Breeding-bird assemblages of calcareous grasslands and heathlands provide evidence for Common juniper (*Juniperus communis*) as a keystone species

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A B S T R A C T

Relative to their biomass or abundance, keystone species have a disproportionate effect on many other organisms. Common juniper (*Juniperus communis*) is an evergreen shrub that has significant impacts on microclimate, composition of plant assemblages and herbivorous insects. However, *J. communis* is currently not considered a keystone species. The present study aims to provide deeper insights into the potential importance of juniper as a keystone species in its two main habitats: calcareous grasslands and heathlands. The response of breeding birds to the occurrence of Common juniper was highly similar in both habitat types. Plots with the presence of *J. communis* had a higher species richness and density of all and shrub-nesting species than absence plots. Additionally, presence plots exhibited a higher density (calcareous grasslands) or richness (heathlands) of threatened species than absence plots. Overall, the occurrence of scattered juniper shrubs boosted species richness and abundance of breeding birds. Responsible for this pattern were (i) the general increase in structural complexity and (ii) two (genuine) properties of the tall, evergreen shrub in particular: dense growth and prickly leaves. Due to the latter, the shrubs provide nesting sites that are strongly sheltered against predation and adverse weather. However, juniper shrubs have also an important function as song posts and perches for hunting. Additionally, the usually scattered distribution of juniper shrubs ensures a maximum territory density in calcareous grasslands and heathlands. Our study provides evidence that *J. communis* should be considered a keystone species in both habitat types of European conservation concern.

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1. Introduction

The recent biodiversity crisis is one of mankind's greatest challenges (Naeem et al., 2012; Cardoso et al., 2020). It jeopardizes ecosystem functioning and human well-being on our planet (Ripple et al., 2017; IPBES, 2019; Cardoso et al., 2020). Therefore, suitable conservation strategies are urgently needed to counteract the dramatic loss of species (Samways et al., 2020). However, budgets are tight and, hence, conservation has to focus on the most effective policies to foster biodiversity (Simberloff, 1998).

Relative to their biomass or abundance, keystone species have a disproportionate effect on many other organisms (Power et al., 1996; Simberloff, 1998). The concept of keystone species was originally introduced by Paine (1966). In his pioneer study, he observed that a starfish species selectively preyed on a certain mussel species. Thus, the starfish inhibited the dominance of the bivalve and favoured coexistence of a variety of other organisms. Since then keystone species have been described across all trophic levels, including carnivores, herbivores, detritivores and primary producers (see Hernández-Agüero et al., 2022). Due to their outstanding importance for ecosystem functioning, Jordán (2009) claimed that conservation biology needs to devote more attention to identifying and conserving keystone species globally.

Among primary producers, in particular several tree species have been determined as keystone species so far (Tews et al., 2004; Manning et al., 2006; Hernández-Agüero et al., 2021). Prominent examples are scattered trees in African savannas such as acacia (*Acacia* spp.) or solitary Holm oaks (*Quercus ilex*) in Iberian wood pastures. They alter microclimatic conditions, nutrient cycling and composition of plant assemblages within the ecosystem. Moreover, they increase structural heterogeneity and provide food sources, shelter and breeding habitats for a large number of animal species.

The genus *Juniperus* is the most diverse of the conifers, containing more than 70 evergreen shrub and tree species (Adams, 2014). Among *Juniperus*, Common juniper (*Juniperus communis*) exhibits the largest range and is widely distributed across the Holarctic (Mao et al., 2010; Adams, 2014). The shrub or small tree has a dense, often columnar growth and very prickly leaves (Nebel et al., 1993; Thomas et al., 2007; Fig. 1c). Previous studies revealed that *J. communis* has significant impacts on microclimate and the composition of plant assemblages (Stoutjesdijk and Barkman, 1992; Thomas et al., 2007). For example, less than 20% of the local precipitation reaches the ground under the shrubs or in the shady north-facing zone adjacent to the shrubs pleurocarpous mosses are often dominant. Moreover, it is characterised by a specific fauna of herbivorous insects, in particular moths (Thomas et al., 2007). Nevertheless, most research on the interactions between juniper and wild animals has focused on frugivorous birds, in particular Thrushes (*Turdus* spp.) that feed on the fleshy fruits and disperse the juniper seeds (García et al., 2001; García and Ortiz-Pulido, 2004; Thomas et al., 2007). However, *J. communis* is currently not considered a keystone species.

Birds are excellent indicators for environmental conditions and overall biodiversity of a habitat (Reif et al., 2016, 2020). In general, habitat heterogeneity is known to be an important driver of species richness and abundance of breeding birds (Benton et al., 2003; Farwell et al., 2020; Brüggeshemke et al., 2022). In particular, birds depend on (i) breeding habitats that provide shelter against nest

Fig. 1. Photographs of typical stands of juniper-rich calcareous grasslands (a) and heathlands (b) as well as juniper shrub (*Juniperus communis*) (c). Photographs: T. Fartmann.
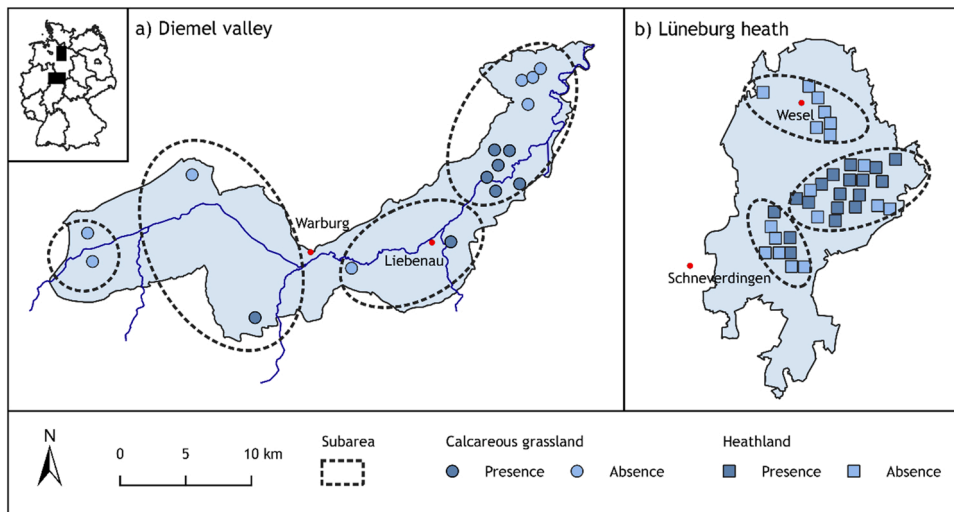
Fig. 2. Location of the two study areas Diemel valley (a) and Lüneburg Heath (b) in Germany.

predators and adverse weather and (ii) suitable foraging habitats with high prey accessibility (Moorcroft et al., 2002; Benton et al., 2003; Fartmann et al., 2018).

Only recently, Brüggeshemke et al. (2022) determined in a comparative study on breeding-bird assemblages of calcareous and mesic grasslands that the area of calcareous grasslands with occurrence of *J. communis* was an important predictor of species richness and abundance of breeding birds in calcareous grasslands. However, local climate also had a strong effect since the investigation was conducted across an elevation and, hence, climate gradient. The present research is a follow-up of this study and aims to provide deeper insights into the potential importance of *J. communis* as a keystone species. In contrast to Brüggeshemke et al. (2022), we now controlled for the effects of local climate by choosing two study areas with low within climatic variability. Moreover, we considered the two main habitats of Common juniper in Central Europe, calcareous grasslands and heathlands (Fig. 1) (Ssymank et al., 2021). Both habitat types are of outstanding importance for biodiversity conservation, and thus they are protected under the EU Habitats Directive. We compared environmental conditions and composition of breeding-bird assemblages in plots with the presence and absence of *J. communis*. Based on our findings, we derive recommendations for further management of calcareous grasslands and heathlands.

