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Novel methods of heathland management promote grasshopper diversity and abundance

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ABSTRACT

Today, the remaining heathlands suffer from habitat degradation, particularly due to unsuitable or absent management. Recently, two novel measures have been implemented to rejuvenate heathlands: moss removal (scarification) and disc harrowing. Here, we studied the effects of five different types of heathland management on Orthoptera (hereinafter referred to as grasshoppers): (i) prescribed burning (BURN), (ii) prescribed burning and subsequent disc harrowing (BURN+DIS), (iii) mowing (MOW), (iv) mowing and subsequent scarification (MOW+SCA) and (v) unmanaged old heathlands (CONTROL). Our study revealed strong differences in habitat structure, and in both species richness and density of grasshoppers between the management types. This was particularly true for CONTROL on the one hand, and BURN + DIS and, to a lesser extent, MOW + SCA on the other hand. CONTROL was dominated by tall stands of dwarf shrubs and had the lowest habitat heterogeneity. MOW + SCA exhibited the shortest swards and had the highest cover of bare ground. Although the cover of bare ground was also high and the turf was also short, BURN + DIS was characterised by the highest habitat heterogeneity. The number of species and density peaked in BURN + DIS, reached the second highest values in MOW + SCA, and were lowest in CONTROL. The application of the two novel heathland management techniques fostered habitat quality for grasshoppers by (i) strongly increasing the cover of bare soil, (ii) creating warm microclimatic conditions, (iii) boosting the availability of food resources, and (iv) favouring heterogeneity. Accordingly, we recommend both management techniques as regular measures to foster grasshoppers in heathlands.

1. Introduction

Human-driven environmental change has led to a rapid decline in biodiversity, threatening ecosystem functioning and human well-being on a global scale (Dirzo et al., 2014; Ripple et al., 2017; IPBES Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Service, 2019; Cardoso et al., 2020). Semi-natural ecosystems such as heathlands are particularly affected by these processes (Fagúndez, 2013).

Originally, heathlands covered 80% of the Central European lowlands (Keienburg and Prüter, 2006). However, from the middle of the 19th century onwards they have extensively been converted to arable fields or have largely disappeared due to afforestation. Today, the remaining heathlands suffer from habitat degradation due to: (i) unsuitable or absent management (Borchard et al., 2013;

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Schirmel and Fartmann, 2014; Brüggeshemke et al., 2025) but also (ii) climate change (Streitberger et al., 2022) and (iii) airborne nitrogen deposition (Vogels et al., 2023). In general, heathlands harbour a variety of rare plant and animal species that are often considered threatened (Vogels et al., 2013; Schirmel and Fartmann, 2014; Fartmann et al., 2022a). Due to the great importance of heathlands for nature conservation and the threats they face, they are now protected throughout Europe by the EU Habitats Directive (EC European Commission, 2013).

Historically, heathlands were shaped and maintained by traditional human management, including grazing, mowing, burning, and sod-cutting, i.e. the removal of vegetation and topsoil layer (Webb, 1998; Niemeyer et al., 2007; Fartmann et al., 2015; Streitberger et al., 2021a, b). Sod-cutting is a highly effective way to rejuvenate heathlands and to foster threatened species (e.g. Streitberger et al., 2021a). However, it produces a lot of waste material resulting in high costs. To reduce costs, recently choppering has been successfully applied as an alternative (Koopmann and Mertens, 2004; Keienburg and Prüter, 2006; Niemeyer et al., 2007; Fartmann et al., 2015). In contrast to sod-cutting, choppering encompasses only chaffing and removing of the largest part of the organic layer (O-horizon) down to the mineral soil. More recently, further attempts were made to reduce waste material and to save costs when rejuvenating heathlands. Since 2014, two novel management measures have been implemented in the study area (Lüneburg Heath, Fig. 1): moss removal (scarification) in mown heathlands (Matevski et al., 2025) and disc harrowing in previously burned heathlands (Verein Naturschutzpark Lüneburger Heide VNP, 2025). Scarification involves the mechanical removal of the moss layer using a rotary scarifier. Disc harrowing likewise disturbs the soil surface and upper soil layers through the use of agricultural disc harrows. In addition to the desired rejuvenation effect, both aim to increase the cover of bare ground in heathlands and thus promote early-successional and often threatened species. So far, well-replicated investigations that studied the effects of both novel management methods on arthropods were missing. Matevski et al. (2025), however, was able to confirm the high value of moss removal (scarification) in mown heathlands for threatened spider species. Moreover, Gardiner (2020) showed, based on a small sample size that the grasshopper species *Myrmeleotettix maculatus* benefits from the sole application of disc harrowing in grassy heathland.

