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ORIGINAL PAPER

# Impact of wild boar (*Sus scrofa*) rooting succession on grasshoppers (Orthoptera) in abandoned calcareous grasslands

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**Abstract**
Many European insect species are bound to open habitats, hence disturbances that reset succession are important for their conservation. These can be employed in the form of low-intensity management or, alternatively, natural processes. Rooting by wild boar (*Sus scrofa*) is an example of such a natural process. In this study, we investigated if and how boar rooting influences Orthoptera (grasshoppers and crickets) communities in calcareous grasslands. We compared three successional stages in abandoned calcareous grasslands in Hainich National Park, Germany: fresh rootings, old rootings and the matrix. We tested for differences in microhabitat, Orthoptera abundance, species composition and demography. We found that crickets and bush-crickets (Ensifera) preferred late successional stages in May and June, whereas grasshoppers and groundhoppers (Caelifera) preferred early successional stages in May, whereas they did not show any preference in June. We found two mechanisms through which rooting by wild boar supported Orthoptera diversity: (1) different microhabitats support different habitat specialists with different life cycles. Habitat mosaics created by wild boar are thus more diverse than just undisturbed grassland and (2) the most diverse microhabitat, characterised by the highest species richness, was created by wild boar. Additionally, our observations also indicated that successional mosaics offer habitats for species requiring different microhabitats throughout their life cycle. Implications for insect conservation: Our results indicate that, at this density, wild boar can help to sustain Orthoptera biodiversity in calcareous grasslands. We advise to take the beneficial role of wild boar into consideration in conservation measures and wild boar population management.

**Keywords** Biodiversity conservation · Habitat quality · Disturbance ecology · Ecosystem engineers · Rewilding · Insect ecology

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## Introduction

Insects are critical to ecosystems due to their important ecological roles (Wagner 2020; Nyffeler et al. 2018), their high diversity (Stork 2018) and their strong declines in recent years (e.g. Hallmann et al. 2017; Wagner 2020). For instance, the International Union for Conservation of Nature reveals that about a quarter of all insects are nowadays near-threatened, threatened, or already extinct (IUCN 2024). Many threatened species are bound to open habitats, in particular grassland ecosystems (Wagner 2020). In forest biomes, grasslands were historically maintained by natural disturbances such as foraging by large herbivores, storms, floods and fires (Brackhane et al. 2021; Navarro et al. 2015; Pearce et al. 2024). Nowadays, however, natural disturbance dynamics have largely been lost from European landscapes (Brackhane et al. 2021). Instead, grasslands are maintained through management practices such as clearing, mowing and livestock grazing. When land is abandoned and these practices stop, they currently undergo vegetation succession towards woodland (Navarro et al. 2015). This process often results in loss of plants and insects adapted to grasslands due to litter accumulation and cooler microclimates (Benton 2012; Bobbink and Willems 1993; Otti 1989). Consequently, a certain level of disturbance is crucial for maintaining grassland biodiversity (Pärtel et al. 2015). The level of disturbance needed to maintain grassland biodiversity, is dependent on the specific context and system (Bakker et al. 2006; Nabe-Nielsen et al. 2021).

One increasingly popular way to re-establish a natural disturbance regime is rewilding with ecosystem engineers (Bakker and Svenning 2018; Navarro et al. 2015); organisms that directly or indirectly modify the availability of resources for other species by altering the physical state of the ecosystem (Jones et al. 1994). However, scientific understanding of how ecosystem engineers contribute to conservation of species associated with grasslands is still limited (Bakker and Svenning 2018). In particular, little is known on how physical disturbances affect insect communities, and risks have been identified as well (van Klink & Wallis DeVries 2018). Given the urgency of insect biodiversity loss, it is important to assess the effect of ecosystem engineers on insect communities (Bakker and Svenning 2018).

One of the most important extant ecosystem engineers in Europe is the wild boar (*Sus scrofa*) (Labadessa and Ancillotto 2023), which roots, often belowground, for arthropods, tubers and other food resources (Ballari and Barrios-García 2014; Bueno et al. 2013). This foraging behaviour sets back vegetation succession by removing vegetation and turning over the topsoil (Horčičková et al. 2019). Subsequently, these disturbances (hereafter referred to as 'rootings') become colonised by pioneer communities (van Leeuwen et al. 2025; Scherer et al. 2025). As succession progresses, ecological communities evolve sequentially (Steffan-Dewenter and Tscharntke 1997; Fig. 1). The hypothesis (Fig. 1) is that up to a certain level, rooting could elevate the biodiversity of ecosystems by creating mosaics of successional stages that provide habitat to a higher diversity of species, because they provide niches to specialists of different vegetation structures (Verberk and Esselink 2003), form combinations of different microhabitats needed throughout insect life cycles (Diacon-Bolli et al. 2012), and offer shelter against stochastic disturbances (Oliver et al. 2010).

In this study, we tested whether rooting by wild boar enhances insect biodiversity in abandoned, species-rich grasslands by adding early successional stages. We focused on grasshoppers, a group of insects tightly associated with grasslands (Fartmann et al. 2012; Helbing et al. 2014). They are important indicators for environmental change, as they prefer specific microhabitats and vegetation structures (Fartmann et al. 2012; Schirmel et al. 2011). Additionally, they play important ecological roles as grazers (Fartmann et al. 2022) and as a food source for many vertebrates (Zahn et al. 2010).

Specifically, we tested the prediction that the abundance, species composition and life stages of grasshoppers differ between fresh and old wild boar rootings, and the matrix. The latter is defined as a closed grassland vegetation without any signs of rooting. Subsequently, we also explored mechanisms behind the observed compositions of Orthoptera species, their life stages, and their occurrence in certain successional stages.