2. Material and methods

2.1. Study species

Common juniper (*Juniperus communis*) is an evergreen, light-demanding gymnosperm shrub or small tree (Nebel et al., 1993; Thomas et al., 2007; Fig. 1c). It has the greatest distribution range of any juniper species, including large areas of the Holarctic (Mao et al., 2010; Adams, 2014). Within Europe, it is widely distributed across the northern and central part but populations further south only occur scattered across the mountain ranges (García et al., 2001). Common juniper has a dense and often columnar growth with very prickly leaves (Nebel et al., 1993; Thomas et al., 2007; Abb. 1c). Although not very palatable (Borchard et al., 2011), juniper is grazed by small and large mammals when food is short, particularly in winter (Thomas et al., 2007). Reproduction appears mainly by seeds on open soil, but rooting of decumbent branches may also occur in some populations (Thomas et al., 2007). Frugivorous birds, in particular thrushes (*Turdus* spp.), are the main dispersers of the seeds (García et al., 2001).

In Central Europe, grazed calcareous grasslands and heathlands are the most important habitats of Common juniper (Ssymank et al., 2021). However, due to agricultural intensification and abandonment, both habitats have strongly declined (Fartmann et al., 2021) and populations of *J. communis* are now often localized and threatened (Thomas et al., 2007). Consequently, juniper formations on calcareous grasslands and heathlands (EU Code 5130) are protected by the EU Habitats Directive (Ssymank et al., 2021).

2.2. Study area

The study was carried out in two ancient cultural landscapes: (i) the middle and lower Diemel valley (hereinafter referred to as Diemel valley; 100–350 m a.s.l.; 51°29'N/8°53'E and 51°38'N/9°25'E; Central Germany) and (ii) the Lüneburg heath (40–169 m a.s. l.; 53°01'N/9°51'E and 53°16'N/9°56'E; Northern Germany) (Fig. 2). Both study areas are characterised by a suboceanic climate.

The Diemel valley has an area of about 315 km^2 along the border between the federal states of North Rhine-Westphalia and Hesse. It covers ~660 ha of calcareous grasslands, which represents the most important stronghold of this grassland type in the northern half

Table 1

Overview of sampled environmental variables (mean ± standard error [SE]; N_{Calc} = 16, N_{Heath} = 36). Differences between the groups were analysed using GLMM (Poisson error structure) with 'subarea' as a random factor (cf. Material and methods). Significant differences are indicated by bold type. n.s. not significant, * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$.

Parameter	Calcareous grassland		P	Heathland		P
	Presence	Absence		Presence	Absence	
a) Local climate						
Elevation (m a.s.l.)	212 ± 12	243 ± 10	n.s.	100 ± 5	89 ± 5	n.s.
Breeding season temperature (°C)	12.8 ± 0.1	12.6 ± 0.1	n.s.	12.4 ± 0.3	12.4 ± 0.4	n.s.
Breeding season precipitation (mm)	383.6 ± 6.1	388.4 ± 4.7	n.s.	410.1 ± 2.2	410.0 ± 2.8	n.s.
b) Habitat composition (ha)						
Arable land	0.33 ± 0.12	0.26 ± 0.18	n.s.	.	.	.
Improved grassland	0.02 ± 0.01	0.37 ± 0.27	n.s.	.	.	.
Semi-natural mesic grassland	0.26 ± 0.12	0.60 ± 0.24	n.s.	.	.	.
Semi-natural calcareous grassland						
Open	**0.09 ± 0.09**	**1.63 ± 0.65**	*	.	.	.
Blackthorn-rich (*Prunus spinosa*)	**0.00 ± 0.00**	**1.04 ± 0.39**	*	.	.	.
Juniper-rich (*Juniperus communis*)	**2.92 ± 0.35**	**0.00 ± 0.00**	***	.	.	.
Mire and wet heathland	.	.	.	0.02 ± 0.01	0.06 ± 0.03	n.s.
Dry grassland and bare ground	.	.	.	0.00 ± 0.00	0.05 ± 0.04	n.s.
Heathland						
Open	.	.	.	**0.13 ± 0.09**	**3.91 ± 0.34**	***
Semi-open	.	.	.	0.27 ± 0.12	1.03 ± 0.36	n.s.
Juniper-rich	.	.	.	**4.32 ± 0.21**	**0.00 ± 0.00**	***
Hedge and copse	**0.20 ± 0.11**	**0.66 ± 0.13**	*	0.04 ± 0.02	0.04 ± 0.03	n.s.
Open and pioneer forest	0.29 ± 0.14	0.22 ± 0.18	n.s.	0.06 ± 0.04	0.00 ± 0.00	n.s.
Closed forest	**0.87 ± 0.36**	**0.21 ± 0.09**	**n.s.**	0.02 ± 0.01	0.00 ± 0.00	n.s.
c) Habitat heterogeneity						
Shannon habitat diversity	1.03 ± 0.11	1.24 ± 0.22	n.s.	0.37 ± 0.09	0.34 ± 0.07	n.s.

of Germany (Fartmann, 2004). The surrounding matrix is dominated by patchworks of woodland, improved grassland and arable fields (Brüggeshemke et al., 2022). Mean annual precipitation is 734 mm, and average annual temperature is 8.8 °C (long-term mean: 1981–2010; weather station Warburg [240 m a.s.l.]; German Meteorological Service, 2021).

The Lüneburg heath has an area of about 234 km² and comprises the eponymous nature reserve in the centre of Lower Saxony. It contains ~4000 ha of *Calluna* heathlands, which is the largest heathland outside military training areas in Germany (Schellenberg and Bergmeier, 2014). The heathlands are embedded in a matrix of non-native coniferous forests (Cordes et al., 1997; Keienburg and Prüter, 2006). Average annual precipitation is 815 mm, and mean annual temperature is 9.0 °C (long-term mean: 1981–2010; weather station Soltau [75 m a.s.l.]; German Meteorological Service, 2021).

2.3. Sampling design

2.3.1. Plots

We studied the two main habitats of Common juniper in Central Europe: calcareous grasslands (Diemel valley) and heathlands (Lüneburg heath) (Fig. 2). We randomly selected square-shaped plots with a size of 5 ha and dominant cover (cover >50%) of calcareous grasslands (N = 16) and heathlands (N = 36), respectively (hereinafter referred to as calcareous grassland and heathland plots, respectively) (cf. Fartmann et al., 2018; Brüggeshemke et al., 2022; Kämpfer et al., 2022). For both habitat types, we compared plots with the presence and absence of juniper (hereinafter referred to as presence and absence plots, respectively). Presence plots had a cover of at least 50% of juniper-rich calcareous grasslands and heathlands, respectively. For each of the two habitat types, we applied a balanced design; (i.e.) the ratio between presence and absence plots was 1: 1.

2.3.2. Environmental conditions

We used digital elevation models with a spatial resolution of 4 ha to calculate the mean elevation of the plots (Geobasis NRW, 2021) (Table 1). Climate data were derived from grid maps with a spatial resolution of 1 km² containing information on long-term averages of temperature and precipitation during the breeding season (March–August) (period 1981–2010; German Meteorological Service, 2021).

