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Original research article

Territory densities of heathland breeding birds are enhanced by fire on military training areas

Jonas Brüggeshemke [a,*,1], Ole Henning [b], Thomas Fartmann [a,c,2]

[a] Department of Biodiversity and Landscape Ecology, Osnabrück University, Barbarastraße 11, Osnabrück 49076, Germany
[b] Otto-Lauffer-Straße 2, Göttingen 37077, Germany
[c] Institute of Biodiversity and Landscape Ecology (IBL), An der Kleimannbrücke 98, Münster 48157, Germany

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ABSTRACT

Heathland ecosystems have experienced severe declines. Today, the remaining heathlands suffer from succession and airborne nitrogen deposition. To counteract the negative effects of both, various management measures such as choppering, grazing, mowing or sod-cutting have been implemented. However, thus far, these measures only partially halted the loss of biodiversity. We compared environmental conditions and territory densities of characteristic heathland breeding bird species on 91 randomly selected plots in two large heathlands that vary in their long-term land use history: a military training area shaped by fire and a nature reserve where grazing dominates. Our study revealed strong differences in environmental conditions and territory densities. In the military training area, very open habitats accounted for more than two thirds per plot. By contrast, in the nature reserve, semi-open habitats had a share of more than one half per plot. Mean territory densities of open heathland species were 1.6 times higher in the training area compared to the nature reserve. By contrast, territory densities of semi-open heathland species did not differ. Overall, fire was assumed as the key driver of territory densities in characteristic heathland breeding birds. In comparison to traditionally managed heathlands, fire management of heathlands favoured breeding birds in two ways: First, through preserving the nutrient balance, which very likely had positive effects on insect food supply and may also on the formation of eggshells. Second, by creating early successional stages rich in bare ground that allow an easy access to invertebrate food resources. Based on our study, heathland management should aim at rejuvenating heathlands and creating early successional stages regularly without causing nutrient imbalances in the long run. Consequently, we recommend an extension of the area and frequency of prescribed burning in a mosaic-like manner in heathlands, especially outside military training areas.

1. Introduction

Biodiversity is in decline at an alarming rate (Naeem et al., 2012; Cardoso et al., 2020). Among the main drivers for biodiversity loss in terrestrial biomes is atmospheric nitrogen deposition (Bobbink et al., 2010; Jones and Power, 2012). Negative effects have been

* Corresponding author.
E-mail address: jonas.brueggeshemke@uos.de (J. Brüggeshemke).
[1] ORCID 0000–0002-7425–4949
[2] ORCID 0000–0002-2050–9221

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found across different trophic levels (Kurze et al., 2018; Stevens et al., 2018). Ecosystems that are adapted to nutrient-poor conditions such as heathlands are particularly vulnerable (Roem et al., 2002; Phoenix et al., 2012; Southon et al., 2013; Vogels et al., 2023).

At the beginning of the 19th century, heathlands covered large parts of Western and Central Europe (Keienburg and Prüter, 2006). Originally, fire was a common tool in maintaining grazing grounds in heathlands (Goldammer et al., 1997; Bowman et al., 2013). However, in the course of land use change during the past two centuries, most heathlands were afforested or transformed into arable land (Fagúndez, 2013; Vogels et al., 2013; Walmsley et al., 2021). Today, the remaining heathlands often lack proper management. Also, prescribed burning diminished and only persisted on military training areas, which became important refuges for heathlands due to their early establishment and the absence of agricultural intensification, but also through regular disturbance caused by military training activity (Warren et al., 2007; Heitkamp et al., 2008; Schellenberg and Bergmeier, 2020; Wittig et al., 2020). Nowadays, heathlands are legally protected by the EU Habitats Directive (EC (European Commission), 2013).

In Central Europe, despite a recent decline, critical loads for atmospheric nitrogen deposition in heathlands are still surpassed by actual rates (Schaap et al., 2018; Bobbink et al., 2022). Problems arising from this nitrogen surplus are acidification, subsequent grass encroachment and degradation of heathlands (Houdijk et al., 1993; Falk et al., 2010; Olmeda et al., 2020). To counteract the effects of both succession and airborne nitrogen deposition, various heathland management measures such as choppering, grazing, mowing or sod-cutting have been implemented (Härdtle et al., 2007; Fartmann et al., 2015; Streitberger et al., 2021a; Walmsley et al., 2021). However, recent research suggests that they lead to nutrient imbalances in the long run (Fottner et al., 2007; Härdtle et al., 2009; Vogels et al., 2019). These imbalances do not only have negative effects on plants and arthropods, but possibly also on vertebrates such as heathland birds (Maskell et al., 2010; Southon et al., 2013; Vogels et al., 2013, 2017; Field et al., 2014). Prescribed burning might be a possible solution to counteract nutrient imbalances in heathlands (Niemeyer et al., 2005). However, fire as a heathland conservation tool is still rarely used in Central Europe unlike, for example, Great Britain or Norway (Gimingham, 1972; Davies et al., 2022).

Heathlands harbour a wide range of threatened bird species that were once very common in nutrient-poor cultural landscapes (Ludwig et al., 2009; Schaub et al., 2010; Tagmann-Ioset et al., 2012; Newton, 2017; Fartmann et al., 2018, 2022b; Schwarz et al., 2018). However, in recent decades, many heathland bird species showed marked declines in Western and Central Europe (Van Turnhout et al., 2007, 2010; Van Strien et al., 2016; Rigal et al., 2023). Most of these species require early successional stages rich in bare ground and heterogeneous habitats. Moreover, usually they are insectivores, which makes them particularly susceptible for potential effects of nutrient imbalances and changed plant stoichiometry (Van Turnhout et al., 2010; Vogels et al., 2013; Nijssen et al., 2017, 2023).

Our study aims to answer the question whether populations of characteristic heathland bird species respond to differences in the availability of early successional stages and nutrient imbalances in heathlands. We hypothesise that there are differences in bird territory densities in traditionally managed heathlands compared to those predominantly shaped by burning. We expect fire influence to have positive effects on in the occurrence of early successional stages and nutrient balances. Both should enhance territory densities of heathland breeding birds.

