments on a previous version of the manuscript. Gwydion Scherer was supported by a PhD scholarship of the Studienstiftung des Deutschen Volkes. At last, we appreciate the constructive feedback provided by two anonymous reviewers.

Appendix

Table A1
Statistics of the binomial GLMMs (model averaging): mesoclimate/vegetation structure (a) and host plant predictors (b) of the frequency (presence/absence) of *E. aurinia* in rooting plots ($n = 50$). Marginal $R^2 = R^2_m$, conditional $R^2 = R^2_c$. Mesoclimate/vegetation structure model: $R^2_m = R^2_c = 0.57–0.71$. Host plant model: $R^2_m = 0.80–0.83$, $R^2_c = 0.85–0.87$. *$P < 0.05$; n.s., not significant

Parameter	Estimate	SE	Z	*p*
(a) Mesoclimate/vegetation structure model				
Intercept	–3.19	5.03	0.63	n.s.
Cover of litter	0.10	0.04	2.33	*
(b) Host plant model				
Intercept	–3.95	1.64	2.35	*
Abundance of *S. columbaria*	0.35	0.14	2.41	*

Table A2
Predictor variables used in the binomial and Poisson GLMMs (model averaging). The variance inflation factor (VIF) of all included variables was < 10. For further information see Section 2.4

Parameter	Binomial models			Poisson models		
	E. aurinia		*M. aurelia*	*E. aurinia*		*M. aurelia*
	FM	RM	RM	FM	RM	RM
Mesoclimate						
Sunshine duration	x	x	x	x	x	x
Heat load index	x	x	x	x	x	x
Vegetation structure						
Cover						
Bare ground	x	x	x	x	x	x
Mosses	x	x	x	x	x	x
Litter	x	x	x	x	x	x
Grasses	x	x	x	x	x	x

(*continued on next page*)

Table A2 (*continued*)

Parameter	Binomial models			Poisson models		
Herbs	x	x	x	x	x	x
Shrubs	x	x	x	x	x	x
Height						
Herbaceous layer	x	x	x	x	x	x
Shrub layer	x	x	x	x	x	x
Host plants						
Abundance						
Dipsacus fullonum	x	x	.	x	x	.
Knautia arvensis	x	x	.	x	x	.
Plantago media	.	.	x	.	.	x
Scabiosa columbaria	x	x	.	x	x	.
Biomass	.	.		.	.	
Dipsacus fullonum	.	.	.	.	.	.
Knautia arvensis	.	.	.	.	.	.
Plantago media	.	.	x	.	.	x
Scabiosa columbaria	x	x	.	x	x	.
No. parameters	**14**	**14**	**12**	**14**	**14**	**12**

Table A3
Statistics of binomial GLMMs (model averaging): environmental predictors of the frequency (presence/absence) of *E. aurinia* and *M. aurelia* in all plots (a; full model: rooting [$n = 50$] and control plots [$n = 50$]) and rooting plots (b and c; rooting model, $n = 50$), respectively. Marginal $R^2 = R^2_m$, conditional $R^2 = R^2_c$. *Euphydryas aurinia*: full model – $R^2_m = R^2_c = 0.66$–0.73, rooting model – $R^2_m = 0.80$, $R^2_c = 0.84$. *Melitaea aurelia*: rooting model – $R^2_m = R^2_c = 0.53$–0.65. $^*P < 0.05$, $^{**}P < 0.01$, $^{***}P < 0.001$; n.s., not significant

Parameter	Estimate	SE	Z	*P*
Euphydryas aurinia				
(a) Full model				
Intercept	–1.51	0.41	3.61	***
Abundance of *S. columbaria*	2.16	0.46	3.82	***
Cover of mosses	–1.93	0.67	2.89	**
Abundance of *D. fullonum*	0.92	0.42	2.16	*
Abundance of *K. arvensis*	0.80	0.38	2.05	*
(b) Rooting model				
Intercept	–5.29	1.84	−2.87	**
Abundance of *S. columbaria*	0.27	0.10	2.64	**
Cover of litter	0.15	0.06	2.59	**
Melitaea aurelia				
(c) Rooting model				
Intercept	–0.68	0.40	1.65	n.s.
Biomass of *P. media*	2.30	0.77	2.91	**

Table A4
Statistics of Poisson GLMMs (model averaging): environmental predictors of the abundance of *E. aurinia* and *M. aurelia* in all plots (a; full model: rooting [$n = 50$] and control plots [$n = 50$]) and rooting plots (b and c; rooting model, $n = 50$), respectively. Marginal $R^2 = R^2_m$, conditional $R^2 = R^2_c$. *Euphydryas aurinia*: full model – $R^2_m = R^2_c = 0.76$–0.80, rooting model – $R^2_m = 0.65$–0.70, $R^2_c = 0.66$–0.78. *Melitaea aurelia*: rooting model – $R^2_m = R^2_c = 0.49$–0.57. $^*P < 0.05$, $^{**}P < 0.01$, $^{***}P < 0.001$; n.s., not significant

Parameter	Estimate	SE	Z	*p*
Euphydryas aurinia				
(a) Full model				
Intercept	–1.60	0.29	5.4	***
Cover of mosses	–1.14	0.34	3.52	**
Abundance of *S. columbaria*	0.89	0.14	6.16	***
Cover of shrubs	0.54	0.14	3.87	***
Vegetation height	–0.53	0.22	2.93	*
(b) Rooting model				
Intercept	–0.36	0.20	1.73	n.s.
Abundance of *S. columbaria*	0.76	0.20	3.74	***
Cover of shrubs	0.56	0.14	4.00	***
Melitaea aurelia				
(c) Rooting model				
Intercept	–0.46	0.20	2.22	*
Biomass of *P. media*	0.88	0.20	4.35	***

Data availability

Data will be made available on request.

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