For each plot, we recorded the habitat composition in the field according to the German habitat classification scheme (scale: 1: 1000; 14 major habitat types [Table 1]; Finck et al., 2017). Later, we digitised the habitat maps using ArcGIS 10.5. Additionally, we used these data to calculate the Shannon habitat diversity (H') of each plot as a measure of habitat heterogeneity (Fartmann et al., 2018; Schwarz et al., 2018):
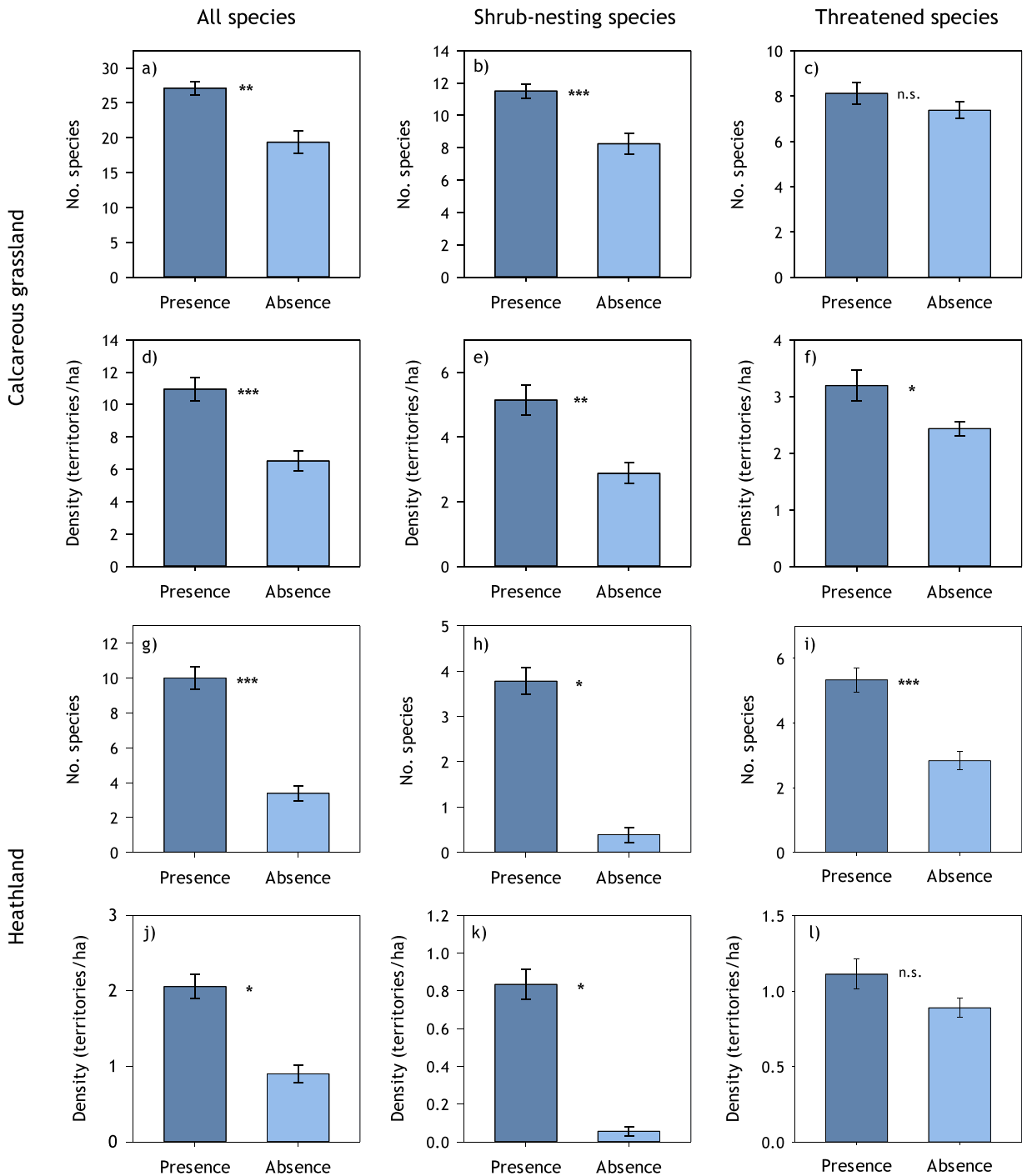
$$H' = -\sum_i p_i \ln p_i$$

Fig. 3. Mean values (± SE) of species richness and territory density of all (a, d, g, j), shrub-nesting (b, e, h, k) and threatened (c, f, i, l) breeding-bird species in plots of calcareous grasslands (*N* = 16) and heathlands (*N* = 36). Differences between the groups were analysed using GLMM (Poisson error structure) with 'subarea' as a random factor. a) Z = 3.199, b) Z = 2.059, c) Z = −0.397, d) Z = 2.773, e) Z = 2.006, f) Z = −0.108, g) Z = −0.057, h) Z = −0.603, i) Z = 3.65, j) Z = 0.66, k) Z = −0.251, l) Z = 0.712. n.s. not significant, *P < 0.05, **P < 0.01, ***P < 0.001.

with $p_i = n_i / N$ where N is the overall area of all habitat types per plot and n_i is the area of the respective habitat type in the plot.

2.3.3. Breeding-bird surveys

We mapped breeding-bird territories in all plots from the beginning of April to July (Fischer et al., 2005). Plots of calcareous grasslands were surveyed in 2019 and those of heathlands in 2021. 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 at each plot early in the morning (between sunrise and 10 a.m.) with a period of at least 10 days between each visit (Fartmann et al., 2018; Fumy and Fartmann, 2021). During each survey, we followed a non-linear route covering the whole plot and noted all signs of territorial behaviour, such as chasing, singing or visual display, on a map (scale 1:1000) (Bibby et al., 2000). 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 (Schmidt et al., 2022).

For further analyses, we used (i) all, (ii) shrub-nesting and (iii) threatened species of breeding birds as response variables. Shrub-nesting species were classified according to Kamp et al. (2021) and threatened ones (including near-threatened species) in accordance with the regional red-data books of breeding birds (Diemel valley: Wolf and Widdig, 2016; Grüneberg et al., 2017; Lüneburg heath: Krüger and Nipkow, 2015).

2.4. Statistical analysis

We performed all statistical analyses using R 3.6.1 (R Core Team, 2021). In order to account for possible spatial autocorrelation, both study areas were divided into subareas according to their landscape configuration (Fig. 2; Fumy and Fartmann, 2021; Brügge-shemke et al., 2022). Subareas had a mean size ($\pm$ SE) of 80.25 ± 26.02 km^2 in the Diemel Valley and 34.00 ± 8.08 km^2 in the Lüneburg heath.

To detect significant differences in environmental parameters (Table 1) as well as in species richness and territory density between presence and absence plots (Fig. 3), we applied generalised linear mixed-effects models (GLMM) (R packages lme4, Poisson error structure; Bates et al., 2020) with 'subarea' as a random factor (Crawley, 2007). 'Presence/absence of juniper' served as a nominal fixed factor and the analysed parameters as dependent variables. We examined the overall effect of juniper occurrence on the environmental parameters by comparing the full models with reduced models without 'presence/absence of juniper' as the fixed factor (intercept-only models) and by applying likelihood-ratio tests (type III tests).

To identify indicator species of presence and absence plots in both calcareous grasslands and heathlands, indicator-species analyses (ISA) were carried out (Dufrêne and Legendre, 1997; Cáceres and Jansen, 2016). The ISA uses the relative abundance and relative frequency of a species to estimate the strength of its association with presence/absence of juniper in both habitat types. The higher the indicator value (IV; scaled from 0 to 1) of a species was, the more abundant and the more frequently it occurred compared to other species in the focal habitat type. The statistical significance of the relationship was tested by permutation tests (4999 permutations).