This study was conducted in the Lüneburg Heath biogeographical region (northern Germany). Within Central Europe, it is the most important stronghold of lowland heathlands and one of the last refuges for many rare heathland species, such as Black Grouse (*Lyrurus tetrix*). We compared environmental conditions and territory densities of characteristic heathland breeding bird species in two large and representative heathlands that vary in their long-term land use history and therefore disturbance regime: a military training area and a nature reserve. The training area has a continuous fire history of more than 130 years and is the area with the greatest and most regular fire influence in Central Europe. By contrast, the nature reserve exhibits the largest heathland outside military training areas in Germany. It has been used for continuous sheep grazing and sod-cutting for at least 200 years. Today's heathland management there mainly consists of sheep grazing. Overall, we sampled environmental conditions and bird territory densities on 91 randomly selected plots with a size of 30 ha and a dominance (cover >50 %) of heathlands (training area: $n = 42$; nature reserve: $n = 49$). Based on our findings, we make recommendations for the management of Central European heathlands that maintains biodiversity across trophic levels in the long run.

2. Material and methods

2.1. Study area

The Lüneburg Heath biogeographical region was chosen as a study area. It belongs to the Northwest German Lowland and is located in the northeast of the German federal state of Lower Saxony (Cordes et al., 1997; Fig. 1). The study area is the most important stronghold of lowland heathlands in Central Europe (Schellenberg and Bergmeier, 2014). Accordingly, it is one of the last refuges for many rare heathland species, such as Black Grouse (*Lyrurus tetrix*) (Mertens et al., 2007; Keller et al., 2020). The study area has a suboceanic climate with an average annual precipitation of 790 mm and a mean annual temperature of 9.2 °C (Soltau weather station, period: 1991–2020; German Meteorological Service, 2024). Within the heathlands brown podzolic soils dominate (NIBIS, 2017). Current nitrogen deposition rates of 17–19 kg ha^{-1} year^{-1} surpass the critical loads of 5–15 kg ha^{-1} year^{-1} for heathlands (Schaap et al., 2018; Bobbink et al., 2022).

The study was carried out in two subareas that contain very large heathlands but strongly differ in their land use history and therefore disturbance regime: (i) Munster-South military training area (hereinafter referred to as 'training area'; 60–98 m a.s.l.; 52°56'44.4"N 10°03'27.4"E) and (ii) Lüneburg heath Nature reserve (hereinafter referred to as 'nature reserve'; 40–169 m a.s.l.; 53°09'01.1"N 9°53'50.0"E) (Fig. 1). The training area covers an area of 6500 ha and is used for military training exercise since 1891 (Bundeswehr Joint Support Service, 2011; Müller et al., 1997). Therefore, it has not been affected by any kind of agricultural

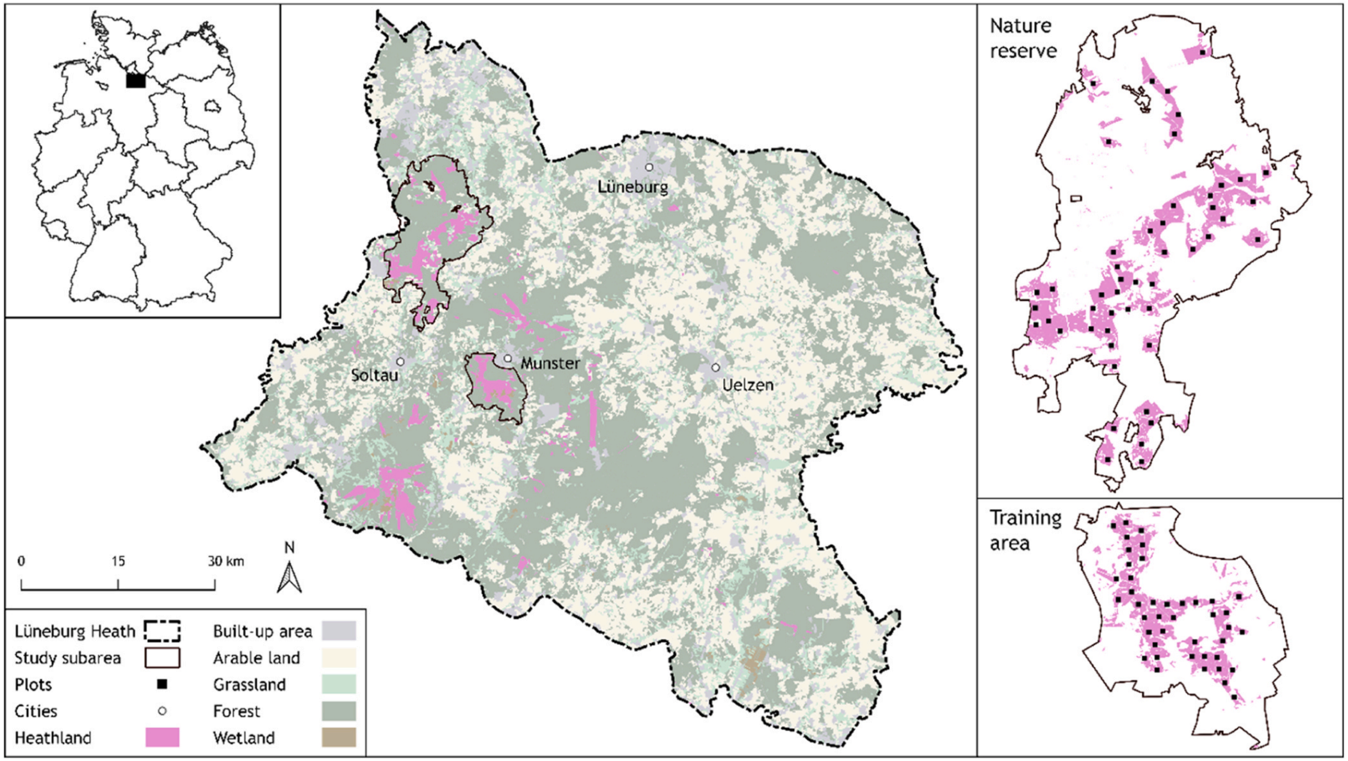

Fig. 1. Location of the study area, two subareas (Munster-South military training area and Lüneburg Heath Nature reserve) and plots in northern Germany.