## Methods

### Study area

The study was conducted in the species-rich calcareous grasslands in the southern part of the Hainich National Park in the German federal state of Thüringen (51° 2' 16'' N; 10° 25' 13.6'' E). The climate is subcontinental (Cfb), with an average annual temperature of approximately 8.5 °C and an average annual precipitation of 700–800 mm (long-term average 1989–2018; Kronenberg et al. 2021). Historically, these grasslands were kept open through sheep grazing and military activities (Großmann 2018). Since 1993, the landscape has been left unmanaged and is kept open solely by large herbivores (Großmann 2018). The most recent estimation of wild boar population density in the study area is around 12 individuals per 100 ha (Klamm et al. 2020).

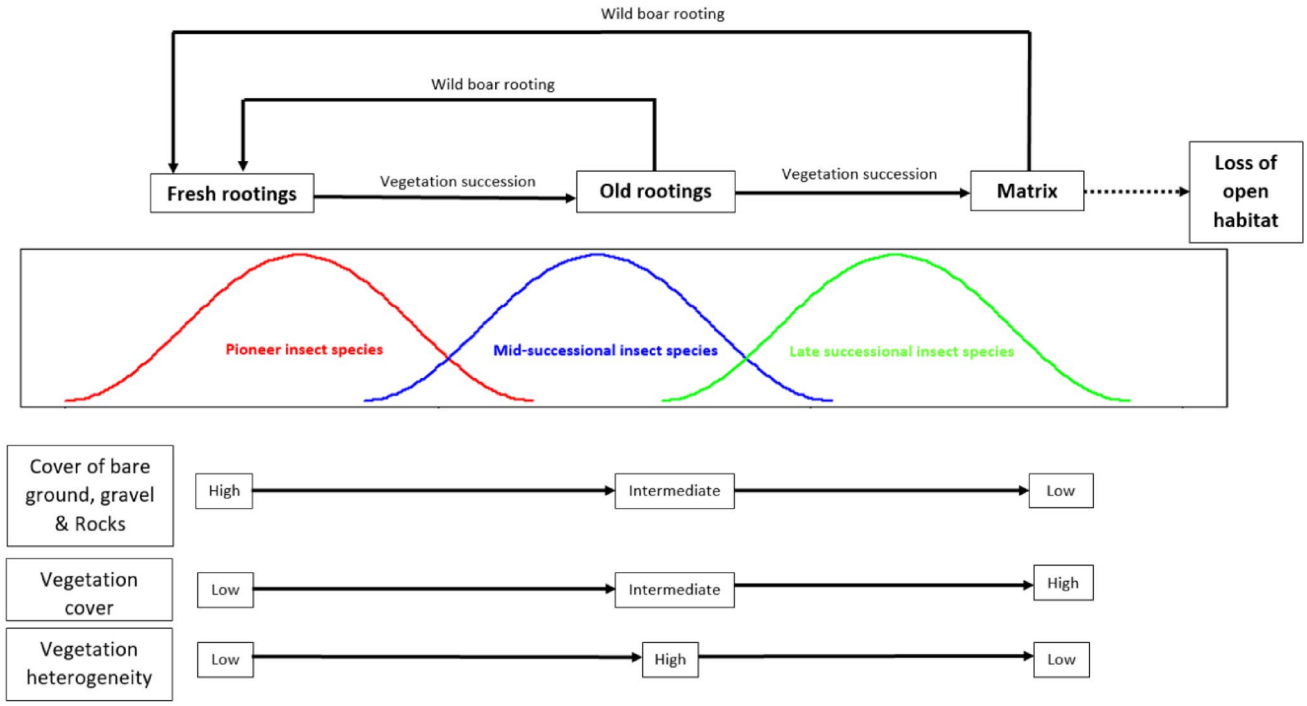


**Fig. 1** Conceptual model of vegetation and grasshopper succession in wild boar rootings in calcareous grasslands. Wild boar create fresh rootings, which subsequently age and eventually converge to surrounding matrix vegetation. The matrix may be rooted again or further develop into shrubland/forest. Changes in insect communities are expected to change with microhabitat quality

## Study design

To study this successional trajectory on wild boar rootings, we used a space-for-time substitution (sensu Pickett 1989). We mapped wild boar rootings and then divided the area into three different successional stages – fresh rootings, old rootings and matrix – based on field characteristics, as in Cabon et al. (2022). Fresh rootings had signs of very recent rooting: a low vegetation cover and a high microrelief. Old rootings were largely overgrown patches which still held signs of wild boar rooting activity. Matrix was grassland vegetation without signs of wild boar rooting. We sampled 40 2 × 2 m plots for each successional stage (total: $N = 120$, Fig. 2). Sets of one fresh rooting, one old rooting and one matrix plot were selected within 8–25 m from each other, representing a block design. All plots were located in areas with a gentle slope (inclination < 10°), and > 10 m from the closest shrub to the south to avoid shading.

## Measurements

Orthoptera communities were sampled in 2023 in two rounds (May and June) using a 2 $m^2$ box quadrat (1,41 × 1,41 m) (as in Fartmann et al. 2024). Sampling did not take place during rain (as in Gardiner and Hassall 2009). Identification was performed using Thommen (2021) for nymphs and Fischer et al. (2020) for adult grasshoppers. Unidentified (escaped) individuals (which escaped too quickly) were included in calculations on abundance, but excluded from species richness calculations. All individuals were identified to (morpho)species level and classified by life stage (young nymph, old nymph, or adult) and suborder (Ensifera and Caelifera). Caelifera are mostly herbivorous, have short antennae (Benton 2012) and are represented by grasshoppers and groundhoppers in the study system (Benton 2012). Ensifera are omnivorous, have long antennae and are represented by crickets and bush-crickets. Old nymphs were defined as nymphs in the last two nymphal stages, in which the wing stubs are no longer in inverted position (Benton 2012). For all plots the Shannon Index and Shannon's evenness were calculated (Weaver and Shannon 1949). For calculating the Shannon Index the function 'diversity' from the 'vegan' package was used (Oksanen et al. 2022).

