Journal of Ornithology (2022) 163:695–707
https://doi.org/10.1007/s10336-022-01972-7

ORIGINAL ARTICLE

# Effects of local climate and habitat heterogeneity on breeding-bird assemblages of semi-natural grasslands

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Received: 12 October 2021 / Revised: 16 February 2022 / Accepted: 21 February 2022 / Published online: 14 March 2022
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## Abstract

The intensification of agricultural land-use, abandonment and afforestation have caused severe loss and degradation of nutrient-poor, semi-natural grasslands across Europe. Calcareous grasslands have an outstanding value for nature conservation due to their highly diverse flora and fauna, including birds. However, knowledge of environmental factors driving the composition of bird communities in calcareous grasslands is still scarce. The aim of our study was to compare the breeding-bird assemblages of calcareous grasslands and the second most common semi-natural grassland type in the study area (Diemel Valley, Central Germany), mesic grasslands, along an elevation (climate) gradient. For each grassland type, we randomly selected 27 square-shaped plots with a size of 5 ha each and a cover of the focal grassland type of at least 50% within the plot. Our study revealed that both the number and density of threatened species of breeding birds were higher in plots of calcareous grasslands than in those of mesic grasslands. Based on multivariable generalised linear mixed-effects models, the most important predictors of overall species richness and density of breeding birds in plots of calcareous grasslands were the area of juniper-rich calcareous grassland and Shannon habitat diversity. By contrast, the number and density of threatened species were in both grassland types mainly driven by breeding-season temperature. Heterogeneous, juniper-rich calcareous grasslands seem to be a key habitat for bird assemblages with high species richness and density. These grasslands usually consisted of small-scale habitat mosaics providing suitable nesting sites and foraging grounds in close proximity. By contrast, mesic grasslands had rather homogeneous swards and shrubs or trees were normally restricted to the edges of the grassland patches. Based on our study, increasing habitat heterogeneity at the landscape scale and within grasslands is the key to enhancing species richness and density of breeding birds.

**Keywords** Abundance · Biodiversity conservation · Calcareous grassland · Elevation gradient · Farmland bird · Generalised linear mixed-effects model · Habitat structure · Indicator-species analysis · Land-use change · Mesic grassland · Species richness · Threatened species

## Zusammenfassung

**Bedeutung des Lokalklimas und der Habitatheterogenität für Brutvogelgemeinschaften des Magergraslandes**

Die Intensivierung und Aufgabe der Landnutzung sowie Aufforstungen haben zu einem starken Flächenrückgang und einer Abnahme der Habitatqualität des Magergraslands in Europa geführt. Kalkmagerrasen haben eine herausragende Bedeutung für den Naturschutz aufgrund ihrer artenreichen Flora und Fauna, inklusive der Vogelwelt. Unser Wissen über die Faktoren, die die Zusammensetzung der Vogelgemeinschaften in Kalkmagerrasen bestimmen ist aber immer noch gering. Das Ziel

Communicated by T. Gottschalk.

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unserer Studie war es, die Zusammensetzung der Brutvogelgemeinschaften in Kalkmagerrasen und dem zweithäufigsten, nährstoffarmen Graslandtyp im Untersuchungsgebiet (dem Diemeltal, Deutschland) – frischem Magergrasland – entlang eines Höhen- bzw. Klimagradienten zu untersuchen. Für jeden Magergraslandtyp wurden 27 quadratische Probeflächen (PF) mit einer Größe von 5 ha und einem Anteil des namengebenden Graslandtyps von mindestens 50% zufällig ausgewählt. Unsere Studie zeigte, dass sowohl die Artenzahl als auch die Dichte an gefährdeten Brutvogelarten in PF der Kalkmagerrasen höher war als in denen des frischen Magergraslands. In multivariablen, generalisierten linearen gemischten Modellen der PF der Kalkmagerrasen waren die Fläche an wacholderreichen Kalkmagerrasen und der Shannon-Habitatdiversitätsindex die wichtigsten Prädiktoren für die Artenzahl und Dichte der Brutvogelarten insgesamt. Im Gegensatz dazu hing die Artenzahl und Dichte gefährdeter Brutvogelarten in beiden Magergraslandtypen vor allem von der Temperatur zur Brutzeit ab. Heterogene, wacholderreiche Kalkmagerrasen scheinen Schlüsselhabitate für arten- und individuenreiche Brutvogelgemeinschaften zu sein. Sie wiesen normalerweise kleinräumige Habitatmosaike auf, die aus geeigneten Brutplätzen und Nahrungshabitaten in unmittelbarer Nachbarschaft bestanden. Im Gegensatz dazu war das frische Magergrasland eher durch eine homogene Grasnarbe gekennzeichnet und Sträucher oder Bäume waren vor allem am Rand der Parzellen vorhanden. Basierend auf unserer Studie ist die Erhöhung der Habitatheterogenität auf der Landschaftsebene und innerhalb des Magergraslandes der Schlüssel zur Förderung arten- und individuenreicher Brutvogelgemeinschaften.