intensification and within the 2260 ha of open habitats, heathlands still cover 1400 ha. The main purpose of the training area is the use as a firing range for barrel and rocket artillery (Bundeswehr Joint Support Service, 2011; Wegner, 2018). Therefore, a very open landscape at a large scale is needed that guarantees clear views on the targets. The most important tool to keep the landscape open on the training area is fire. Prescribed burning is applied to rejuvenate old heathlands. Furthermore, accidental fires also occur to a considerable extent due to military training activity (Bundeswehr Joint Support Service, 2011; Wegner, 2018). Annual area of wildfires and controlled burning varies between 124 and 539 ha with an annual mean of 355 ha, which corresponds to 16 % of the open habitats that burn per year (own analysis based on Sentinel-2-satellite data from 2016–2022; cf. Heim et al., 2022). This makes the training area the area with the greatest and most regular fire influence in Central Europe with a continuous fire history of more than 130 years (Copernicus Emergency Management Service, 2024). To avoid any unintended expansion of fires, the training area is covered by a network of firebreaks (lanes that are regularly milled) but also of tracks and roads to allow for an easy access of firefighters. In addition, solitary trees and groups of shrubs are selectively removed to ensure distance vison (Wegner, 2018).

The nature reserve was established in 1922 and is one of the oldest and largest nature reserves of the German mainland (Cordes et al., 1997). Today, it covers an area of about 23,440 ha. It contains 4300 ha of heathlands, which is the largest heathland outside military training areas in Germany (Schellenberg and Bergmeier, 2014). The heathlands are embedded in a matrix of coniferous forests dominated by Scots Pine (*Pinus sylvestris*) (Cordes et al., 1997; Keienburg and Prüter, 2006). The nature reserve has been used for continuous sheep grazing and sod-cutting for at least 200 years. By contrast, fire was rarely applied (Lütkepohl and Stubbe, 1997). Today's heathland management mainly consists of sheep grazing (Walmsley et al., 2021). Choppering, mowing, prescribed burning and sod-cutting are in each case applied annually on less than 1 % of the heathlands (period 2016–2022; annual mean and range per measure: 20 ha and 0–70 ha, respectively). Prescribed burning occurs in autumn and late winter. Furthermore, extensive thinning of forests has been carried out in an area of 3500 ha in order to increase ecotone length between heathland and woodland (Mertens et al., 2007; Keller et al., 2020). These measures aimed at promoting species of semi-open landscapes, in particular Black Grouse.

2.2. *Sampling design*

2.2.1. *Plots*

Before the start of fieldwork, we randomly selected 91 square-shaped plots with a size of 30 ha and a dominance (cover >50 %) of heathlands in the training area ($n = 42$) and nature reserve ($n = 49$).

2.2.2. *Sampling of environmental parameters*

For each plot, we recorded the habitat composition in the field according to the German habitat classification scheme (15 major habitat types [Table 1]; Finck et al., 2017). Heathland and forest habitat types were further differentiated depending on their tree density: open heathland (< 5 trees/ha) vs. semi-open heathland (5–20 trees/ha) and open forest (20–100 trees/ha) vs. dense coniferous forest (>100 trees/ha).

Moreover, we calculated the Normalized Difference Vegetation Index (NDVI) (Seto et al., 2004). It measures the greenness of vegetation, therefore the NDVI is a proxy for vegetation productivity and acts anti-proportional to the level of disturbance. To derive NDVI data, we used a grid image of ESA satellite mission Sentinel-2 with a grid length of 10 m. The satellite image was acquired on 23 June 2022 for the training area and on 18 June 2021 for the nature reserve to depict habitat conditions during the respective breeding season. From these images we calculated NDVI values for each grid cell based on the following equation (Sellers, 1985):

Table 1
Overview of habitat types and Normalized Difference Vegetation Index (NDVI) (mean ± standard error [SE]) in heathland plots in the training area ($n = 42$) and nature reserve ($n = 49$); ha = hectares. Differences between the two subareas were tested by using Mann-Whitney U test. n.s. not significant, *$P < 0.05$, ** $P < 0.01$, *** $P < 0.001$.

Parameter	Study subarea		*U*	*P*
	Training area	Nature reserve		
(a) Habitat type (ha)				
Agricultural land	0.11 ± 0.03	0.15 ± 0.07	972.0	n.s.
Burned area	3.10 ± 0.63	0.00 ± 0.00	318.5	***
Open heathland	16.06 ± 1.02	11.14 ± 1.11	600.0	***
Semi-open heathland	2.36 ± 0.53	9.16 ± 0.95	411.0	***
Juniper (*Juniperus communis*) heathland	0.01 ± 0.01	3.34 ± 0.98	765.0	**
Wet heathland	1.03 ± 0.27	0.46 ± 0.15	757.0	*
Broom (*Cytisus scoparius*) scrub	0.23 ± 0.11	0.01 ± 0.01	853.0	**
Dry grassland	1.72 ± 0.54	0.50 ± 0.23	635.0	***
Mesic grassland	0.31 ± 0.12	0.26 ± 0.10	1011.0	n.s.
Open forest	0.90 ± 0.34	2.74 ± 0.59	628.0	**
Dense coniferous forest	3.39 ± 0.56	1.65 ± 0.30	751.5	*
Fringe	0.23 ± 0.05	0.15 ± 0.01	770.0	*
Firebreak	0.52 ± 0.09	0.00 ± 0.00	269.5	***
Track	0.78 ± 0.08	0.37 ± 0.04	506.0	***
Built-up area and road	0.32 ± 0.06	0.07 ± 0.03	500.0	***
(b) NDVI	0.27 ± 0.01	0.29 ± 0.01	73.0	*

$$NDVI = \frac{(B8 - B4)}{(B8 + B4)}$$

with B8 being the near-infrared band (8) and B4 being the red band (4) of the Sentinel-2 satellite image. Based on the NDVI values for each grid cell we calculated mean NDVI values for each plot.