Microhabitat was measured by estimating cover (in 5% increments) of bare ground, bare rock and gravel, mosses, lichens, herbs, grasses, shrubs (height: >50 cm), litter and flowers (as in Fijen et al. 2019), and anthills (as ants might also function as ecosystem engineers that create habitats for early successional species, cf. Streitberger and Fartmann 2015; van Leeuwen et al. 2025). Moreover, we measured vegetation height with a yardstick at five regularly


**Fig. 2** Aerial photograph showing the locations of the plots used in the field study in Hainich National Park, Germany. The white dots indicate fresh rootings, the light blue dots indicate old rootings and the dark blue dots indicate matrix plots. The different subareas, used as random factors in the statistical analysis, are indicated in orange. The white ellipses indicate the clusters of plots, these are also used as random factors in the analysis (GDI-Th; dl-de/by-2-0)

distributed locations per plot, and calculated the average and standard deviation.

## Data analysis

Data analysis was conducted in R version 4.3.1 (R Core Team 2023). Predictions on grasshopper abundance, life stages, species richness and habitat quality and were tested by GLMM's using the 'lme4' package (Bates et al. 2015), with successional stage and measurement round as fixed factors and subareas and predefined clusters within each subarea (Fig. 2) as random factors. The model family was determined by visually assessing the data distribution using histograms. We used post-hoc tests from the 'multcomp' package (Hothorn et al. 2008). Multiple testing correction was applied according to the false discovery rate (FDR) method (Benjamini and Hochberg 1995). In the models with successional stage and measurement round as fixed factors and the habitat quality variables, grasshopper abundance and species richness, we checked the Poisson models for overdispersion using the 'AER' package (Kleiber & Zeileis 2008). When a significant overdispersion was detected, the Poisson models were substituted negative binomial GLMM's.

The specificity and sensitivity of all (morpho)species to (combinations) of successional stages were calculated using an indicator species analysis with the package 'indicspecies' (Cáceres and Legendre 2009). As input data, the sum of grasshopper abundances was pooled for both May and June.

To visualise the data and test the prediction on if grasshopper communities differed between different successional stages, NMDS ordination was used. NMDS ordinations were based on grasshopper abundance using the 'Vegan' package (Oksanen et al. 2022). Again, the sum of grasshopper abundances was pooled for both May and June as input data. Due to the presence of a relatively high number of zeros in the dataset, the Euclidean distance measure was used with a maximum of 100 random starts. A PERMANOVA test was conducted to test whether the point clouds of the different successional stages significantly differed from each other, with a post-hoc test using the package 'pairwiseAdonis' (Martinez Arbizu 2017).

To test for a relationship of species richness with microhabitat quality, we used GLMMs with the abundances of all grasshoppers or grasshopper suborders as response variables, habitat quality parameters as fixed factors, and subarea and cluster as random factors. Environmental variables were scaled. As bare soil cover, total vegetation cover and grass cover were highly intercorrelated (Pearson correlation

coefficient > 0.7), we included only bare soil cover, as this variable is the ecologically most important for many Orthoptera species, providing warm microclimates (Wünsch et al. 2012; Schirmel et al. 2010). We then used model averaging based on an information-theoretic approach. Different candidate models were formulated by including all possible combinations of habitat quality variables into the models, using the 'MuMIn' package in R (Burnham and Anderson 2004). The best-fitting models were selected using the small-sample corrected Akaike's information criterion (AICc). Using model averaging, the values from the top-rank models (ΔAICc < 3) were combined to estimate the final coefficients for all habitat quality variables. As this modelling technique cannot deal with missing values, the few missing values in the first round were filled up as described in Online Appendix 3. Due to a large number of missing values in the second round, 8 plots containing missing values for at least one variable were removed from the dataset. The 'ggplot2' package was used for data visualisation (Wickham 2009).

**Table 1** Average (±SE) values of vegetation S.ructure parameters in fresh rootings, old rootings and matrix in abandoned calcareous grasslands in Hainich National Park, Germany

| Parameter | Fresh rooting | Old rooting | Matrix | Post-hoc test |
|---|---|---|---|---|
| Cover (%) | | | | |
| Vegetation total | 52.44 ± 2.87 | 91.46 ± 0.98 | 98.26 ± 0.34 | F < O, M |
| Herb layer | 51.67 ± 2.98 | 91.46 ± 0.98 | 98.2 ± 0.34 | F < O, M |
| Shrubs | 1.04 ± 0.65 | 0.93 ± 0.45 | 1.96 ± 0.86 | n. s. |
| Grasses | 20.64 ± 2.51 | 79.39 ± 2.29 | 91.6 ± 1.49 | F < O < M |
| Forbs | 40.26 ± 2.80 | 39.86 ± 2.25 | 26.84 ± 2.06 | F, O > M |
| Grass/forb ratio | 0.62 ± 0.11 | 2.34 ± 0.19 | 4.51 ± 0.43 | F < O < M |
| Mosses | 1.81 ± 0.36 | 15.70 ± 2.54 | 52.5 ± 3.71 | F < O < M |
| Litter | 7.27 ± 0.90 | 30.74 ± 3.35 | 69.14 ± 3.58 | F < O < M |
| Bare soil | 45.00 ± 2.76 | 8.50 ± 0.99 | 1.84 ± 0.35 | F > O > M |
| Rocks and stones | 5.83 ± 0.51 | 2.28 ± 0.27 | 0.09 ± 0.07 | F > O > M |
| Anthills | 3.06 ± 0.67 | 3.54 ± 0.55 | 5.74 ± 1.15 | n.s. |
| Flowers | 2.90 ± 0.41 | 1.70 ± 0.27 | 1.27 ± 0.13 | F > M |
| Average vegetation height (cm) | 6.75 ± 0.42 | 11.9 ± 0.39 | 16.53 ± 0.87 | F < O < M |
| StdDev vegetation height (cm) | 3.77 ± 0.46 | 4.10 ± 0.30 | 4.71 ± 0.53 | n.s. |

The last column S.ows S.gnificant differences between S.ages from post-hoc z-tests. N. S. N.t S.gnificant. Significant differences are based on $P < 0.05$

## Results

### Vegetation structure

Vegetation structure clearly differed between successional stages. Vegetation cover, including forbs, grasses, mosses and litter was highest in the matrix and lowest in fresh rootings (Table 1). Forb cover was significantly lower in the matrix than in fresh and old rootings but did not differ between these latter two successional stages (Table 1). Bare soil, rocks and stones had decreasing covers in fresh rootings, old rootings and matrix plots respectively. Flower cover was significantly higher in fresh rootings than in the matrix, with intermediate values in old rootings. The grass-to-forb cover ratio and the average vegetation height increased significantly from fresh rootings to old rootings and the matrix respectively (Table 1).