Non-metric multidimensional scaling (NMDS, function metaMDS, package vegan, Oksanen et al., 2019) was applied to detect differences in bird assemblages among calcareous grasslands and heathlands, respectively, with presence/absence of juniper. Bray-Curtis was used as a distance measure and maximum random starts was set at 500 to search for a stable solution. Species occurring in less than 15% of the plots (calcareous grassland: > 2 plots; heathlands: > 5 plots) were excluded from the NMDS. Environmental variables with significant impact ($P < 0.05$) were used as an overlay (function envit, package vegan, Oksanen et al., 2019]). We only used non-intercorrelated variables (function ggpairs, Spearman correlation coefficient [r_s] $|r_s| < 0.5$, package GGally, Schloerke et al., 2021). For calcareous grasslands the following variables were excluded from the NMDS due to intercorrelations: elevation (temperature: $r_s = -0.77$), open semi-natural calcareous grassland (juniper-rich semi-natural calcareous grassland: $r_s = -0.58$), blackthorn-rich semi-natural calcareous grassland (juniper-rich semi-natural calcareous grassland: $r_s = -0.69$; hedge and copse: $r_s = 0.63$; Shannon habitat diversity: $r_s = 0.63$) and hedge/copse (juniper-rich semi-natural calcareous grassland: $r_s = -0.55$) (Tab. A1). In the heathland NMDS the following variables were excluded: temperature (elevation: $r_s = -0.86$; precipitation: -0.92; mire/wet heathland: 0.53), precipitation (elevation: $r_s = 0.89$; temperature: $r_s = -0.92$; mire/wet heathland: $r_s = -0.56$), open heathland (juniper-rich heathland: $r_s = -0.80$) and Shannon habitat diversity (semi-open heathland: $r_s = 0.65$) (Table A2).

3. Results

3.1. Environmental conditions

Local climate and habitat heterogeneity did not differ between presence and absence plots either in calcareous grasslands or in heathlands (Table 1). However, plots of calcareous grasslands were much more heterogeneous than those of heathlands. Shannon habitat diversity was more than two and a half times higher in both presence and absence plots of calcareous grasslands compared with those of heathlands.

By contrast, habitat composition strongly differed between presence and absence plots in both calcareous grasslands and heathlands (Table 1). In calcareous grasslands, presence plots were dominated by juniper-rich calcareous grasslands. Within these juniper-

Table 2

Results of indicator species analysis (ISA) (Dufrêne and Legendre, 1997; Cáceres and Jansen, 2016) for plots of calcareous grasslands ($N = 16$) and heathlands based on territory densities ($N = 36$). IV = indicator value; relative abundance/relative frequency (percentage of plots within each group of calcareous grassland and heath with occurrence of the species). Shrub-nesting species (SN): Kamp et al. (2021). Threat status (TS): Diemel valley – Wolf and Widdig (2016), Grüneberg et al. (2017); Lüneburg heath – Krüger and Nipkow (2015); threat status within each study area is only displayed if the species was detected in the respective study area. Grey-hatched: species are indicator species for this group; bold-type values: species are threatened in the respective study area. n.s. not significant, * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$.

Species	SN	Calcareous grassland					Heathland				
		TS	IV	*P*	Presence	Absence	TS	IV	*P*	Presence	Absence
Blackbird (*Turdus merula*)	✓	.	64.4	*	64/100	36/100	.	38.9	***	100/39	0/0
Chaffinch (*Fringilla coelebs*)	✓	.	73.5	**	74/100	26/88	.	55.6	***	100/56	0/0
Tree sparrow (*Passer montanus*)	.	✓	75.0	**	0/0	**100/75**	.	.	.	./.	./.
Tree pipit (*Anthus trivialis*)	.	✓	53.0	n.s.	61/88	39/75	✓	53.7	*	64/83	36/50
Skylark (*Alauda arvensis*)	.	✓	45.0	n.s.	10/13	90/50	✓	86.2	***	9/28	**91/94**
Greenfinch (*Carduelis chloris*)	✓	.	90.0	**	90/100	10/13	.	59.1	***	97/61	3/6
Yellowhammer (*Emberiza citrinella*)	✓	✓	53.8	n.s.	54/100	46/100	✓	79.3	***	95/83	5/11
Lesser whitethroat (*Sylvia curruca*)	✓	✓	68.2	*	68/100	32/75	.	22.2	n.s.	100/22	0/0
Woodlark (*Lullula arborea*)	.	✓	16.7	n.s.	33/13	67/25	✓	48.1	*	67/72	33/33
Red-backed shrike (*Lanius collurio*)	✓	✓	75.9	*	76/100	24/38	✓	84.8	***	95/89	5/6
Willow warbler (*Phylloscopus trochilus*)	✓	✓	61.0	n.s.	61/100	39/100	.	27.8	*	100/28	0/0
Long-tailed tit (*Aegithalos caudatus*)	✓	.	75.8	**	87/88	13/25	.	11.1	n.s.	100/11	0/0
Song thrush (*Turdus philomelos*)	✓	.	67.6	*	68/100	32/75	.	5.6	n.s.	100/6	0/0
Chiffchaff (*Phylloscopus collybita*)	✓	.	61.2	*	61/100	39/100	.	5.6	n.s.	100/6	0/0

rich stands *J. communis* had a mean cover ±SE of 22.1 ± 3.8%. Additionally, the area of closed forests was greater in presence than in absence plots (Table 1). By contrast, in absence plots, open calcareous grasslands had the largest area, followed by blackthorn-rich calcareous grasslands. Moreover, hedges and copses had a larger extension in absence than in presence plots.

In heathlands, most of the entire presence plot was covered by juniper-rich heathlands (Table 1), exhibiting a mean cover ±SE of *J. communis* of 23.3 ± 2.9%. By contrast, in absence plots, open heathlands clearly dominated (Table 1).

3.2. Relationship between environmental conditions and breeding-bird assemblages

Altogether, we detected 55 species of breeding birds in the 16 calcareous grassland plots and 45 in the 36 heathland plots (Table A3). In plots of calcareous grasslands, 20 of these species were threatened, and in heathland plots, this was true for 21 species. The most common species in calcareous grassland plots (i.e. > 40 territories in all plots) were in decreasing order: Yellowhammer (*Emberiza citrinella*), Blackcap (*Sylvia atricapilla*), Chiffchaff (*Phylloscopus collybita*), Blackbird (*Turdus merula*) and Willow warbler (*Phylloscopus trochilus*). The dominant threatened species (i.e. > 21 territories) were in declining frequency: Yellowhammer, Willow warbler, Common linnet (*Carduelis cannabina*) and Lesser whitethroat (*Sylvia curruca*). In heathland plots, the most frequent species (i. e. > 14 territories) were with decreasing order: Skylark (*Alauda arvensis*), Tree pipit (*Anthus trivialis*), Red-backed shrike (*Lanius collurio*), Yellowhammer and Greenfinch (*Carduelis chloris*). Except Greenfinch, all are considered threatened.

Species richness and density of all three response variables were much higher (more than 2.5 and 5 times, respectively) in presence and absence plots of calcareous grasslands than in those of heathlands (Fig. 3). The difference was smaller only for the number of threatened species in presence plots. Nevertheless, the response of breeding birds to the occurrence of Common juniper was highly similar in both habitats. Presence plots in calcareous grasslands and heathlands had a higher species richness and density of all and shrub-nesting species compared with absence plots. Additionally, presence plots exhibited a higher density (calcareous grasslands) or richness (heathlands) of threatened species than absence plots.