Soil samples were gathered in 10 randomly pre-selected heathland plots per subarea (20 samples in total). They comprised the inorganic soil after removal of the humus layer and were taken with a soil corer (3 cm diameter) at a soil depth of 10 cm as mixed samples from three randomly chosen sub-samples per plot. Air-dried soil samples were sieved (2 mm mesh size). Calcium (Ca) and magnesium (Mg) were analysed using ion chromatography (Metrohm 761 Compact IC). We used an eluent consisting of 1.7 mmol/L nitric acid and 1.7 mmol/L dipicolinic acid. For potassium (K) and soluble phosphorus (P), 5 g soil was shaken out with 100 ml of calcium-acetate-lactate (CAL). The phosphorus extracted from the soil with the CAL solution is considered to be plant-available. The plant-available phosphorus was measured with a Libra S11 photometer using a SPECTROQUANT phosphate test from Merck. Orthophosphate ions form molybdatophosphoric acid with molybdate ions in a sulphuric acid solution. This was converted with ascorbic acid to phosphomolybdenum blue, which was determined photometrically. The measured values, which were determined with the aid of the calibration lines, refer to mg phosphate/L. After milling, the soil samples were analysed for percentage total nitrogen (N) using an elemental auto-analyser (NA 1500, Carlo Erba, Milan, IT). N:P ratio was calculated as mass percentage. The soil reaction was measured using $CaCl_2$ as detergent (10 g soil with 25 ml $CaCl_2$ [0.01 mol/L]). All soil analyses were run twice accepting a maximum deviation of 10 % between duplicates. We calculated mean values of duplicates for further analyses.

2.3. Bird surveys

We mapped breeding-bird territories from March to June, in the nature reserve in 2021 and in the training area in 2022 (Fischer et al., 2005). Breeding birds show generally little variation in densities regarding two consecutive years (Bengtsson et al., 1997; Järvinen et al., 1977). Short-term temporal variability is mainly driven by habitat changes (Söderström et al., 2001). Particularly, relatively stable habitat types, such as forests or heathlands, exhibit usually only a low inter-annual variation. Territory mapping ranks among the most precise sampling technique for estimating species richness and abundance of breeding birds (Bibby et al., 2000). In total, we conducted five surveys early in the morning and three surveys in the evening after sunset with an interval of at least 10 days between each visit (Fartmann et al., 2018; Fumy and Fartmann, 2021). During every survey, we followed a non-linear route covering the whole plot and noted all signs of territorial behaviour or breeding activity, such as singing, on a digital map using QField for QGIS. Breeding was assumed if a bird showed territorial behaviour during at least two surveys (Fischer et al., 2005). We counted single observations as a territory only if breeding (e.g., nestlings in a nest) was documented (Brüggeshemke et al., 2022; Fartmann et al., 2022b).

For further analyses, we identified bird species characteristic for Central European heathlands following Flade (1994): Black Grouse (*Lyrurus tetrix*), Great Grey Shrike (*Lanius excubitor*), Hoopoe (*Upupa epops*), Nightjar (*Caprimulgus europaeus*), Red-backed Shrike (*Lanius collurio*), Skylark (*Alauda arvensis*), Stonechat (*Saxicola rubicola*), Tree Pipit (*Anthus trivialis*), Woodlark (*Lullula arborea*) and Yellowhammer (*Emberiza citrinella*). These species reach particularly high densities in this habitat type. Moreover, we added Wryneck (*Jynx torquilla*) to the list of characteristic heathland species following new findings that almost 70 % of the population in Lower Saxony occurs in dry habitat with sparse vegetation, such as heathlands (Dankelmann, 2022). All the species, except Stonechat, are considered threatened in Lower Saxony (Krüger and Sandkühler, 2021).

2.4. Statistical analysis

We performed all statistical analyses using R 4.3.2 (R Development Core Team, 2024). Differences in environmental conditions and heathland birds' territory densities between heathland plots in the training area and nature reserve were tested by using the Mann-Whitney U test. Non-metric multidimensional scaling (NMDS, function metaMDS, package vegan, Oksanen et al., 2022) was applied to detect preferences of heathland bird species and differences in the composition of habitat types between heathland plots in the training area and nature reserve. Bray-Curtis was applied as a distance measure and maximum random starts was set at 200 to search for a stable solution. Environmental variables with significant impact ($P < 0.05$) were used as an overlay (function envit, package vegan, Oksanen et al., 2022]). We only used non-intercorrelated variables (function ggpairs, Spearman correlation coefficient [r_s], $| r_s | < 0.6$, package GGally, Schloerke et al., 2023).

3. Results

3.1. Environmental conditions

Habitat type composition and soil conditions varied strongly between the two subareas (Table 1). Overall, burned area, open heathland, wet heathland, Broom (*Cytisus scoparius*) scrub, dry grassland, dense coniferous forest, fringe, firebreak, track and built-up area/road covered on average a larger area in the training area than in the nature reserve. By contrast, semi-open heathland, Juniper (*Juniperus communis*) heathland and open forest had on average a higher cover in the nature reserve compared to the training area.

In the training area, open heathland on average covered alone more than one half of the 30 ha large plots. Together with burned area, track and firebreak very open habitats even accounted for more than two thirds per plot. Overall, their cover was 1.8 times higher in the training area compared to the nature reserve. Moreover, dense coniferous forest and semi-open heathland had jointly a mean share of more than one fifths per plot. By contrast, in the nature reserve, semi-open habitats, i.e. semi-open heathland, Juniper heathland and open forest, had on average a share of more than 50 % per plot. Compared to the training area, the mean cover of these semi-open habitats was 4.7 times higher. Open heathland was on average found on more than one third per plot in the nature reserve. No further habitat type had on average a cover of more than 2 ha per plot across the two subareas. In line with aforementioned differences in habitat type composition, mean NDVI reached higher figures in the nature reserve than in the training area.