Heathlands are inhabited by a variety of Orthoptera (hereinafter termed 'grasshopper') species, among them are many specialised ones (Marshall and Haes, 1988; Schirmel et al., 2011; Fartmann and Poniatowski, 2025). Grasshoppers frequently constitute the dominant arthropod herbivores in open habitats (Samways, 2005) and serve as a crucial prey base for insectivorous vertebrates, particularly birds (Ingrisch and Köhler, 1998; Birkhofer et al., 2026). Consequently, they play a central functional role in heathland

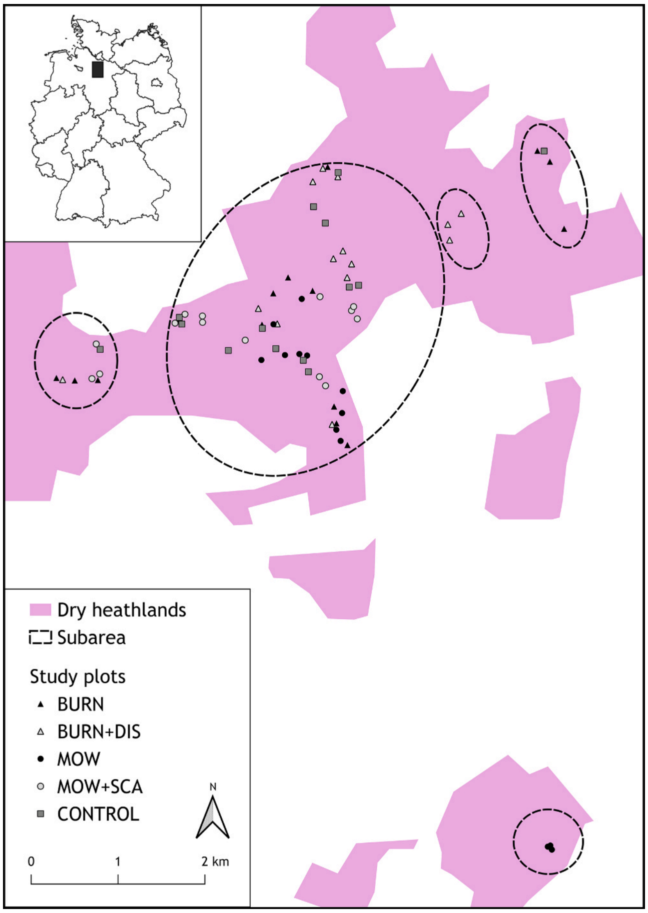

Fig. 1. Location of the study area, five subareas and plots in northern Germany.

ecosystems. Grasshoppers depend on specific vegetation structures (Gardiner et al., 2002; Poniatowski and Fartmann, 2008; Fartmann et al., 2012) and closely associated microclimatic conditions (Willott and Hassall, 1998; Gardiner and Dover, 2008, Fartmann et al., 2022b). As a consequence, they respond sensitively and rapidly to land-use changes (Uchida and Ushimaru, 2014; Theron et al., 2022), which makes them valuable bioindicators both in general (Poniatowski and Fartmann, 2008; Bazelet and Samways, 2011) and, in particular, for assessing restoration and management interventions (Kiehl and Wagner, 2006; Borchard et al., 2013; Kenyeres et al., 2020).

Our study was conducted in the Lüneburg heath nature reserve, the largest area of well-connected heathlands outside military training areas in Germany (Fig. 1). Overall, we studied five different types of heathland management, including the two novel methods: (i) prescribed burning (BURN), (ii) prescribed burning and subsequent disc harrowing (BURN+DIS), (iii) mowing (MOW), (iv) mowing and subsequent scarification (moss removal; MOW+SCA) and (v) unmanaged old heathlands (CONTROL). In particular, we address the following questions:

- How do the five heathland management types differ in habitat-structure characteristics and grasshopper assemblage composition?
- Do the two novel methods of heathland management (BURN+DIS; MOW+SCA) have the desired effect?
- What management recommendations can be derived from the results of the study for the promotion of grasshopper species richness and density in heathlands?

2. Material and methods

2.1. Study area

The research was carried out in the Lüneburg heath nature reserve in the centre of the German Federal State of Lower Saxony (Fig. 1; 70–169 m a.s.l.; 53°9'N/9°55'E; Northern Germany). The study area is characterized by a suboceanic climate. Average annual precipitation is 786 mm and mean annual temperature is 9.2 °C (long-term mean: 1991–2020; weather station Soltau [75 m a.s.l.]; German Meteorological Service, 2025). The nature reserve covers an area of about 234 km^2. It contains ~4000 ha of *Calluna* heathlands, which is the largest area of well-connected heathlands outside military training areas in Germany (Schellenberg and Bergmeier, 2014; Fartmann et al., 2022c). The heathlands are embedded in a matrix of coniferous forests dominated by Scots pine (*Pinus sylvestris*) (Cordes et al., 1997, Keienburg and Prüter, 2006). Heathland management in the nature reserve traditionally consisted of sheep grazing, mowing, prescribed burning, sod-cutting and choppering (Mertens et al., 2007). However, since 2014, the two novel management measures have been implemented: moss removal (scarification) in mown heathlands (Matevski et al., 2025) and disc harrowing in previously burned heathlands (Verein Naturschutzpark Lüneburger Heide VNP, 2025). Compared to sod-cutting and choppering, these two novel management measures are considerably less cost-intensive and generate substantially less waste material (Table 1).