Altogether, we identified 14 indicator species; of these, shrub-nesting birds clearly dominated with ten species. All indicator species were typical of presence plots—except two threatened species, Tree sparrow (*Passer montanus*) (calcareous grasslands) and Skylark (heathlands), which were characteristic of absence plots (Table 2). Blackbird, Chaffinch (*Fringilla coelebs*), Greenfinch and Red-backed shrike were indicative of presence plots in both calcareous grasslands and heathlands. The latter is considered threatened in both study areas. Lesser whitethroat, Long-tailed tit (*Aegithalos caudatus*), Song thrush (*Turdus philomelos*) and Chiffchaff were further indicator species of presence plots in calcareous grasslands. The former is a threatened species in the study area. The three regionally threatened
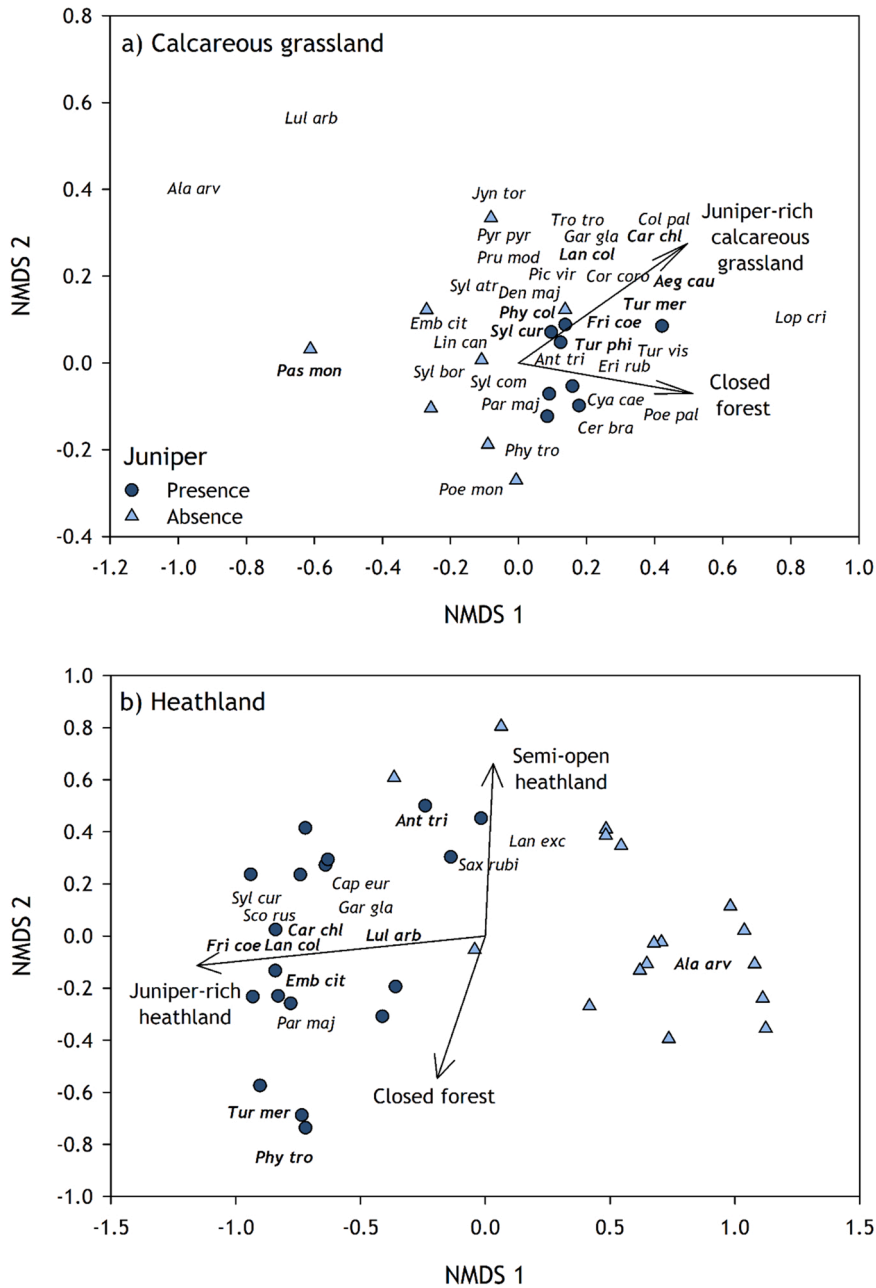
Fig. 4. NMDS ordination for plots of calcareous grasslands (a) ($N = 16$) and heathlands (b) ($N = 36$), and significant environmental variables as an overlay ($P < 0.05$). a) Four dimensions, stress: 0.06; b) four dimensions, stress: 0.08. Indicator species for plots with presence and absence of juniper are highlighted in bold type (cf. Table 2). Abbreviations of species consist of the first three letters of the scientific genus and species name (cf. Table A3). For further explanations see Section 2.4.

species Tree pipit, Yellowhammer and Woodlark (*Lullula arborea*) as well as Willow warbler were identified as indicator species of presence plots in heathlands.

In calcareous grasslands and heathlands, plots with presence and absence of juniper were clearly separated along the first NMDS axis (Fig. 4). In calcareous grasslands, plots with presence of juniper were correlated with the cover of juniper-rich calcareous grassland, which was negatively correlated with the cover of open and blackthorn-rich calcareous grasslands as well as hedges/copses (Table A1), and the cover of closed forest (Fig. 4a). In heathlands, plots with presence of juniper were correlated with the cover of juniper-rich heathland, which was negatively correlated with the cover of open heathland (Table A2, Fig. 4b). In both, calcareous grasslands and heathlands, most species had a strong affinity to presence plots and only a few species were associated with absence plots. Moreover, both NMDS confirm the preferences of the indicator species detected by the indicator species analyses.

4. Discussion

Although our study revealed strong differences in environmental conditions and assemblage composition between calcareous grasslands and heathlands, the response of breeding birds to the occurrence of Common juniper was highly similar in both habitat types. In calcareous grasslands and heathlands, presence plots had a higher species richness and density of all and shrub-nesting species than absence plots. Additionally, presence plots exhibited a higher density (calcareous grasslands) or richness (heathlands) of threatened species than absence plots. Moreover, all but two of the 14 indicator species were typical of presence plots.

Due to their base-rich soils and high habitat heterogeneity, calcareous grasslands are hotspots of plant and insect diversity (Wallis De Vries et al., 2002; Krämer et al., 2012; Bonari et al., 2017; Löffler et al., 2020; Helbing et al., 2021). Recently, Brüggeshemke et al. (2022) showed that they are also key habitats for many bird species. Heathlands are characterised by a specific flora and insect fauna, too (Streitberger et al., 2021a; 2021b; Fartmann et al., 2022). However, heathlands have naturally poorly buffered soils, and the shortage of base cations constrains species richness of vascular plants and also limits the number of species and abundance of insects (Vogels et al., 2017, 2021). This is especially true for heathlands that are characterised by further loss of base cations such as phosphorus due to acidifying deposition (NO_x, NH_y, SO_x) or intensive heathland management such as sod cutting (Härdtle et al., 2009; Vogels et al., 2021). Both apply to the study area Lüneburg heath (Härdtle et al., 2009). In our study, Shannon habitat diversity was more than two and a half times higher in presence and absence plots of calcareous grasslands compared with those of heathlands. Species richness and density of all, shrub-nesting and threatened species were also much higher (>2.5 and 5 times, respectively) in plots of calcareous grasslands than in those of heathlands; the difference was smaller only for the number of threatened species in presence plots. Habitat heterogeneity ranks among the most important drivers of breeding-bird assemblage composition (Benton et al., 2003; Farwell et al., 2020; Brüggeshemke et al., 2022). Therefore, we attribute the much higher species richness and density of breeding birds in calcareous grasslands compared with heathlands especially to the higher habitat heterogeneity of the former. However, the deficiency of base cations likely constrains insect abundance in the studied heathlands. Since insects are an important food source for many bird species, at least for their chicks (Newton, 2017), this may additionally hamper higher species richness and abundance of breeding birds in heathlands.