### Grasshopper communities

We found 15 grasshopper (morpho)species, including 6 Caelifera and 9 Ensifera species. Samples ranged 0–42 individuals of 0–6 species per plot, with a median of 2 individuals of 2 species. In May, 28% of the plots had no grasshoppers. In June, this was 8%. No significant differences in grasshopper abundance were found between successional stages in both rounds, neither overall, nor for specific life stages (Fig. 3a and Tables A2a and A2b).

In May, overall species richness did not significantly differ between successional stages (Table 2). However, Caelifera species richness was significantly higher in fresh and old rootings compared to the matrix, while Ensifera species richness was significantly higher in the matrix and old rooting plots than in fresh rootings. In June, overall species richness was significantly higher in old rootings than in fresh rootings, which were both not significantly different from the matrix. In this month, no significant differences in species richness for either Caelifera or Ensifera specifically were found. Neither the Shannon index or Shannon evenness did differ significantly between the successional stages in neither May or June.

In May, Caelifera were significantly more abundant in fresh and old rootings than in the matrix (Fig. 3b and Table A2a). In June, no differences in Caelifera abundance between the successional stages were found (Fig. 3b and Table A2b). Ensifera were significantly more abundant in old rootings and the matrix in both May and June (Fig. 3c and Tables A2a and A2b).

Three species emerged as indicator species. *Metrioptera brachyptera* and *Roeseliana roeselii* were significantly biased towards old rootings and the matrix, and *Tetrix*

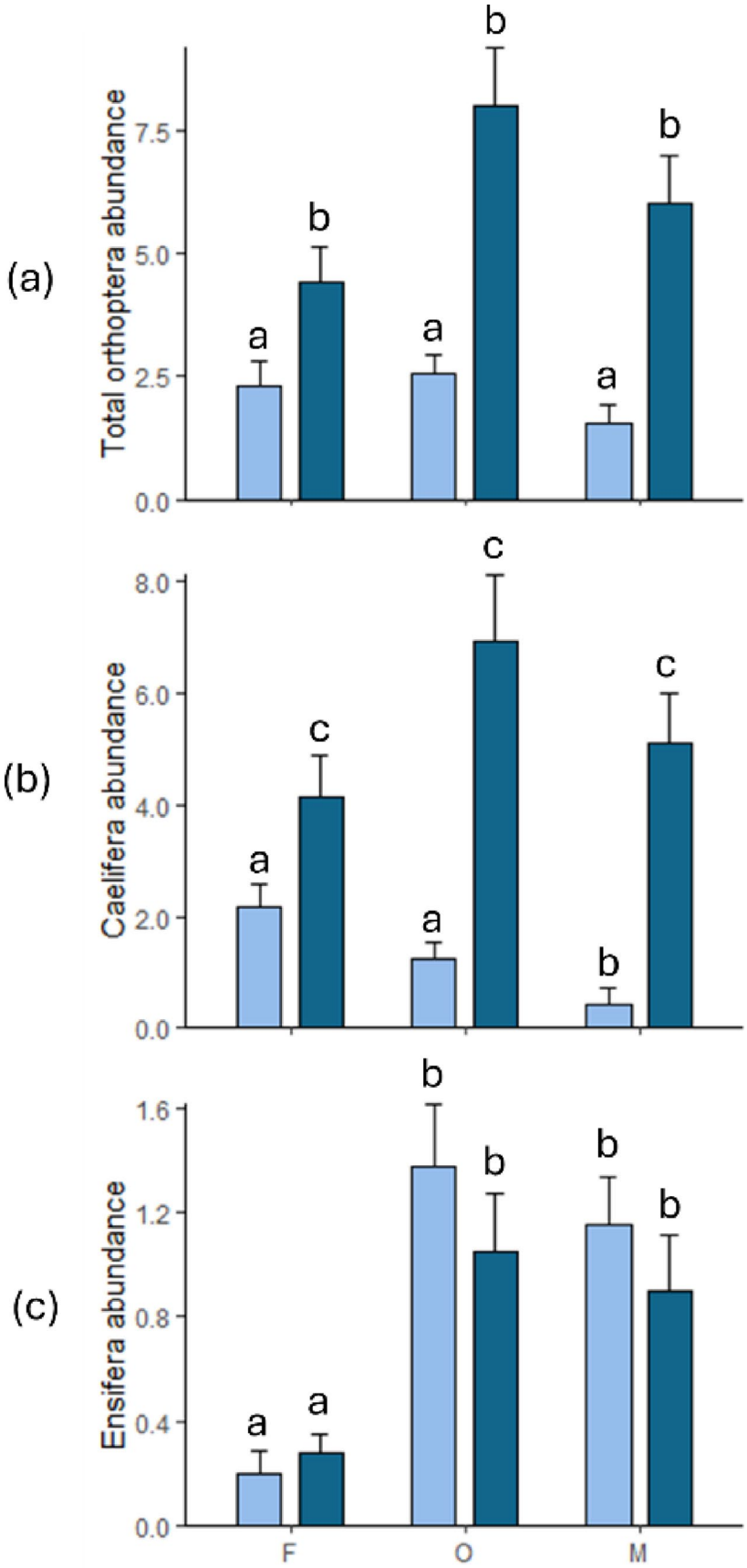


**Fig. 3** Abundances of grasshoppers and crickets (Orthoptera) in fresh rootings (F), old rootings (O) and matrix (M) with SE in in calcareous grasslands in Hainich National Park, Germany, measured in May (light blue) and June (dark blue). Values are means with SE. **a** total Orthoptera abundance, **b** Caelifera and **c** Ensifera. Letters indicate significant differences as found in the GLMM's