Among the soil parameters, average values of phosphate, potassium, calcium, magnesium and total N were higher in the training area than in the nature reserve (Fig. 2, Fig. A1). By contrast, mean N:P ratio was higher in the nature reserve. Solely, mean pH did not differ between the two subareas.

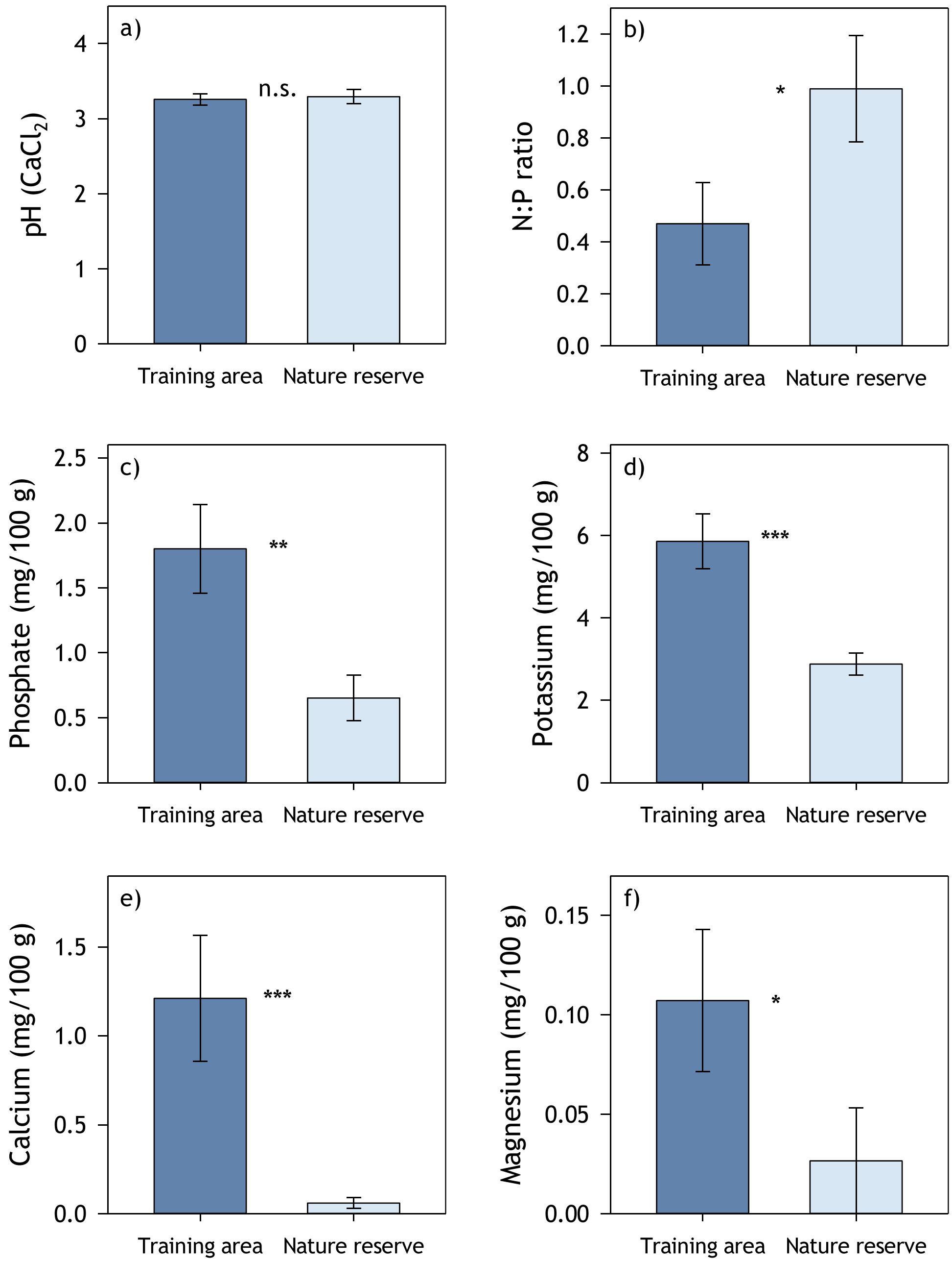

Fig. 2. Mean values (± SE) of soil parameters in heathland plots in the training area ($n = 10$) and nature reserve ($n = 10$). Differences between the two subareas were tested by using Mann-Whitney U test. n.s. not significant, ** $P < 0.01$, *** $P < 0.001$.

3.2. Response of heathland breeding birds to environmental conditions

In total, we recorded eleven heathland bird species with 2496 territories on the 91 heathland plots (Tab. A1). Five were classified as species of open heathland and six as species of semi-open heathland. The most common species (i.e. > 200 territories in all plots) were in decreasing order: Tree Pipit, Skylark, Woodlark, Stonechat and Yellowhammer. Mean territory density of open heathland species was higher in the training area than in the nature reserve (Fig. 3). By contrast, territory density of semi-open heathland species did not differ between the two subareas (Fig. 3). Both, the most common open heathland species, Skylark (*Alauda arvensis*), and the most common semi-open heathland species, Tree Pipit (*Anthus trivialis*), had higher densities in the military training area compared to the nature reserve (Fig. 4). All other nine heathland bird species did not differ in their density between the two subareas. In the NMDS analysis, the first axis showed a gradient of heathland openness with characteristic breeding bird species of semi-open heathland and open forest clustered on the left side (Nightjar *Caprimulgus europaeus*, Red-backed Shrike *Lanius collurio*, Tree Pipit *Anthus trivialis*, Woodlark *Lullula arborea*, Wryneck *Jynx torquilla* and Yellowhammer *Emberiza citrinella*) and characteristic breeding bird species of open heathlands on the right side (Black Grouse *Lyrurus tetrix*, Great Grey Shrike *Lanius excubitor*, Hoopoe *Upupa epops*, Skylark *Alauda arvensis* and Stonechat *Saxicola rubicola*) (Fig. 5).