The study of Brüggeshemke et al. (2022) has demonstrated that the area of juniper-rich calcareous grasslands fosters overall species richness and abundance of breeding birds in calcareous grasslands. Our study now provides further insights into the importance of scattered juniper shrubs for breeding birds in calcareous grasslands and, for the first time, also in heathlands. Despite the general differences in environmental conditions and composition of bird assemblages, the effects of juniper presence were highly similar for both habitat types. Occurrence of *J. communis* favoured species richness and density of all and shrub-nesting species. Additionally, the availability of juniper had beneficial effects on threatened species by increasing their density (calcareous grasslands) and species richness (heathlands). Moreover, presence plots were characterised by a highly specific breeding-bird assemblage, harbouring 86% of the indicator species detected in our study. Shannon habitat diversity based on the cover of habitat types did not differ between presence and absence plots in either calcareous grasslands or in heathlands. However, we have to consider that the index is a rather rough measure of habitat heterogeneity because it does not reflect the sometimes highly three-dimensional structural diversity within a certain habitat type (Cooper et al., 2020). In our study, *J. communis* shrubs grew usually scattered (own observation, cf. Fig. 1c) and had a mean cover of less than 25% within juniper-rich calcareous grasslands and heathlands. Consequently, occurrence of juniper strongly increased the structural complexity in both habitat types, which, as already mentioned, boosts species richness and abundance of breeding birds. Absence plots in calcareous grasslands were also characterised by a higher share of shrub-rich parts (i.e., blackthorn-rich calcareous grasslands and hedges/copses), but species richness and abundance of breeding birds were nevertheless clearly lower. Accordingly, it is not only the general increase of the three-dimensional structural diversity due to the occurrence of shrubs but rather the genuine properties of *J. communis* that have beneficial effects on the assemblages of breeding birds.

Nest predation is the main cause of reproductive failure in most bird species (Götmark et al., 1995). Therefore, birds often choose concealed sites for nesting. Under the temperate climate of Central Europe, broad-leaved woody plants clearly dominate over ever-green ones (Ellenberg and Leuschner, 2010). Nonetheless, Gatter and Mattes (2018) pointed out that many shrub-nesting bird species disproportionately often use evergreen woody plants for breeding. They explain this pattern by citing the higher degree of concealment

of the nest in comparison with broad-leaved woody plants in general and particularly in early spring, when the latter are leafless. Moreover, they argue that the more balanced microclimate within evergreen woody plants also enhances survival of the offspring. Both assumptions are highly true for juniper shrubs. Juniper belongs to those evergreen woody plants with the densest growth and most prickly leaves (Thomas et al., 2007). This results in a very high concealment of the nests (Brüggeshemke et al., 2022) and, even in case of nest detection, strongly hampers access of predators larger than the breeding birds. Nests inside juniper are also strongly protected against rain- and snowfall since less than 20% of the local precipitation reaches the ground under the shrubs, which is a very low throughfall even among conifers (Stoutjesdijk and Barkman, 1992). Additionally, temperature amplitude and wind speed are sharply reduced within juniper shrubs.

Juniper is a light-demanding species that mainly reproduces by seeds on open soil (Thomas et al., 2007). As a result, seedling establishment is often aggregated in the most open areas away from older shading juniper shrubs, although these microsites are characterised by the lowest seed deposition by birds. Such a reproduction strategy leads to groups of scattered shrubs across a habitat. Additionally, conservation management in both habitat types aims to create open grasslands and heathlands with interspersed juniper shrubs due to reasons of landscape aesthetics (e.g. Cordes et al., 1997; Keienburg and Prüter, 2006; own observation).

Open grasslands and heathlands serve as important nesting habitats for ground-breeding species and as the major foraging habitats of most birds (cf. Brüggeshemke et al., 2022). Hence, even for some of the ground-nesting birds, juniper shrubs are also important song posts and hunting perches. Accordingly, the scattered distribution of juniper shrubs ensures a maximum exploitation of the habitat for territory establishment, nesting and foraging in birds that (i) depend on taller shrubs as song posts (e.g. Tree pipit and Woodlark; Fartmann et al., 2018; Schwarz et al., 2018; Kämpfer et al., 2022), (ii) are shrub-nesting and/or (iii) use shrubs as hunting perches (e.g. Red-backed shrike; Stoos et al., 2017).

Blackthorn (*Prunus spinosa*) shrubs covered large areas in absence plots of calcareous grasslands. However, they did not have the same beneficial effects on bird assemblages as juniper. Due to its clonal growth, blackthorn usually builds large thickets (Ellenberg and Leuschner, 2010), which should also secure a certain protection against predation although the shrub is broad-leaved. However, Stoos et al. (2017) observed for the Red-backed shrike that the accessibility of food resources rather than the amount of shrubs limits breeding-territory densities. In most species of open habitats, patches of low-growing vegetation and bare ground are the main foraging habitats (Moorcroft et al., 2002; Tagmann-Ioset et al., 2012; Kämpfer and Fartmann, 2019; Fumy and Fartmann, 2021). Therefore, we argue that not only the characteristics of the individual juniper plants but also their scattered distribution in the open grasslands and heathlands were responsible for the high species richness and abundance of breeding birds.

In calcareous grasslands and heathlands, plots with presence and absence of juniper were clearly separated along the first NMDS axis. Overall, both NMDS confirm the preferences of the indicator species detected by the indicator species analyses. Among the 12 indicator species of the presence plots, the vast majority (83%) were shrub-nesting ones. At least three of them, Blackbird, Song thrush and Chiffchaff, prefer evergreen over broad-leaved woody plants for breeding (Gatter and Mattes, 2018). Another three species, Greenfinch, Lesser whitethroat and Long-tailed tit, are even strongly associated with juniper if the shrub species is present in their habitat (Assmann and Kratochwil, 1995; Hölzinger, 1997, 1999; Gatter and Mattes, 2018; Brüggeshemke et al., 2022). These figures additionally underpin the prime importance of juniper shrubs as sheltered nesting habitats for birds.

Two of the indicator species of presence plots, Tree pipit and Woodlark, are ground-nesting birds that depend on bare ground or low-growing vegetation for foraging (Burton, 2007; Fartmann et al., 2018; Bosco et al., 2019; Kämpfer et al., 2022). However, they require adjacent tall shrubs or trees as song posts in their territories. In heathlands, such structures were largely lacking in absence plots in comparison with presence plots. Here, juniper was the clearly dominating woody plant. Accordingly, we explain the preference of both bird species for presence plots mainly by the value of juniper as a song post. The species indicative of absence plots in calcareous grasslands (the cavity-breeding Tree sparrow) and heathlands (the ground-breeding Skylark) are known to prefer semi-open habitats with some hedges or copses and large open habitats, respectively (Bauer et al., 2005). In our study, the absence plots provided exactly such environmental conditions.