2.2. Sampling design

2.2.1. Plots

We investigated five heathland management types: (i) prescribed burning (BURN), (ii) prescribed burning and subsequent disc harrowing (BURN+DIS), (iii) mowing (MOW), (iv) mowing and subsequent scarification (moss removal using a rotary scarifier; MOW+SCA), and (v) unmanaged old heathlands (CONTROL), where no management interventions had been applied during the past five years, apart from continuous sheep grazing across the entire nature reserve, which did not differ in intensity among plots. Cutting height in both management types where mowing had been applied was 5 cm (Matevski et al., 2025). Cut material was removed afterwards. The respective management measure took place in winter preceding the survey in late summer. For each management type, we randomly selected 14 rectangular plots with a total size of 200 m^2 ($N = 70$). Due to the stripwise arrangement of areas subjected to BURN + DIS and MOW + SCA management, each plot had a minimum distance of 10 m to the neighbouring management type, which was in all cases unmanaged, old heathland. In order to account for possible spatial autocorrelation, plots were assigned to five subareas (Fig. 1; Fumy et al., 2021; Brüggeshemke et al., 2022).

Table 1
Overview of the costs associated with the implementation of intensive heathland management measures (Euros per hectare), as well as the amount of waste material generated. The two novel management approaches prescribed burning and subsequent disc-harrowing (BURN+DIS) and mowing and subsequent scarification (MOW+SCA) are compared with two traditional intensive management measures, sod-cutting and choppering.

Management measure	Costs (€/ha)	Waste (m^3/ha)
Traditional		
Sod-cutting	4.000–7.000	1.000–1.300
Choppering	1.500–2.500	400–600
Novel		
Prescribed burning + subsequent disc-harrowing	ca. 720	0
Mowing + subsequent scarification	700–1.000	225–445

Source: Dirk Mertens (Verein Naturschutzpark e.V.) personal communication.

2.2.2. Environmental conditions

For each plot, we assessed several parameters of habitat structure at the beginning of August 2020 (Table 2). Per plot, we ascertained environmental parameters in a randomly selected part of the plot with a size of 3 m × 3 m. The plots were highly homogeneous, as each entire area was subjected to the respective management regime. Consequently, we considered the sampled part to be representative of the entire 200 m^2 plot. We recorded the following parameters of horizontal vegetation structure with an accuracy of 5%: cover of dwarf shrubs, grasses, herbs, mosses, lichens, litter, bare ground and gravel. In cases in which the cover was above 95% or below 5%, 2.5% steps were used (Poniatowski and Fartmann, 2008). To calculate habitat heterogeneity, we counted the number of the following habitat layers per plot: dwarf shrubs, grasses, herbs and bare ground. We only considered layers with a minimum cover of 10% (cf. Fumy and Fartmann, 2023). We selected a threshold of 10% cover to ensure a minimum level of ecologically relevant coverage that could potentially exert population-level effects on grasshopper species richness and abundance. Cover values below 10% would likely represent only isolated occurrences of a given layer, whereas a threshold of 15% was considered too high and therefore too coarse in resolution. As a result, the values of the habitat-heterogeneity score in our study ranged between one and four per plot. Furthermore, vertical vegetation structure was ascertained by measuring vegetation height at an accuracy of 2.5 cm (Fartmann et al., 2012).

2.2.3. Grasshopper sampling

Grasshopper assemblages were recorded in each plot using a box quadrat (1.41 m × 1.41 m ≙ 2.0 m^2), which ranks among the most accurate sampling methods to ascertain species richness and abundance of grasshoppers (Gardiner and Hill, 2006; Fartmann et al., 2024). Sampling occurred in early August 2020. To avoid edge effects (Schirmel et al., 2010; Gardiner, 2020), the box quadrat was randomly dropped at 10 different points in the centre of the plot, covering a total area of 20 m^2 per plot (Fartmann et al., 2024). Accordingly, the grasshopper assemblages were very distinct and for example species characteristic of old heathlands (*Metrioptera brachyptera* and *Phaneroptera falcata*) were rarely and never found, respectively, in plots were heathland management measures had been applied (cf. Table 3). Within the box quadrat, grasshoppers were captured by sweep netting and hand. Species identification was done in the field by using Fischer et al. (2020). The scientific nomenclature of the species follows Fischer et al. (2020). Habitat specialists were classified according to Fartmann and Poniatowski (2025). Threatened species (including near-threatened ones) were derived from Helbing et al. (2025).