## Introduction

Most of Europe's biodiversity is associated with agricultural land (Donald et al. 2006; Henle et al. 2008; Kleijn et al. 2009). For centuries, traditional farmland-management practices have contributed to the creation of semi-natural ecosystems hosting an outstanding biodiversity (Plieninger et al. 2006, 2015; Löffler and Fartmann 2017; Poschlod 2017). However, since the beginning of the industrial era, land-use change has led to a dramatic loss of wild biota in agricultural habitats (Donald et al. 2006; Bengtsson et al. 2019). Consequently, maintaining farmland biodiversity has become increasingly difficult throughout Europe (Donald et al. 2006; Flohre et al. 2011).

The intensification of agricultural land-use, abandonment and afforestation have caused severe loss and degradation of nutrient-poor, semi-natural grasslands across Europe (Wallis De Vries et al. 2002; Baur et al. 2006; Löffler et al. 2020). As a result, large-scale grasslands of conservation concern, such as calcareous grasslands, are now mainly restricted to mountain ranges, that are usually characterised by a low land-use intensity (MacDonald et al. 2000; Plieninger et al. 2006). Calcareous grasslands have an outstanding value for nature conservation due to their highly diverse flora and insect fauna (Poschlod and Wallis De Vries 2002; van Swaay 2002). Therefore, calcareous grasslands in general and those with occurrence of juniper (*Juniperus communis*) shrubs are now protected under the EU Habitats Directive (EC 2007). Previous studies on the biodiversity of calcareous grasslands have primarily concentrated on plants and insects (e.g., Poschlod and Wallis De Vries 2002; Poniatowski and Fartmann 2008; Krämer et al. 2012; Helbing et al. 2021). Recent work revealed that these grasslands may also play a vital role as refuges for species-rich bird assemblages in Central European landscapes (Köhler et al. 2016; Ernst et al. 2017). However, knowledge of environmental factors driving the composition of bird assemblages in calcareous grasslands is still scarce and sometimes findings have even been contradictory. While Köhler et al. (2016) showed that year-round grazing favoured species richness in calcareous grasslands, Ernst et al. (2017) detected a higher richness and abundance of farmland birds in abandoned calcareous grasslands. In comparison to calcareous grasslands, our knowledge on the biodiversity of mesic grasslands is even worse since they suffered more severely from habitat loss due agricultural intensification (Poschlod 2017; Fartmann et al. 2021).

Birds are excellent indicators of farmland biodiversity and human-driven habitat alterations in semi-natural grasslands (Fuller 2012; Newton 2017; Reif and Hanzelka 2020). In particular, specialised species are highly sensitive to land-use change and, as a consequence, have frequently become threatened in recent decades (Reif et al. 2008; Correll et al. 2019; Keller et al. 2020). They are mainly affected by changes in food supply and breeding habitats caused by altered farmland-management practices (Benton et al. 2002; Newton 2004). Additionally, temperature is another important driver of bird species richness and density (Pearce-Higgins and Green 2014; Keller et al. 2020; Fumy and Fartmann 2021).

Our study area, the Diemel valley in Central Germany (Fig. 1), is rich in nutrient-poor semi-natural grasslands with low land-use intensity (Fartmann 2004). For calcareous grasslands, it is even the most important stronghold in the northern half of Germany. The aim of our study was to compare the breeding-bird assemblages of calcareous grasslands and the second most common semi-natural grassland type in the study area, mesic grasslands (Fig. 2). We compared the species richness and density of breeding birds as well as environmental conditions between the two grassland types along the elevation (climate) gradient of the study area. Moreover, we assessed indicator species for each grassland type by their relative abundance and relative frequency using