**Table 2** Mean ± sd of species richness, Shannon index and Shannon evenness for the two grasshopper suborders in the calcareous grasslands of Hainich National park, Germany in May and June

| Parameter | Fresh rooting | Old rooting | Matrix | Post-hoc |
|---|---|---|---|---|
| Orthoptera species richness | | | | |
| May | | | | |
| Caelifera | 1.10 ± 1.15 | 0.70 ± 0.992 | 0.15 ± 0.533 | F, O > M |
| Ensifera | 0.18 ± 0.45 | 1.08 ± 1.02 | 0.875 ± 0.88 | F < O, M |
| *Overall* | *1.28 ± 1.20* | *1.78 ± 1.12* | *1.03 ± 1.14* | *n.s.* |
| June | | | | |
| Caelifera | 1.60 ± 1.26 | 2.30 ± 0.992 | 1.73 ± 1.20 | n.s. |
| Ensifera | 0.275 ± 0.452 | 0.70 ± 0.791 | 0.65 ± 0.802 | n.s. |
| *Overall* | *1.88 ± 1.36* | *3.00 ± 1.26* | *2.38 ± 1.60* | *F < O* |
| Shannon index | | | | |
| May | 0.32 ± 0.43 | 0.52 ± 0.45 | 0.22 ± 0.38 | n.s. |
| June | 0.45 ± 0.48 | 0.85 ± 0.43 | 0.70 ± 0.53 | n.s. |
| Shannon evenness | | | | |
| May | 0.64 ± 0.46 | 0.83 ± 0.36 | 0.58 ± 0.49 | n.s. |
| June | 0.78 ± 0.35 | 0.89 ± 0.11 | 0.77 ± 0.35 | n.s. |

The last column indicates significant differences as found in the glmm's. N.s. Not significant. Significant differences are based on $P < 0.05$

*tenuicornis* was significantly biased to young and old rootings (Table 3).

### Habitat quality affecting grasshopper abundance

In May, the total grasshopper abundance was positively related to distance to the nearest shrub and negatively by the standard deviation of the vegetation height and the moss cover. The Caelifera were positively influenced by the standard deviation of the vegetation height and the distance to the nearest shrub and negatively by the average vegetation height in May. Ensifera were positively influenced by the cover of anthills and negatively by the standard deviation of the vegetation height, and the covers of bare soil, forbs and mosses in May (Fig. 4). In June, the results were different. The total grasshopper abundance and the Caelifera abundance were positively correlated with the forb cover and negatively by the rock cover and the cover of anthills. The Ensifera abundance, in contrast, was positively correlated with the standard deviation of the vegetation height and negatively by the covers of bare soil and mosses (Fig. 4).

### Succession of grasshopper communities

For the NMDS, we used 4 dimensions (k = 4). This resulted in a stress value of 0.097. The NMDS showed that Grasshopper community composition in samples differed between the three successional stages (Fig. 5). The grasshopper communities in the matrix differed from those in the fresh and old rootings (permanova test), while these latter two successional stages hosted similar grasshopper communities. Cover of bare soil, forbs and mosses and the average vegetation height were the main habitat quality variables that explained differences in community composition. Early successional stages were characterised by high covers of bare soil and forbs. Late successional stages were characterised by high vegetations with a high moss cover.

## Discussion

Rooting by wild boar has been put forward as a natural process that conserves insect communities of open habitats by resetting vegetation succession in grasslands. In this study, we tested whether rooting by wild boar increases Orthoptera biodiversity in abandoned calcareous grasslands by enhancing microhabitat heterogeneity. Our study expands on previous studies on wild boar rooting by dividing the successional trajectory into three stages, instead of the two stages used in many earlier studies (but see Cabon et al. 2022).

We found significant differences in microhabitat structure between the successional stages. Rooting thus indeed produced a mosaic of patches with contrasting microhabitats. As we also found significant differences in grasshopper communities from fresh and old rootings to matrix plots along a successional axis, we conclude the mosaic supports a more diverse Orthoptera community than the matrix alone (Fig. 5).

We found clear differences in species abundance, richness, and composition between the successional stages. These may be explained by changes in microhabitat and vegetation structure during succession, as our data shows that successional stages differ in vegetation structure and

**Table 3** Results of the indicator species analysis on orthoptera communities in calcareous grasslands in the Hainich National Park, Germany

| | | Successional stage | | | | | | |
|---|---|---|---|---|---|---|---|---|
| Species | Life stage | Fresh | Old | Matrix | Spec. | Sens. | IV | *P* |
| *Roeseliana roeselii* | Young nymphs | . | ✓ | ✓ | 1.000 | 0.375 | 0.612 | ** |
| *Metrioptera brachyptera* | Young nymphs | . | ✓ | ✓ | 0.921 | 0.325 | 0.547 | ** |
| *Tetrix tenuicornis* | Adult females | ✓ | ✓ | . | 0.973 | 0.262 | 0.505 | ** |