2.3. Statistical analysis

We performed all statistical analyses using R 4.3.1 (R Core Team, 2025). To detect differences in environmental parameters (Table 2) as well as in species richness and densities between plots of different management types (Fig. 2), we applied generalised linear mixed-effects models (GLMM) (R package lme4, negative-binomial structure; Bates et al., 2015) with 'subarea' as a random factor (Crawley, 2007). 'Management type' served as a nominal fixed factor and the analysed parameters as dependent variables. Pairwise comparisons among management types were conducted using estimated marginal means with Tukey adjustment implemented in the R package emmeans. To identify indicator species of different management types an indicator-species analysis (ISA) was carried out (Dufrêne and Legendre, 1997; De Cáceres and Jansen, 2016). The ISA uses the relative abundance and relative frequency of a species to estimate the strength of its association with a management type. The higher the indicator value (IV; scaled from 0 to 1) of a species was, the more abundant and frequently it occurred in the focal management type. The statistical significance of the relationship was tested by permutation tests (4999 permutations).

Table 2

Overview of sampled environmental parameters (mean ± standard error [SE]) for plots of five different types of heathland management ($N = 70$). Differences between the groups were analysed by using generalised linear mixed-effects models and Dunn's test for pairwise comparisons. n.s. not significant, $^{*}P < 0.05$, $^{**}P < 0.01$, $^{***}P < 0.001$.

Parameter	Management type					*P*
	BURN	BURN + DIS	MOW	MOW + SCA	CONTROL	
Cover (%)						
Dwarf shrubs	45.7 ± 5.1^{c}	21.8 ± 2.3^{b}	52.9 ± 3.6^{cd}	11.4 ± 4.1^{a}	86.8 ± 1.8^{d}	***
Grasses	5.9 ± 2.0^{ab}	19.6 ± 2.4^{b}	8.9 ± 3.1^{b}	11.4 ± 2.4^{b}	1.6 ± 0.6^{a}	***
Herbs	1.4 ± 0.4^{ab}	7.9 ± 1.5^{c}	0.4 ± 0.2^{a}	5.4 ± 2.2^{bc}	0.0 ± 0.0^{a}	***
Litter	10.7 ± 3.2^{b}	3.4 ± 0.6^{a}	34.3 ± 0.9^{c}	6.6 ± 1.3^{ab}	22.9 ± 2.7^{c}	***
Mosses	3.9 ± 2.2^{b}	0.7 ± 0.4^{a}	14.3 ± 4.6^{bc}	0.4 ± 0.4^{a}	45.0 ± 6.3^{c}	***
Lichens	$0.9 \pm 0.3^{\cdot}$	$0.5 \pm 0.3^{\cdot}$	2.1 ± 0.6	$0.0 \pm 0.0^{\cdot}$	$0.9 \pm 0.4^{\cdot}$	n.s.
Gravel	$0.5 \pm 0.3^{\cdot}$	$0.5 \pm 0.3^{\cdot}$	0.2 ± 0.2	0.0 ± 0.0	0.0 ± 0.0	n.s.
Bare ground	39.3 ± 3.3^{c}	51.3 ± 4.4^{cd}	9.3 ± 2.1^{b}	71.1 ± 4.1^{d}	2.5 ± 0.5^{a}	***
Habitat heterogeneity	2.3 ± 0.1^{bc}	3.2 ± 0.2^{c}	1.8 ± 0.2^{ab}	2.1 ± 0.3^{b}	1.0 ± 0.0^{a}	***
Vegetation height (cm)	8.4 ± 0.9^{b}	6.2 ± 0.7^{ab}	8.6 ± 0.4^{b}	4.4 ± 1.3^{a}	36.5 ± 2.0^{c}	***

Table 3
Results of indicator species analysis (ISA) for plots of five different types of heathland management ($N = 70$). IV = indicator value; relative abundance/relative frequency (percentage of plots within each group of heathland management). Indicator species for a certain group are hatched in grey. n.s. not significant, * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$.

Species	IV	*P*	Management type				
			BURN	BURN+DIS	MOW	MOW+SCA	CONTROL
Chorthippus biguttulus	8.0	n.s.	21 / 14	37 / 21	29 / 14	0 / 0	13 / 7
Chorthippus brunneus	41.8	***	23 / 21	73 / 57	4 / 7	0 / 0	0 / 0
Chorthippus mollis	38.6	**	18 / 57	54 / 71	11 / 57	14 / 57	3 / 21
Decticus verrucivorus	26.8	*	13 / 7	74 / 36	13 / 7	0 /0	0 / 0
Metrioptera brachyptera	49.1	***	9 / 14	4 / 14	2 / 7	0 / 0	85 / 57
Myrmeleotettix maculatus	39.1	***	12 / 71	39 / 100	18 / 86	29 / 100	2 / 29
Oedipoda caerulescens	33.0	**	20 / 79	18 / 71	23 / 79	39 / 86	0 / 0
Omocestus haemorrhoidalis	40.4	***	15 / 36	51 / 79	6 / 21	28 / 57	0 / 0
Omocestus viridulus	7.1	n.s.	0 / 0	0 / 0	0 / 0	0 / 0	100 / 7
Phaneroptera falcata	42.9	***	0 / 0	0 / 0	0 / 0	0 / 0	100 / 43
Platycleis albopunctata	20.4	*	14 / 14	29 / 21	0 / 0	57 / 36	0 / 0
Pseudochorthippus parallelus	9.5	n.s.	0 / 0	33 / 7	0 / 0	0 / 0	67 / 14
Stenobothrus lineatus	8.6	n.s.	25 / 29	30 / 29	30 / 29	15 / 14	0 / 0
Stenobothrus stigmaticus	24.7	*	23 / 21	69 / 36	0 / 0	8 / 7	0 / 0
Tettigonia viridissima	7.1	n.s.	0 / 0	0 / 0	0 / 0	100 / 7	0 / 0