4. Discussion

Our study revealed strong differences in environmental conditions and territory densities of characteristic heathland breeding bird species in two large Central European heathlands that varied in their long-term land use history and thus disturbance regime. In the military training area, mainly shaped by fire, open heathland on average covered alone more than one half per plot. Together with burned area, track and firebreak, very open habitats even accounted for more than two thirds per plot. By contrast, in the nature reserve, traditionally managed by sheep grazing, semi-open habitats (semi-open and Juniper heathland, open forest) had a share of more than 50 % per plot. Accordingly, the mean NDVI reached higher figures in the nature reserve than in the training area. Mean territory densities of open heathland species were 1.6 times higher in the training area compared to the nature reserve. By contrast, territory densities of semi-open heathland species did not differ between the two subareas.

Primary purpose of military training areas is not nature conservation, but military training (Zentelis and Lindenmayer, 2014; Zentelis et al., 2017). At the studied training area, the main military objective was to create a very open landscape at a large scale that can be used as a firing range for artillery. This goal was particularly achieved by (i) prescribed burning, (ii) accidental fires due to military shooting activity and (iii) additional removal of solitary trees or groups of shrubs. Consequently, the training area is the area with the greatest and most regular fire influence in Central Europe. To avoid any unintended expansion of fires, the training area was additionally covered by a network of firebreaks as well as of tracks that allow an easy access of firefighters. Accordingly, the applied disturbance regime, has resulted in a landscape with dominance of very open habitats, particularly open heathlands but also burned areas, tracks and firebreaks, and a sharp gradient between open habitats and woodlands. Overall, the aforementioned open habitats covered more than two thirds of the plots, which was 1.7 times more compared to the nature reserve. By contrast, in the nature reserve, the applied conservation measures mainly included (i) regular heathland management by grazing and (ii) extensive thinning of forests to create heterogeneous and soft ecotones between heathland and woodland. As a result, semi-open habitats, i.e, semi-open heathland, Juniper heathland and open forest, had a share of more than 50 % in the plots, which was 4.7 times higher compared to the training area. Accordingly, the higher territory densities of open heathland bird species in general and the Skylark in particular, as a characteristic species of open heathlands, in the training area can at least partially be explained by the higher cover of very open habitats. By contrast, the territory densities of semi-open heathland bird species did not differ between the training area and nature reserve. Additionally, the Tree Pipit, a characteristic species of semi-open heathlands, was even more abundant in the training area. Both

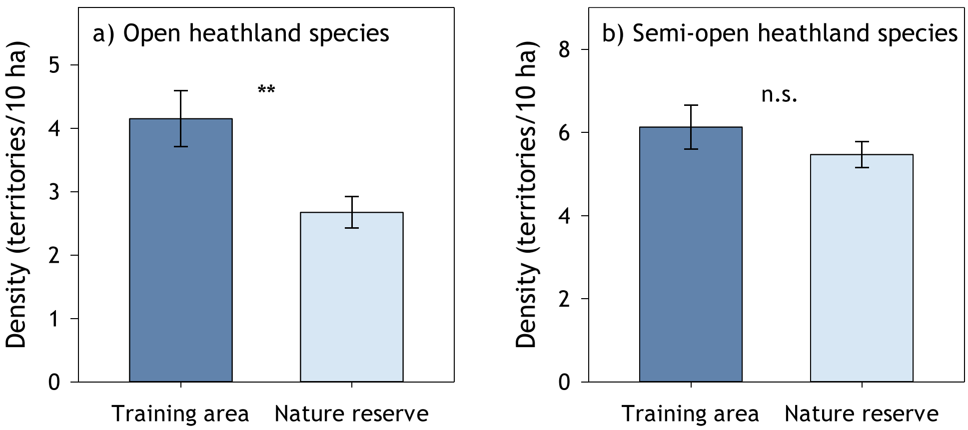

Fig. 3. Mean values (± SE) of overall territory density of open (a) and semi-open heathland (b) breeding bird species in plots in the training area ($n = 42$) and nature reserve ($n = 49$). Differences between the two subareas were tested by using Mann-Whitney U test. n.s. not significant, ** $P < 0.01$, *** $P < 0.001$.

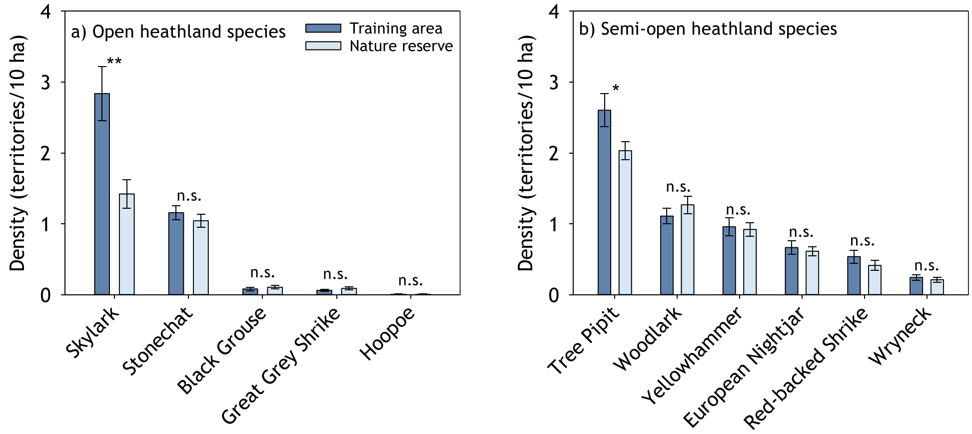

Fig. 4. Mean values (± SE) of species-specific territory density of open (a) and semi-open heathland (b) breeding bird species in plots in the training area ($n = 42$) and nature reserve ($n = 49$). Differences between the two subareas were tested by using Mann-Whitney U test. n.s. not significant, * $P < 0.05$, ** $P < 0.01$.