*Spec.* Specifity, *Sens.* Sensitivity

iv = indicator value (test statistic), for P, * < 0.05, ** < 0.01, *** < 0.001

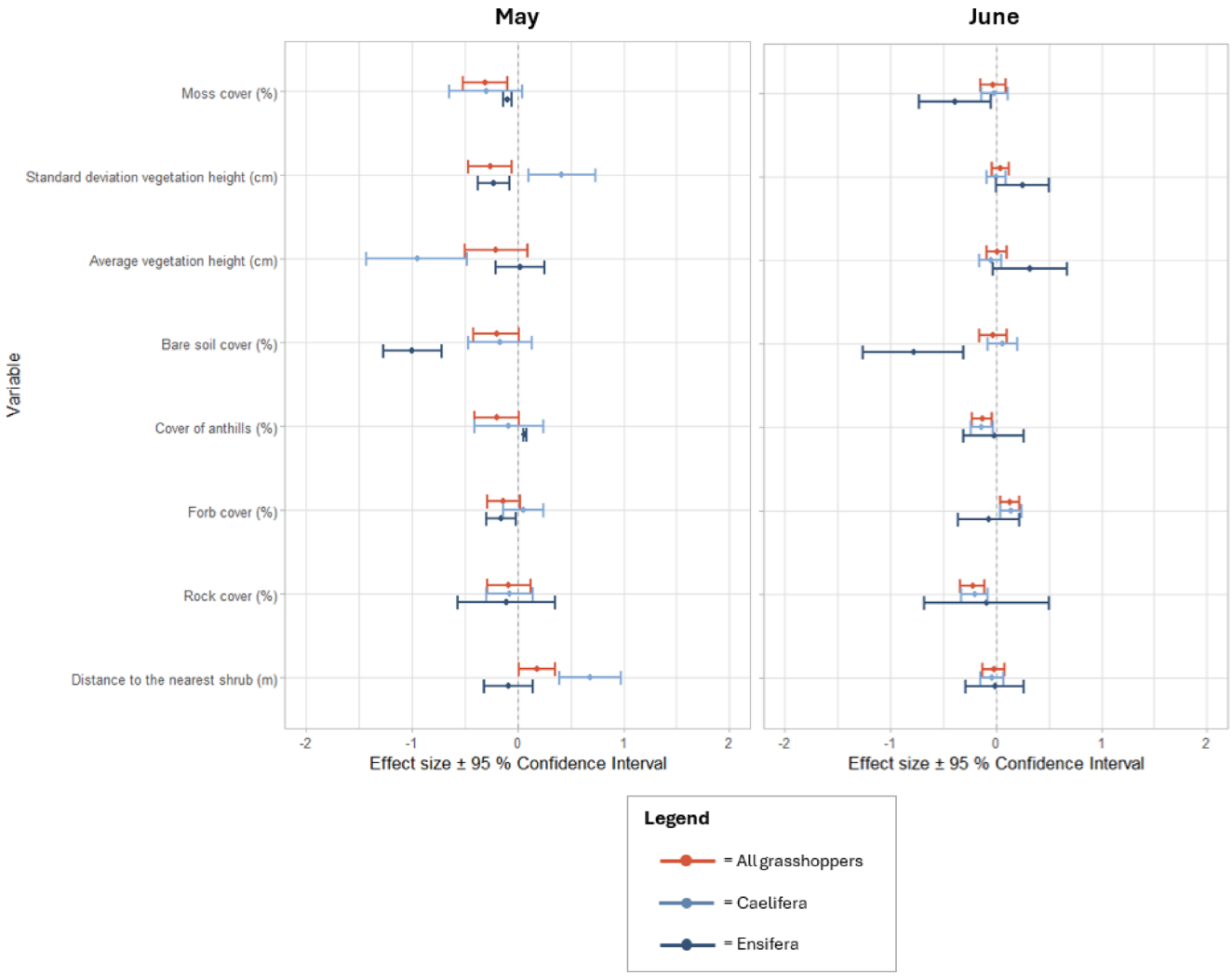


**Fig. 4** Associations of Orthoptera with microhabitat variables in calcareous grasslands in the Hainich National Park, Germany. The figure shows the estimated effect size of the different measured habitat quality variables as derived from the model averaging. The shown values for the estimated effect sizes and confidence intervals are the conditional averages of the top-rank models (ΔAICc < 3). Their effects on the abundances of total Orthoptera, as well as specifically on the suborders Caelifera and Ensifera, were tested. The left panel shows the results for May, and the right panel those for June. The error bars indicate the 95% Confidence intervals around the estimated values of the effect size. This means that the effect sizes of which the conditional averages do not overlap with 0 are significant ($p < 0.05$). Subarea and spatial clusters were used as random factors

that the different successional stages harbour grasshoppers with different life cycle characteristics (see Online Appendix 3). Vegetation structure is important for Orthoptera, because it determines opportunities for thermoregulation, hiding for predators, oviposition and finding mates (Schirmel et al. 2010; Schwarz and Fartmann 2022; Wünsch et al. 2012). In contrast to vegetation structure, Orthoptera depend less on plant species composition, as most grasshoppers are generalist feeders, feeding on a broad range of plants (both Caelifera and Ensifera) and animals (only Ensifera) (Kleukers et al. 2004; Löffler and Fartmann 2017).

The observed differences in grasshopper community composition between the successional stages are expected to link to oviposition preferences, as the majority of the recorded grasshoppers were young nymphs. Nymphal habitat choice of Orthoptera often reflects the oviposition preferences of adult females, as young grasshopper nymphs have a limited mobility, and hence stay close to where they hatched (Cherrill and Brown 1992; Wünsch et al. 2012). To identify microhabitat preferences of adult grasshoppers, further research is needed (Cherrill and Brown 1992; Wünsch et al. 2012). The differences in preferred habitats of Ensifera and Caelifera in May might be explained by their species-specific life cycles. Ensifera were most abundant in old rootings and matrix in both May and June and their species richness was highest in these two stages in May as well. Of the 7 Ensifera species observed, almost all have a (facultative) biannual or perennial life cycle (except for the