3. Results

3.1. Effects of heathland management on habitat structure

Habitat structure varied strongly between the five different types of heathland management (Table 2). The difference was most pronounced for CONTROL on the one hand and BURN + DIS and MOW + SCA on the other hand. CONTROL was dominated by tall stands of dwarf shrubs and additionally exhibited a high cover of mosses and litter. Overall, CONTROL had the highest cover of dwarf shrubs and mosses, lowest cover of grasses, herbs and bare ground, lowest habitat heterogeneity and tallest vegetation. By contrast, BURN + DIS and MOW + SCA were dominated by large areas of bare ground, which was particularly true for the latter, and very short swards. BURN + DIS and MOW + SCA also had the highest cover of bare ground, grasses and herbs, the lowest cover of dwarf shrubs, litter and mosses as well as the shortest swards. Moreover, BURN + DIS had the highest habitat heterogeneity. By contrast, the cover of lichens and gravel was always low and did not differ between the five management types.

3.2. Response of grasshopper assemblages to heathland management

Altogether, we sampled 1134 individuals of 15 different grasshopper species on the 70 plots (Tab. A1). Nine of them were habitat specialists and seven were considered threatened ones. The most common species were *Myrmeleotettix maculatus* (586 individuals), *Chorthippus mollis* (185) and *Oedipoda caerulescens* (109). In accordance with the strong variation in habitat structure, both species richness and density of grasshoppers differed markedly between the management types, particularly between CONTROL on the one hand, and BURN + DIS and weaker MOW + SCA on the other hand (Fig. 2). The number of species and density peaked for all species, habitat specialists and threatened species in BURN + DIS and was lowest in CONTROL. MOW + SCA reached always the second highest values but did not differ significantly from BURN + DIS.

In detail, overall species richness was highest in BURN + DIS and differed from those in MOW and CONTROL. Species richness of habitat specialists and threatened species did not differ significantly between BURN, BURN + DIS, MOW and MOW + SCA. Densities of all species, habitat specialists, and threatened species were highest in BURN + DIS and differed from those observed in CONTROL and BURN and, for overall species density and habitat specialist density, also from those in MOW. Densities in MOW + SCA were higher than in CONTROL but did not differ significantly from those in BURN or MOW.

Indicator species were only identified for three of the five management types (Table 3). BURN + DIS had by far the most indicator species. The following six species were characteristic of this management type: *Chorthippus brunneus*, *C. mollis*, *Decticus verrucivorus*, *M. maculatus*, *Omocestus haemorrhoidalis* and *Stenobothrus stigmaticus*. The four latter species were considered threatened (Tab. A1). For MOW + SCA, *O. caerulescens* and *Platycleis albopunctata* were typical, for CONTROL, this was true for *Metrioptera brachyptera* (threatened species) and *Phaneroptera falcata* (Table 3 and A1). All mentioned indicator species were habitat specialists, except *C. brunneus* and *P. falcata* (Tab. A1).