Previous research has revealed that Common juniper (i) has strong effects on microclimate, in particular on temperature, humidity and wind speed (Stoutjesdijk and Barkman, 1992), (ii) acts as a nurse plant for other plant species by ameliorating or changing environmental conditions (Stoutjesdijk and Barkman, 1992; Thomas et al., 2007), (iii) is characterised by a specific fauna of herbivorous insects, in particular moths (Thomas et al., 2007) and (iv) supplies important food resources for frugivorous birds, in particular thrushes (*Turdus* spp.) in their wintering areas or during migration, and small mammals (García et al., 2001; García and Ortiz-Pulido, 2004; Thomas et al., 2007). Our study now provided consistent evidence that scattered juniper shrubs foster species richness and density of all and shrub-nesting bird species, and partly also threatened species. This was the case for the two main habitats of Common juniper in Central Europe, calcareous grasslands and heathlands. Consequently, we recommend considering *J. communis* as a keystone species in these habitats protected under the EU Habitats Directive. So far, mainly scattered trees have been considered keystone structures in open habitats (Manning et al., 2006). However, in our study, scattered trees were missing in the studied habitats (cf. Table 1).

To sum up, the occurrence of scattered juniper shrubs boosted species richness and abundance of breeding birds. Primarily responsible for this pattern were (i) the general increase in structural complexity and (ii) two (genuine) properties of the tall, evergreen shrub in particular: dense growth and prickly leaves. Due to the latter, the shrub provides nesting sites that are strongly sheltered against predation and adverse weather. However, it also has an important function as a song post and perch for hunting. Additionally, the usually scattered distribution of the juniper shrubs ensures a maximum exploitation of calcareous grasslands and heathlands by many breeding pairs. Based on the evidence of previous research and our study, *J. communis* should be considered a keystone species in both habitat types of European conservation concern.

5. Implications for conservation

Large portions of the threatened plant and insect species of calcareous grasslands and heathlands depend on early- and mid-successional stages (Bourn and Thomas, 2002; Fartmann et al., 2012, 2022; Poniatowski et al., 2020; Helbing et al., 2021; Streitberger et al., 2021a, 2021b). As a result, conservation management in both habitat types aims to counteract succession and to establish short swards rich in bare ground (Dekoninck et al., 2007; Poniatowski et al., 2018; Fartmann et al., 2022). However, as our study highlights, many bird species, among them several threatened ones, strongly benefit from the occurrence of the keystone species Common juniper. In juniper-rich stands in our study, *J. communis* had a cover of less than 25% and a scattered distribution. For future habitat management, we recommend acknowledging the crucial importance of the keystone species and fostering a scattered occurrence of single junipers or small groups of the shrubs. However, large areas of low-growing vegetation and bare ground as foraging habitats are also decisive for a high species richness and abundance of breeding birds. We recommend a juniper cover of less than 25% as the target, in particular for many of the threatened indicator species such as Tree pipit, Red-backed shrike or Woodlark (Stoos et al., 2017; Fartmann et al., 2018; Kämpfer et al., 2022). However, for some threatened target species, such as Skylark, large open grasslands and heathlands are also indispensable (cf. Fig. 4) (Bauer et al., 2005). Although many rare plant and insect species exhibit a preference for early- and mid-successional stages of calcareous grasslands and heathlands (see above), detailed studies on the conservation value of juniper-rich stands for these taxonomic groups are still missing. Thus, for a fine adjustment of management recommendations for both habitats, we suggest research comparable to our study also for plants and relevant insect groups.

Overall, in both calcareous grasslands and heathlands, low-intensity rough or year-round grazing systems combined with shrub cutting from time to time seem to be suitable management tools (Köhler et al., 2016; Brüggeshemke et al., 2022). For heathlands, additionally, in the long run, rejuvenation measures such as sod cutting and choppering are necessary (Härdtle et al., 2009; Streitberger et al., 2021a, 2021b; Fartmann et al., 2022).

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.

Data availability

Data will be made available on request.

Appendix

(See here Appendix Tables A1, A2, A3).

Table A1
Overview of Spearman correlation coefficients (r_s) among environmental variables in calcareous grasslands. Intercorrelated variables ($|r_s| > 0.5$) that were excluded from the NMDS are displayed in bold type. Shannon = Shannon habitat diversity. n.s. = not significant; * $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$.

Parameter	Temp.	Preci.	Arable land	Impr. rass.	Mesic grass.	Calca. open	Calca. black	Calca. junip.	Hedge/ copse	Pioneer forest	Closed forest	Shannon
Elevation	–0.77***	0.27 n.s.	–0.51*	0.14 n.s.	0.15 n.s.	0.31 n.s.	0.39 n.s.	–0.48 n.s.	0.22 n.s.	–0.42 n.s.	–0.14 n.s.	0.02 n.s.
Temperature	\	–0.48 n.s.	0.45 n.s.	–0.27 n.s.	0.10 n.s.	–0.20 n.s.	–0.36 n.s.	0.34 n.s.	–0.22 n.s.	0.31 n.s.	–0.03 n.s.	–0.02 n.s.
Precipitation	.	\	–0.22 n.s.	–0.22 n.s.	0.24 n.s.	0.43 n.s.	–0.04 n.s.	–0.03 n.s.	–0.04 n.s.	–0.21 n.s.	–0.11 n.s.	0.01 n.s.
Arable land	.	.	\	–0.25 n.s.	–0.01 n.s.	–0.36 n.s.	0.10 n.s.	0.15 n.s.	–0.10 n.s.	–0.08 n.s.	0.37 n.s.	0.41 n.s.
Improved grassland	.	.	.	\	–0.05 n.s.	–0.35 n.s.	0.52*	–0.26 n.s.	0.34 n.s.	0.29 n.s.	0.14 n.s.	0.34 n.s.
Mesic grassland	.	.	.	.	\	0.12 n.s.	0.33 n.s.	–0.09 n.s.	0.39 n.s.	0.05 n.s.	–0.39 n.s.	0.39 n.s.
Open calcareous grassland	.	.	.	.	.	\	0.03 n.s.	–0.58*	–0.04 n.s.	–0.37 n.s.	–0.23 n.s.	–0.04 n.s.
Blackthorn-rich calcareous grassland	.	.	.	.	.	.	\	–0.69**	0.63**	–0.12 n.s.	–0.06 n.s.	0.63**
Juniper-rich calcareous grassland	.	.	.	.	.	.	.	\	–0.55*	0.18 n.s.	0.18 n.s.	–0.44 n.s.
Hedge and copse	.	.	.	.	.	.	.	.	\	–0.31 n.s.	–0.38 n.s.	0.15 n.s.
Open and pioneer forest	.	.	.	.	.	.	.	.	.	\	–0.12 n.s.	0.22 n.s.
Closed forest	.	.	.	.	.	.	.	.	.	.	\	0.34 n.s.

Table A2

Overview of Spearman correlation coefficients (r_s) among environmental variables in heathlands. Intercorrelated variables ($|r_s| > 0.5$) that were excluded from the NMDS are displayed in bold type. Shannon = Shannon habitat diversity. n.s. = not significant; * $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$.