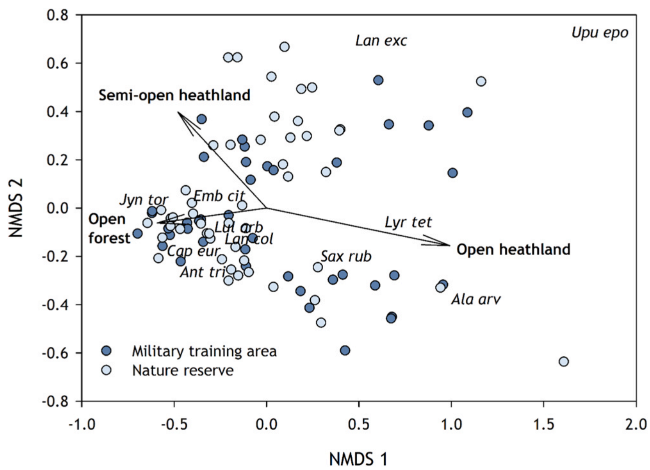

Fig. 5. NMDS ordination of plots in the training area ($n = 42$) and nature reserve ($n = 49$), and significant environmental variables as an overlay (P < 0.05). Four dimensions, stress: 0.09; Abbreviations of species consist of the first three letters of the scientific genus and species name (cf. Table A1). For further explanations see Section 2.4.

findings were very surprising, since in the nature reserve semi-open habitats strongly dominated and edges between heathland and woodland were soft. Accordingly, differences in the quality of the habitats very likely explain the disproportionally high densities of semi-open heathland species in the training area (cf. Fuller, 2012).

Suitable foraging habitats that exhibit a high abundance and accessibility of food strongly influence territory densities of breeding birds (Moorcroft et al., 2002; Benton et al., 2003; Fartmann et al., 2018). The chicks of all eleven heathland species detected in this study are insectivorous (Bauer et al., 2005). In a recent study, Fartmann et al. (2022b) showed that calcareous grasslands are characterized by a much higher abundance of breeding birds than heathlands. They argued that the deficit of base cations in the heathlands compared to calcareous grasslands likely constrained insect abundance and thus a limited food supply was probably one reason for the lower territory densities. Also within heathlands, similar observations have been made. A shortage of base cations causes a decrease in plant species richness (Maskell et al., 2010; Southon et al., 2013; Field et al., 2014) and has negative effects on invertebrates (Siepel et al., 2018), which in turn may also is responsible for declines in heathland bird populations (Vogels et al., 2013; Nijssen et al., 2017, 2023).

Acidification through nitrogen surplus from atmospheric deposition in naturally poorly buffered habitats, such as heathlands, leads to depletion of base cations (Horswill et al., 2008). This process is further accelerated by management measures that promote an increase in the nitrogen/phosphorus (N:P) ratio (Vogels et al., 2013, 2019). In the study area, current nitrogen deposition rates of 17–19 kg ha^{-1} year^{-1} still surpass the critical loads for heathlands of 5–15 kg ha^{-1} year^{-1} (Schaap et al., 2018; Bobbink et al., 2022). Heathland management in the past mainly focused on removing as much of this nitrogen as possible from the system without considering nutrient balances (Vogels et al., 2019). Management measures such as sod-cutting, choppering, mowing and grazing successfully dislodge excess nitrogen but also led to nutrient imbalances by removing both nitrogen and minerals such as phosphorus, calcium, magnesium and potassium equally (Härdtle et al., 2009; Vogels et al., 2019). While nitrogen is replenished very fast due to airborne deposition, the main source for phosphorus and other crucial minerals is weathering, which takes much more time to replenish (Vogels et al., 2013). Accordingly, these management measures led in the long term to heathland vegetation and soils that are depleted in mineral elements and have a high N:P ratio (Fottner et al., 2007; Vogels et al., 2019).

By contrast, fire does not generate nutrient imbalances, since ash deposit is rich in phosphorus, calcium, magnesium and potassium (Niemeyer et al., 2005; Walmsley et al., 2021). In the long run, nutrient balances therefore are much better preserved by fire than by traditional heathland management (Niemeyer et al., 2005; Vogels et al., 2013, 2019). In line with this, soil conditions strongly differed between the fire shaped training area and traditionally managed nature reserve. The mean values of phosphate, potassium, calcium and magnesium were higher in the training area than in the nature reserve. By contrast, mean N:P ratio was lower. Consequently, we explain the disproportionally high densities of birds of semi-open heathlands on the military training area at least partially by the positive effects of fire on insect food supply due to a better nutrient balance.

Moreover, the higher availability of calcium on the training area may additionally had direct positive effects on territory densities of heathland birds. Calcium is of crucial importance for the life cycle of birds, since it is indispensable for the formation of eggshells (Graveland and Drent, 1997). Calcium deficiency on a landscape scale therefore leads to lower productivity and reproductive fitness in birds (Graveland and Drent, 1997; Mänd et al., 2000; Nijssen et al., 2023). Moreover, recent research also suggests that birds occupy larger territories and hence have a lower territory density at the landscape scale in acidified landscapes charaterised by calcium shortage (Pintar and Olsen, 2021).

Fire management on the training area did not only favour the occurrence open habitat types and nutrient balance, it had also strong effects on the vegetation structure within the habitats. On average 16 % of the open habitats on the training area have been burnt per year. In contrast to prescribed burning, accidental fires due to military training activity are not restricted to the cool winter season. In particular, when these fires occur during dry summer periods they cause strong changes in habitat structure. Due to the dry conditions, the above ground vegetation, including the litter and moss layer, is often completely burnt after such fires creating habitats rich in bare ground (Schmidtmann, 2022). By contrast, prescribed burning in winter and sheep grazing do usually not destroy the moos layer and only partially the litter layer. The more intensive disturbance and more widespread occurrence of earlier successional stages in the training area compared to the nature reserve is also acknowledged by the lower NDVI in the prior. Except the Nightjar, all detected heathland bird species forage mostly on the ground (Bauer et al., 2005). The two heathland species that had higher densities on the training area, Skylark and Tree Pipit, are particularly known to require short turf or bare ground for successful hunting (Fartmann et al., 2018; Hološková et al., 2024; Schwarz et al., 2018; Kämpfer et al., 2022). Accordingly, we also explain the high territory densities in the training area by the short swards rich in bare ground that favour access to food resources and hence increase hunting success.