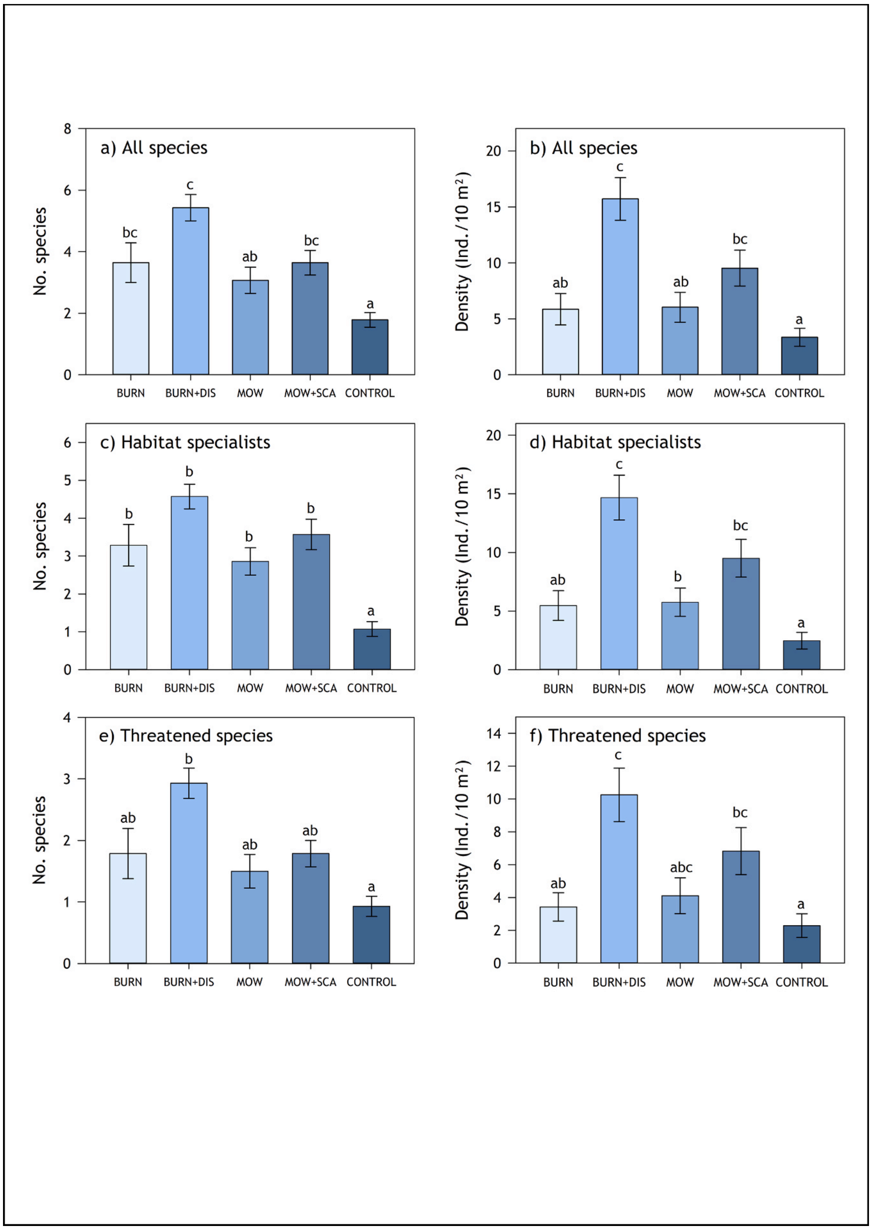

Fig. 2. Mean values (± SE) of species richness and density of grasshoppers, considering all (a, b), habitat specialists (c, d) and threatened species (e, f) for plots of five different types of heathland management ($N = 70$). Differences between the groups were analysed by using generalised linear mixed-effects models and Dunn's test for pairwise comparisons. n.s. not significant, $^{*}P < 0.05$, $^{**} P < 0.01$, $^{***} P < 0.001$.

4. Discussion

Our study revealed strong differences in habitat structure between the five heathland management types. This was particularly true for CONTROL on the one hand, and BURN + DIS and weaker MOW + SCA on the other hand. CONTROL was dominated by tall stands of dwarf shrubs and had the lowest habitat heterogeneity. MOW + SCA exhibited the shortest swards and had the highest cover of bare ground. Although the cover of bare ground was also high and the turf was also short, BURN + DIS was characterised by the highest habitat heterogeneity. In accordance with the strong variation in habitat structure, both species richness and density of grasshoppers differed markedly between the management types. The number of species and density peaked for all species, habitat specialists and threatened species in BURN + DIS, reached the second highest values in MOW + SCA and were lowest in CONTROL.

At the habitat level, habitat heterogeneity is known to be the main driver of species richness in general (Brose, 2001; Tews et al., 2004; Fartmann et al., 2021) and grasshoppers in particular (Fartmann et al., 2024; Kenyeres et al., 2024; Fartmann and Poniatowski, 2025). According to Fartmann et al. (2024), a high habitat heterogeneity favours species richness of grasshoppers in three different manners:

(i) Structurally-rich habitats are mandatory for many grasshopper species, since they undergo microhabitat preference shifts during their life cycle. Among the detected species, for heathlands, this has been shown for *Decticus verrucivorus*, *Myrmeleotettix maculatus* and *Platycleis albopunctata* (Schirmel et al., 2010; Wünsch et al., 2012). In these species, warm microhabitats rich in bare ground are used for oviposition and by the young nymphs. By contrast, the larger older nymphs and especially adults, prefer taller vegetation that serves as a shelter against predators and high temperatures in summer.
(ii) Overall, the high variety of microhabitats in heterogeneous habitats fosters the coexistence of many grasshopper species with sometimes very different habitat requirements (Joern, 2005; Schirmel et al., 2010; Löffler and Fartmann, 2017).
(iii) In contrast to homogenous habitats, heterogeneous ones and their assemblages are more resistant and resilient against the pervasive effects of climate change and generally against environmental alterations (Bladon et al., 2024; Fartmann at al., 2024). This has also been shown for grasshopper populations (Kindvall, 1996; Fartmann et al., 2022a). Thus, habitat heterogeneity favours the long-term viability of grasshopper populations.