Parameter	Temp.	Preci.	Mire	Bare ground	Open heath	Semi. heath	Juniper heath	Hedge/ copse	Pioneer forest	Closed forest	Shannon
Elevation	−0.86***	0.89***	−0.42*	−0.10 n.s.	−0.30 n.s.	−0.08 n.s.	0.39*	−0.02 n.s.	0.24 n.s.	0.02 n.s.	−0.18 n.s.
Temperature	\	−0.92***	0.53**	0.09 n.s.	0.16 n.s.	−0.14 n.s.	−0.12 n.s.	0.18 n.s.	−0.25 n.s.	0.04 n.s.	0.17 n.s.
Precipitation	.	\	−0.56***	−0.22 n.s.	−0.18 n.s.	0.13 n.s.	0.14 n.s.	0.01 n.s.	0.19 n.s.	−0.01 n.s.	−0.12 n.s.
Mire and wet heathland	.	.	\	0.09 n.s.	0.37*	−0.14 n.s.	−0.32 n.s.	0.13 n.s.	0.02 n.s.	−0.02 n.s.	0.21 n.s.
Dry grassland and bare ground	.	.	.	\	0.06 n.s.	−0.17 n.s.	−0.00 n.s.	−0.17 n.s.	−0.12 n.s.	−0.14 n.s.	0.05 n.s.
Open heathland	.	.	.	.	\	−0.08 n.s.	−0.80***	−0.04 n.s.	−0.13 n.s.	−0.41*	0.03 n.s.
Semi-open heathland	.	.	.	.	.	\	−0.40*	−0.09 n.s.	0.03 n.s.	−0.00 n.s.	0.65***
Juniper-rich heathland	.	.	.	.	.	.	\	−0.00 n.s.	0.14 n.s.	0.28 n.s.	−0.30 n.s.
Hedge and copse	.	.	.	.	.	.	.	\	−0.17 n.s.	0.02 n.s.	0.14 n.s.
Open and pioneer forest	.	.	.	.	.	.	.	.	\	0.40*	0.14 n.s.
Closet forest	.	.	.	.	.	.	.	.	.	\	0.27 n.s.

Table A3

Overview of detected breeding-bird species, indication of shrub-breeding species, number of territories and threat status in the studied plots of calcareous grasslands ($N = 16$) and heathlands ($N = 36$). Common name: Newton (2017); scientific name: Barthel and Helbig (2005). Shrub-nesting species (SN): Kamp et al. (2021). Threat status (TS): Diemel valley – Grüneberg et al. (2017), Wolf and Widdig (2016); Lüneburg heath – Krüger and Nipkow (2015); threat status within each study area is only displayed if the species was detected in the respective study area. No. territ. = number of territories.

Common name	Scientific name	SN	Calcareous grassland No. territ.	TS	Heathland No. territ.	TS
Black Grouse	*Lyrurus tetrix*	.	.	.	2	✔
Black woodpecker	*Dryocopus martius*	.	2	.	.	.
Blackbird	*Turdus merula*	✔	44	.	6	.
Blackcap	*Sylvia atricapilla*	✔	57	.	1	.
Blue tit	*Cyanistes caeruleus*	.	20	.	2	.
Bullfinch	*Pyrrhula pyrrhula*	✔	8	.	2	.
Carrion crow	*Corvus corone*	.	3	.	1	.
Chaffinch	*Fringilla coelebs*	.	34	.	13	.
Chiffchaff	*Phylloscopus collybita*	.	49	.	1	.
Coal tit	*Periparus ater*	.	1	.	.	.
Common buzzard	*Buteo buteo*	.	2	.	.	.
Common grasshopper warbler	*Locustella naevia*	.	2	✔	.	.
Common Redstart	*Phoenicurus phoenicurus*	.	.	.	3	✔
Crested tit	*Lophophanes cristatus*	.	3	.	3	.
Cuckoo	*Cuculus canorus*	.	1	✔	1	✔
Dunnock	*Prunella modularis*	✔	28	.	.	.
Eurasian Curlew	*Numenius arquata*	.	.	.	1	✔
Eurasian nuthatch	*Sitta europaea*	.	1	.	.	.
European nightjar	*Caprimulgus europaeus*	.	.	.	9	✔
European robin	*Erithacus rubecula*	.	25	.	2	.
European turtle dove	*Streptopelia turtur*	.	2	✔	.	.
Fieldfare	*Turdus pilaris*	.	1	✔	.	.
Firecrest	*Regulus ignicapilla*	.	2	.	.	.
Garden warbler	*Sylvia borin*	✔	14	.	.	.
Goldcrest	*Regulus regulus*	.	2	.	.	.
Goldfinch	*Carduelis carduelis*	.	2	✔	.	.
Great grey shrike	*Lanius excubitor*	✔	.	.	5	✔
Great tit	*Parus major*	.	39	.	7	.
Great-spotted woodpecker	*Dendrocopos major*	.	5	.	.	.
Green woodpecker	*Picus viridis*	.	9	.	.	.
Greenfinch	*Carduelis chloris*	✔	20	.	15	.
Grey partridge	*Perdix perdix*	.	.	.	2	✔

(continued on next page)

Table A3 (*continued*)

Common name	Scientific name	SN	Calcareous grassland		Heathland	
			No. territ.	TS	No. territ.	TS
Grey-headed woodpecker	*Picus canus*	.	1	✔	.	.
Hawfinch	*Coccothraustes coccothraustes*	.	1	.	.	.
Hobby	*Falco subbuteo*	.	.	.	1	✔
Hoopoe	*Upupa epops*	.	.	.	1	✔
Icterine warbler	*Hippolais icterina*	✔	1	✔	.	.
Jay	*Garrulus glandarius*	.	4	.	3	.
Lesser spotted woodpecker	*Dryobates minor*	.	1	✔	.	.
Lesser whitethroat	*Sylvia curruca*	✔	22	✔	4	.
Linnet	*Linaria cannabina*	✔	33	✔	1	✔
Long-eared owl	*Asio otus*	.	.	.	1	✔
Long-tailed tit	*Aegithalos caudatus*	✔	15	.	2	.
Magpie	*Pica pica*	.	2	.	.	.
Marsh tit	*Poecile palustris*	.	6	.	3	.
Meadow pipit	*Anthus pratensis*	.	.	.	2	✔
Mistle thrush	*Turdus viscivorus*	.	3	.	2	.
Quail	*Coturnis coturnix*	.	.	.	3	✔
Raven	*Corvus corax*	.	1	.	1	.
Red kite	*Milvus milvus*	.	1	✔	.	.
Red-backed shrike	*Lanius collurio*	✔	15	✔	22	✔
Short-toed treecreeper	*Certhia brachydactyla*	.	3	.	.	.
Skylark	*Alauda arvensis*	.	5	✔	52	✔
Song thrush	*Turdus philomelos*	✔	19	.	1	.
Spotted flycatcher	*Muscicapa striata*	.	1	.	1	✔
Stock dove	*Columba oenas*	.	1	.	.	.
Stonechat	*Saxicola rubicola*	.	.	.	17	.
Tree pipit	*Anthus trivialis*	.	19	✔	30	✔
Tree sparrow	*Passer montanus*	.	9	✔	.	.
Western yellow wagtail	*Motacilla flava*	.	.	.	2	.
Whitethroat	*Sylvia communis*	✔	39	.	3	.
Willow tit	*Poecile montanus*	.	4	✔	.	.
Willow warbler	*Phylloscopus trochilus*	.	41	✔	6	.
Wood pigeon	*Columba palumbus*	.	6	.	4	.
Woodcock	*Scolopax rusticola*	.	.	.	7	✔
Woodlark	*Lullula arborea*	.	3	✔	18	✔
Wren	*Troglodytes troglodytes*	✔	7	.	1	.
Wryneck	*Jynx torquilla*	.	5	✔	2	✔
Yellowhammer	*Emberiza citrinella*	✔	60	✔	21	✔

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