Another potential factor that influences heathland soil nutrient balances on military training areas is soil disturbance by the impact of artillery shells. We did not study this parameter since the main impact area of artillery shells in our study area was not substantially covered by heathland and therefore did not fulfil the criteria for our study plots (see Section 2.2). However, soil disturbance by the impact of artillery shells represents another factor that potentially could influence breeding bird densities in heathlands. This topic largely lacks scientific studies and could be an important avenue for future research.

In conclusion, fire was identified as the key driver of territory densities in characteristic heathland breeding birds. In comparison to heathlands that were traditionally managed, mainly by sheep grazing, fire management of heathlands on a military training favoured breeding birds in two ways: First, through preserving the nutrient balance, which very likely had positive effects on insect food supply and may also on the formation of eggshells. Second, by creating early successional stages rich in bare ground that allow an easy access to invertebrate food resources, which increases overall hunting success.

5. Implications for conservation

Based on our study, heathland management should aim at rejuvenating heathlands and creating early successional stages regularly without causing nutrient imbalances in the long run. Early seral stages in heathlands do not only foster characteristic breeding birds but also many other specialized heathland taxa (Schirmel et al., 2014; Wittig et al., 2020; Streitberger et al., 2021b; Fartmann et al., 2015, Fartmann et al., 2022a). The Heath Bush-cricket (*Gampsocleis glabra*), for example, is in Germany restricted to heathlands on military training areas that are rich in bare soil due to regular fires, including the studied training area (Brüggeshemke, 2025).

Consequently, we recommend an extension of the area and frequency of prescribed burning in a mosaic-like manner in heathlands, especially outside military training areas. To remove also the litter and moss layer, especially burning during dry periods in late summer is suggested. Since expertise in the application of prescribed burning and large-scale fire management is nowadays restricted to very few organisations and particularly military fire brigades in Central Europe, we recommend to intensify exchange of experience. To compensate for atmospheric nitrogen inputs by prescribed burning alone, a fire every five years is necessary (Niemeyer et al., 2005).

However, fire can have negative effects on certain types of heathland. Common Juniper (*Juniper communis*) is considered a keystone species in heathlands (Fartmann et al., 2022b) and Juniper heathland is protected by the EU Habitats Directive (EC (European Commission), 2013). The coniferous shrub is highly sensitive to burning (Mallik and Gimingham, 1985; Thomas et al., 2007). Consequently, Juniper heathland was almost absent on the training area while it covered large areas in the nature reserve. Accordingly, the application of fire should be avoided in this heathland type. In heathlands already threatened by grass encroachment burning alone can further promote grass dominance and heathland degradation (Jacquemyn et al., 2005). If combined with high-intensity follow up sheep grazing for several years, however, grass-encroached heathlands can be restored successfully into heathland with ericaceous shrub dominance (pers. comm. J. Vogels, 2024).

In areas where a nutrient deficiency already can be observed, liming by adding rock flour can help to reverse nutrient imbalances (Vogels et al., 2015). However, this has to be done with caution to avoid negative consequences on reproductive performance of arthropods (Vogels et al., 2021). Apart from in situ management measures it is therefore absolutely necessary to further decrease atmospheric nitrogen inputs in order to restore heathland biodiversity (Power et al., 2006).

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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

Table A1
Overview of detected characteristic breeding-bird species of heathlands, their classification as species of open heathland (OH; <5 trees per hectare) and semi-open heathland (SH; 5–20 trees per hectare), the number of territories in heathland plots in the training area (TA, $n = 42$), nature reserve (NR, $n = 49$) and in total ($N = 91$), the percentage of the population in Lower Saxony (LS) and the threat status in Lower Saxony. Population size and threat status in Lower Saxony: Krüger and Sandkühler (2021)

Common name	Scientific name	OH	SH	No. territories			Population LS (%)	Threat status
				TA	NR	Total		
Black Grouse	*Lyrurus tetrix*	✓	.	11	16	27	30.3	✓
European Nightjar	*Caprimulgus europaeus*	.	✓	84	91	175	8.0	✓
Great Grey Shrike	*Lanius excubitor*	✓	.	8	14	22	13.8	✓
Hoopoe	*Upupa epops*	✓	.	1	1	2	5.7	✓
Red-backed Shrike	*Lanius collurio*	.	✓	68	61	129	1.4	✓
Skylark	*Alauda arvensis*	✓	.	358	209	567	0.5	✓
Stonechat	*Saxicola rubicola*	✓	.	146	154	300	3.3	-
Tree Pipit	*Anthus trivialis*	.	✓	328	299	627	0.8	✓
Woodlark	*Lullula arborea*	.	✓	140	187	327	5.0	✓
Wryneck	*Jynx torquilla*	.	✓	31	32	63	12.6	✓
Yellowhammer	*Emberiza citrinella*	.	✓	121	136	257	0.1	✓

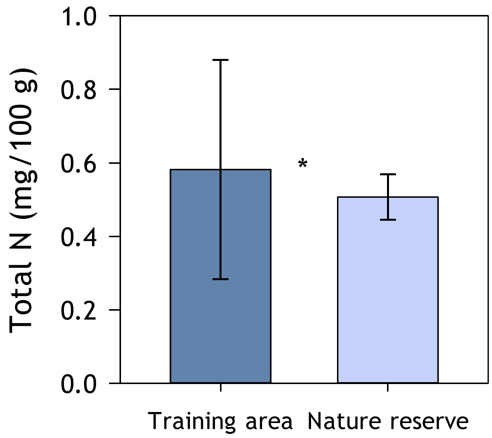

Fig. A1. Mean values (± SE) of total N in soil samples of heathland plots in the training area ($n = 10$) and nature reserve ($n = 10$). Differences between the two subareas were tested by using Mann-Whitney U test., * $P < 0.05$

Data availability

Data will be made available on request.

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