This is in line with our study. BURN + DIS had the highest habitat heterogeneity and as a result the highest species richness of all and threatened species as well as of habitat specialists. By contrast, the homogeneous CONTROL, characterised by tall and dense stands of dwarf shrubs and the lowest habitat heterogeneity had for all three groups the lowest species richness. The three other management types had an intermediate habitat heterogeneity and species richness. Importantly, however, species richness did not differ significantly between the simple management measures (BURN and MOW) and the combined treatments (BURN+DIS and MOW+SCA). This suggests that the conventional management measures might already be sufficient to maintain characteristic heathland grasshopper assemblages. Nevertheless, BURN + DIS had the highest number of indicator species (six species). Among them were two (*D. verrucivorus*, *M. maculatus*) of the three species mentioned before that fulfil microhabitat shifts during their ontogenetic development.

Density of grasshoppers also peaked in BURN + DIS, was second highest in MOW + SCA and lowest in CONTROL for all three groups of grasshoppers. Grasshopper abundance is usually a trade-off between a warm microclimate and sufficient food (Fartmann et al., 2024). Particularly MOW + SCA but also BURN + DIS were characterised by very short swards (on average 4.4 and 6.2 cm, respectively) and very high cover of bare ground (71.1 and 51.3%, respectively), hence warm microclimatic conditions (Stoutjesdijk and Barkman, 2014). The majority of the detected grasshopper species in the heathlands were herbivores that mainly feed on grasses but also herbs (Ingrisch and Köhler, 1998; Schlumprecht and Waeber, 2003; König et al., 2022). This also applies for the three dominant grasshopper species in this study, *M. maculatus*, *Chorthippus mollis* and *Oedipoda caerulescens*, which accounted for more than 75% of all observed individuals. Since the average cover of grasses and herbs was much lower in MOW + SCA (17%) than in BURN + DIS (28%), we explain the lower grasshopper densities in the former by food shortage. By contrast, we attribute the low density of grasshoppers in the dense stands of dwarf shrubs in CONTROL by both an adverse (cool) microclimate and a low food availability (absence of herbs, very low cover of grasses) (cf. Schirmel et al., 2010, 2011; Wünsch et al., 2012; Borchard et al., 2013). In BURN and MOW, vegetation structure characteristics and hence, microclimate, as well as the availability of grasses and herbs were at an intermediate level. Accordingly, the same was true for grasshopper densities. Differences in the densities of all species, habitat specialists, and threatened species were detected between the BURN and BURN + DIS treatments, whereas no such differences were found between MOW and MOW + SCA. These findings suggest that the benefits of BURN + DIS relative to the conventional BURN treatment are more pronounced than those of MOW + SCA relative to MOW. This more pronounced effect might be a result of the higher habitat heterogeneity in BURN + DIS plots.

Bare ground plays a key role for oviposition of grasshoppers (Wünsch et al., 2012; Gardiner, 2020; Fartmann and Poniatowski, 2025). More than 70% of the German grasshopper species use bare soil for egg-laying (Fartmann et al., 2021). MOW + SCA and BURN + DIS were dominated by bare ground and had the highest cover of bare soil. Consequently, both indicator species of MOW + SCA (*Oedipoda caerulescens* and *Platycleis albopunctata*) and all six indicator species of BURN + DIS (*Chorthippus brunneus*, *C. mollis*, *D. verrucivorus*, *M. maculatus*, *Omocestus haemorrhoidalis* and *Stenobothrus stigmaticus*) lay their eggs at least partly into the soil (Fartmann and Mattes, 1997; Detzel, 1998). All these indicator species are habitat specialists (except *C. brunneus*), considered threatened (except *C. brunneus* and *C. mollis*) and species of early to mid-successional seral stages (Detzel, 1998; Schlumprecht and Waeber, 2003; Fartmann and Poniatowski, 2025). By contrast, in the dense stands of CONTROL, bare ground was almost absent and the two indicator species, *Metrioptera brachyptera* and *Phaneroptera falcata*, lay their eggs mainly into plant material (Fartmann and Mattes, 1997; Detzel, 1998) and are typical of late-successional stages (Detzel, 1998; Schlumprecht and Waeber, 2003; Fartmann and Poniatowski, 2025). One of the two species was habitat specialist and considered threatened (*M. brachyptera*).