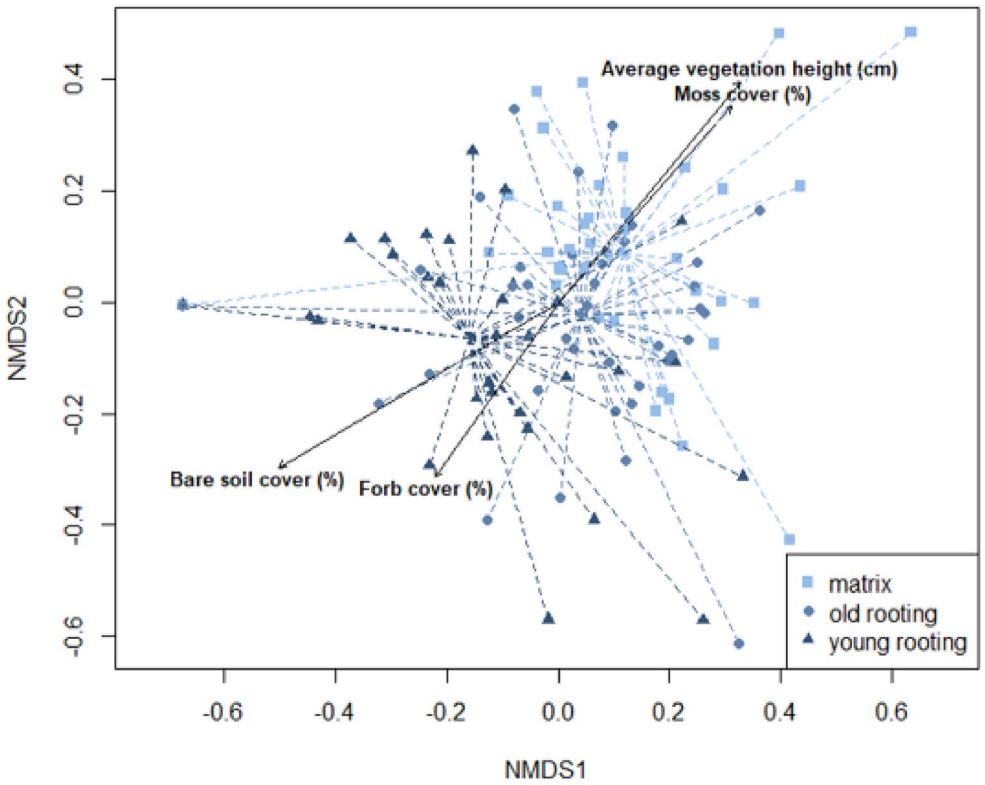


**Fig. 5** NMDS ordination of grasshopper communities for three successional stages in abandoned calcareous grassland in Hainich National Park, Germany. Although they largely overlap the grasshopper communities in the matrix significantly differed from those in the young and old rooting (PERMANOVA test), as shown by the spider diagrams (dotted lines). See for the exact numerical results Online Appendix 5

occasionally occurring *Phaneroptera falcata* and the once observed *Oecanthus pellucens*; see Online Appendix 3). This means that their eggs hibernate twice or more before hatching, and hence are also present during summer (Benton 2012; Kleukers et al. 2004). Grasshopper eggs are sensitive to desiccation (Ingrisch 1986). This makes them vulnerable for warm and dry conditions during summer (Poniatowski et al. 2020). The vegetation in old rooting and matrix sites is relatively dense, which likely results in higher humidity levels (Barkman and Stoutjesdijk 1987). This may explain why Ensifera, like the two indicator species *Roeseliana roeselii* and *Metrioptera brachyptera*, prefer old rootings and matrix for oviposition. Hence, early nymphal stages of such species can also be expected to occur mostly in old rootings and matrix. This is mainly caused by their limited mobility (Cherrill and Brown 1992; Wünsch et al. 2012). However, the nymphs might also profit from the microhabitat in the later successional stages, as these provide them with shelter and sufficient food (Kleukers et al. 2004). The observed negative responses of Ensifera abundance to bare soil (May and June) and forb cover (May) are in line with this.

In contrast, a combination of all successional stages after disturbance seems important for Caelifera. The majority of Caelifera belong to the *Chorthippus biguttulus*-group, which therefore influences the overall trend for this order (Online Appendix 5). They only seem to have a preference for early successional stages in May, as in June, we found no differences in Caelifera abundance between the successional stages. This can be interpreted as an ontogenetic niche shift. Both *C. biguttulus* and *C. brunneus* are indeed known to oviposit in bare soil (Kleukers et al. 2004), which has a higher cover in young and old rootings than in the matrix. Such early successional stages provide warm microclimates (Barkman and Stoutjesdijk 1987), which are known to be ideal for nymphal development of several Caelifera species (Schirmel et al. 2010; Wünsch et al. 2012). This preference for warm microclimates is supported by observations that in May, Caelifera abundance was positively influenced by factors that contribute to warmer microclimates, such as greater distance from the nearest shrub and low vegetation cover (Barkman and Stoutjesdijk 1987). In contrast, Caelifera were negatively influenced by a higher rock cover and a higher cover of anthills, different habitat factors that indicate short and open vegetations.

The ontogenetic niche shift of Caelifera indicates that a successional mosaic not only increases biodiversity because different successional stages support different species, but also because certain species are specifically dependent on a combination of successional stages throughout their life cycle (de Nooij et al. 2006; Verberk and Esselink 2003). This is also supported by the positive response of the abundances of Caelifera in May and Ensifera in June on the variation in vegetation height.

The importance of different successional stages during grasshopper development is in line with earlier findings. It is known that during development, nymphs of several

grasshopper species are in increasing need for higher and denser vegetations. Expectedly, this is because their dependence on shelter and food increases, since they become increasingly attractive as prey for insectivores and need increasing amounts of food during growth respectively (Cherrill and Brown 1992; Wünsch et al. 2012).