Today, nitrogen deposition and mild winters favour the expansion of competitive pleurocarpous mosses, such as *Pleurozium schreberi*, in heathlands, which results in the disappearance of bare ground (Streitberger et al., 2022). Both prescribed winter burning and mowing are traditional techniques of heathland management (Gimingham, 1992; Webb, 1998; Symes and Day, 2003). However, as our study showed, under the current environmental conditions, if applied alone, they (particularly MOW) were less effective in (i) creating the key structure bare soil, (ii) removing the litter and moss layer, and (iii) favouring the establishment of grasses and herbs in comparison to the two novel management techniques. Mowing occurred in a height of 5 cm (Matevski et al., 2025), which is usually above the height of the moss layer and thus had little effects on the cover of mosses (cf. Symes and Day, 2003). Moreover, cut material (particularly small plant fragments) was often only partially removed resulting in litter accumulation. Prescribed burning is nowadays mostly applied during late winter (Symes and Day, 2003; Valkó et al., 2014; Valkó and Deák, 2021), when the moss and litter layer are often relatively moist (own observation). As a result, the combustion of both layers is usually incomplete (Ruprecht et al., 2013; Jacobs et al., 2015). By contrast, summer burning, which was not applied in the study area, is known to be highly effective in destroying the litter and moss layer due to the dry conditions during that period of the year (Brüggeshemke et al., 2025).

In conclusion, the two novel heathland management techniques had the desired effects on the grasshopper assemblages. Their application fostered the habitat quality of the heathlands by (i) strongly increasing the cover of the key structure bare soil, (ii) creating warm microclimatic conditions, (iii) boosting the availability of food resources (grasses but also herbs) and (iv) building heterogeneous stands of heathlands. Consequently, both grasshopper species richness and population densities were higher than under the CONTROL treatment. In contrast, when compared with the conventional management measures BURN and MOW, differences were observed primarily in population densities rather than species richness. These findings suggest that the conventional management measures BURN and MOW are generally effective in maintaining characteristic heathland grasshopper assemblages, although they appear less successful in supporting high population densities. Among the two novel techniques, BURN + DIS was most powerful in favouring species richness and density of grasshoppers since it created the most heterogeneous stands and that exhibited the highest cover of grasses and herbs.

5. Implications for conservation

Based on our findings, we recommend the implementation of both novel management techniques as standard practices to promote grasshoppers in heathland ecosystems. From an economic perspective, these approaches are considerably more cost-effective, generating substantially lower expenses and less waste material than traditional methods that aim at restoring early-successional heathlands such as sod-cutting and choppering (cf. Table 1).

Moreover, they facilitate the development of key habitat structures, particularly bare ground. Bare ground is not only a key structure for grasshoppers but also many other arthropods (Fartmann et al., 2021; 2022b; Matevski et al., 2025) and for the germination of a lot of less competitive and rare plant species (Grime et al., 2007; Gardiner, 2020; Streitberger et al., 2021a, b, 2022). Heathland birds are also favoured by the large availability of early-successional stages (Brüggeshemke et al., 2025). Accordingly, all these taxa should also benefit from the application of the two measures.

Prescribed summer burning might be a further alternative since it also destroys the litter and moss layer (Brüggeshemke et al., 2025). In general, fires help to maintain a balanced nutrient supply in heathland soils and vegetation, supporting the diversity of flora and fauna especially in areas that are subject to a high amount of atmospheric nitrogen deposition (Brüggeshemke et al., 2025). Thus far, the effects of summer burning in heathlands have not been tested for grasshopper assemblages. However, for one species, *Gampsocleis glabra*, its importance has already been proven. It has become extremely rare in Central Europe (Grzędzicka and Vahed, 2020; Hawlitschek et al., 2023; Van Kleef et al., 2025) and its occurrence in Germany is today limited to active military training areas, where high-intensity summer fires occur regularly as part of the military training practice (Brüggeshemke, 2025).

Due to the great importance of habitat heterogeneity for species richness (see Discussion section), heathland management should be applied in a mosaic-like manner on a small scale (Fartmann et al., 2015, 2022b; Matevski et al., 2025). Since later stages of heathland succession also may harbour some typical and threatened habitat specialists (e.g. *Metrioptera brachyptera*) they should be a part of such mosaics. As long as detailed data are missing, we recommend management intervals of 10–15 years. However, further studies that consider successional speed due to differences in soil conditions and climate are necessary for a fine adjustment of this suggestion.

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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

Tab. A1
Overview of sampled grasshopper species, their status as threatened species (according to Helbing et al., 2025) and habitat specialists (according to Fartmann and Poniatowski, 2025) as well as the number of detected individuals

Species	Habitat specialist	Threatened species	No. individuals
Chorthippus biguttulus	.	.	24
Chorthippus brunneus	.	.	26
Chorthippus mollis	✓	.	185
Decticus verrucivorus	✓	✓	8
Metrioptera brachyptera	✓	✓	57
Myrmeleotettix maculatus	✓	✓	586
Oedipoda caerulescens	✓	.	109
Omocestus haemorrhoidalis	✓	✓	68
Omocestus viridulus	.	✓	1
Phaneroptera falcata	.	.	19
Platycleis albopunctata	✓	.	14
Pseudochorthippus parallelus	.	.	3
Stenobothrus lineatus	✓	✓	20
Stenobothrus stigmaticus	✓	✓	13
Tettigonia viridissima	.	.	1
Sum	**9**	**7**	**1134**

Data Availability

Data will be made available on request.

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