Nevertheless, it is also important to note that the total Caelifera abundance in June was much higher compared to May. This might provide an alternative explanation for the fact that Caelifera were most abundant in fresh and old rootings in May and showed no preference for specific successional stages in June. The difference in total abundance could also be caused by the fact that in the warmer microclimates in earlier successional stages (Barkman and Stoutjesdijk 1987), the temperature sum needed for the eggs to hatch was simply achieved earlier in the season (Bieringer and Zulka 2003; Willott and Hassall 1998). This might have led to a temporary Caelifera (or *Chorthippus biguttulus group*) peak in fresh and old rootings.

Summarising, we conclude that rooting wild boar can contribute positively to grasshopper species richness, but not necessarily to the Shannon index and evenness in calcareous grasslands. We indeed found clear differences in community composition between different successional stages, so a mosaic supports more species than a homogenous matrix vegetation. Grasshopper species may be classified as either early successional species (mostly occurring in fresh and old rootings; like the indicator species *T. tenuicornis*), late successional species (mostly occurring in old rootings and the matrix; like the indicator species *M. brachyptera* and *R. roeselii*) or habitat generalists (no preference for a specific successional stage); differences that might be explained by differences in life cycles. Moreover, we found that old rootings, a microhabitat specifically created by wild boar, supports most Orthoptera species in June. As old rootings represented an intermediate stage of grassland succession, this is also in line with studies assessing adult Orthoptera, that also found the highest Orthoptera densities within intermediate stages (Fartmann et al. 2012; Helbing et al. 2014). Finally, our results indicate that the successional mosaics in the grasslands are used by Caelifera species that use the combination of successional stages throughout their life cycle. This points to the idea that the species richness of mosaics is higher than just the sum of specialists of the different patches (Diacon-Bolli et al. 2012).

Although we found a few species that profit from the presence of rootings, it should be remarked that the number of indicator species for the different successional stages was limited, although calcareous grasslands are generally known for their high Orthoptera diversity (Fumy et al. 2020; Fartmann et al. 2024). Additionally, it can be remarked, that although we found significant differences in species richness between the successional stages, there were no differences in either Shannon Index or Evenness. This probably reflects the fact that the communities were often dominated by a few common species, and that other species only occurred in low abundances. In comparison to the species pool of calcareous grasslands in the surrounding landscape (Köhler 2001), several characteristic species, like *Oedipoda caerulescens* or *Platycleis albopunctata*, are lacking or very rare in the study area (own observation). This might imply that the rootings are not necessarily effective for early successional grasshoppers in general, but that only certain early successional specialists can profit from it. The grasslands in the study area have already been abandoned for nearly 30 years, and the matrix is characterized by a high grass cover, litter accumulation and shrub encroachment (Scherer et al. 2025; Schröer et al. 2024). Grasshoppers are generally known to be negatively affected by shrub encroachment (Helbing et al. 2014; Reif et al. 2023). We therefore expect this might explain why some early successional species are not present in the species pool of the national park, and hence are not able to profit from the rootings.

In the Hainich National Park, wild boar densities are sufficient to create mosaics of different successional stages, in which both rooted and unrooted patches are still present (own observation). By increasing the habitat heterogeneity, rooting by a wild boar population at this density contributes positively to Orthoptera biodiversity in calcareous grasslands (Cabon et al. 2022). Earlier studies also showed rooting wild boar can have positive effects on the biodiversity of other species groups (Horčičková et al. 2019; Labadessa and Ancillotto 2023; de Schaetzen et al. 2018; Scherer et al. 2025; van Leeuwen et al. 2025). That wild boar can also positively contribute to biodiversity is an important conclusion, as wild boar is often regarded as a problem species (Ballari and Barrios-García 2014). In the study area, there are currently no other ecological disturbances that create microhabitats comparable to the rooting patches (own observation). However, if rooting intensity would be higher or lower, the grasslands would probably be less heterogenous, and the positive effects of wild boar would be less pronounced. This might explain why in other contexts, negative effects on biodiversity have been observed as well (Barrios-Garcia and Ballari 2012).

## Conclusion

Based on the fact that the grasshopper communities differed significantly between different successional stages and that Caelifera differed in the use of successional stages between May and June, we conclude that wild boar rooting is beneficial for Orthoptera biodiversity in the study area. Wild

boar benefit Orthoptera through two different mechanisms: (1) different microhabitats support different habitat specialists with different life cycles, meaning that habitat mosaics are more diverse than just undisturbed grassland and (2) the most diverse microhabitat (Old rootings), characterised by the highest species richness, was created by wild boar. Additionally, our observations also indicated that successional mosaics offer habitats for species that require different microhabitats throughout their life cycle. Our results thus support the idea that wild boar can play an important role as ecosystem engineers for grasshoppers in calcareous grassland ecosystems. Providing room for natural processes like wild boar rooting might be a useful tool for insect conservation. Therefore, we advise to take the beneficial role of wild boar into consideration in conservation measures and wild boar population management.

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**Author contributions** Q.T.: Conceptualization, Data Curation, Formal Analysis, Methodology, Investigation, Visualisation, Writing – original draft, Writing – review & editing. B.v.L.: Conceptualization, Methodology, Formal analysis, Investigation, writing – review & editing, P.V.: Supervision, Conceptualization, Methodology, Formal analysis, Validation, Project administration, Writing-Review & editing G.S: Supervision, Conceptualization, Methodology, Formal analysis, Validation, Project administration, Writing-Review & editing, Project administration, Funding acquisition. T.F.: Supervision, Conceptualization, Methodology, Formal analysis, Validation, Project administration, Writing-Review & https://submission.springernature.com/new/submission/5ab1b61b-4a3a-4039-87bf-c85feeaf327c/declarationsediting, Project administration, Funding acquisition., P.J.: Supervision, Conceptualization, Methodology, Formal analysis, Validation, Project administration, Writing-Review & editing.

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**Data availability** We will make the data and analysis scripts available via a Data repository soon.

## Declarations

**Competing interests** The authors declare no competing interests.



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