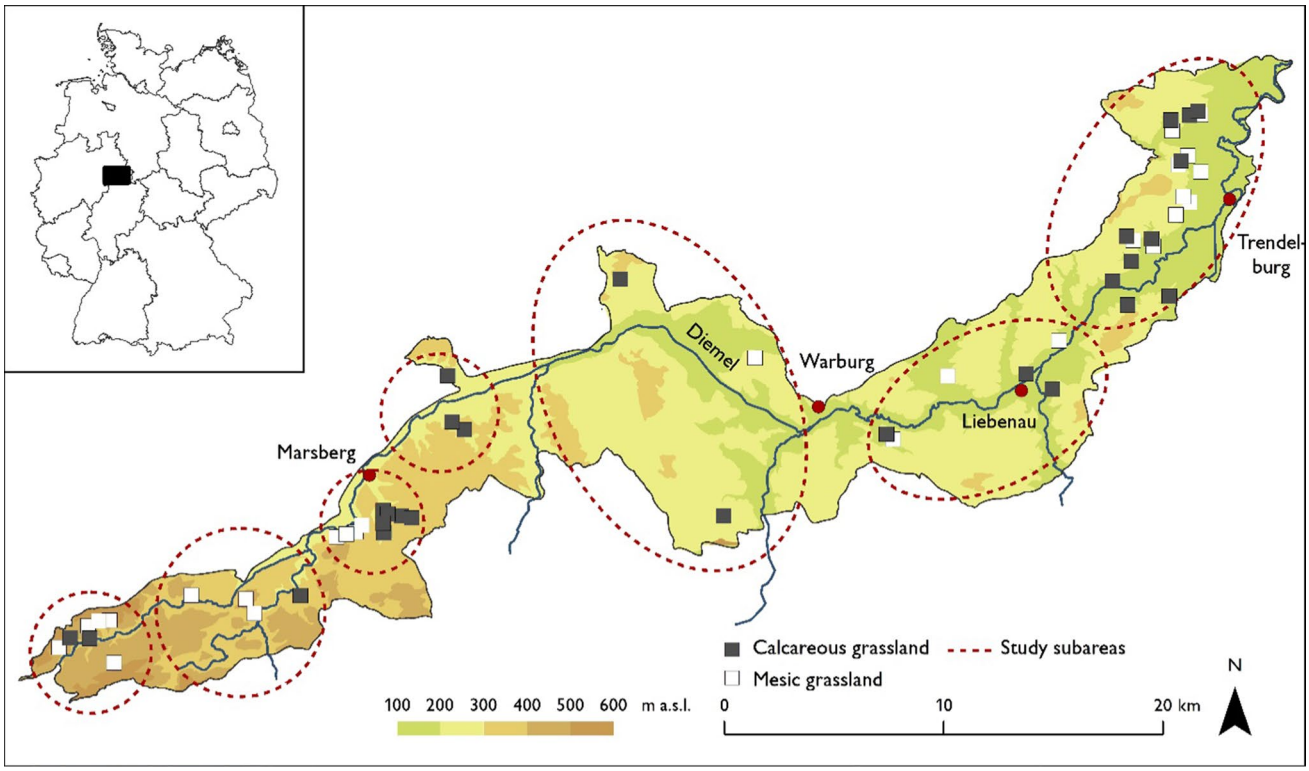


**Fig. 1** Location of the Diemel Valley and plots in Central Germany

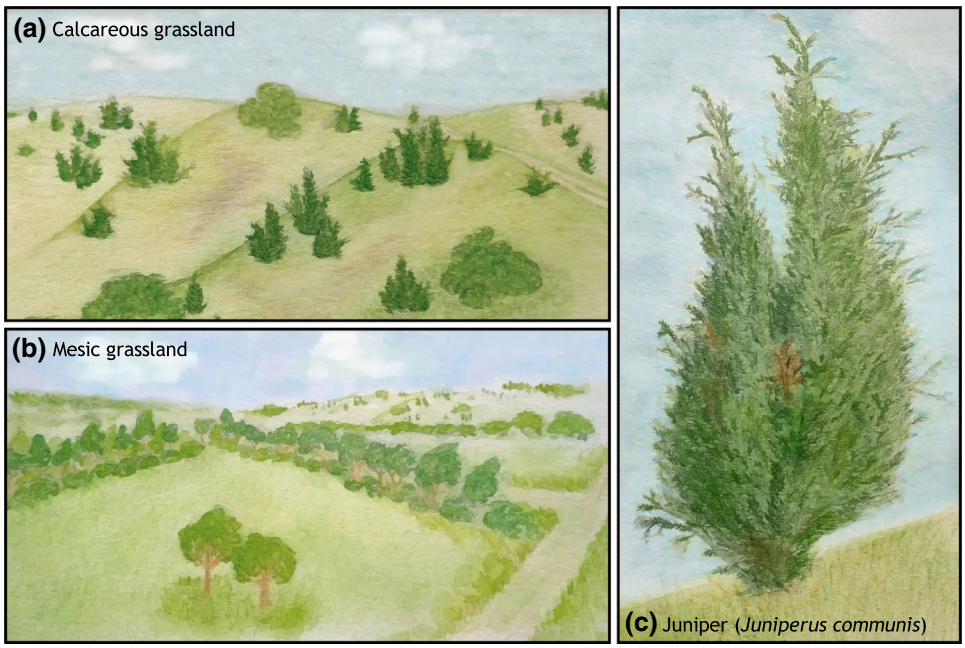


**Fig. 2** Schematic drawing of typical stands of the two focal grassland types, calcareous (**a**) and mesic grasslands (foreground) (**b**), and juniper shrub (*Juniperus communis*) (**c**) as a characteristic keystone structure in calcareous grasslands of the study area. Drawing: M. Freienstein

an indicator-species analysis. Key drivers of bird diversity and density were identified by generalised linear mixed-effects models to derive evidence-based measures for future habitat management in calcareous and mesic grasslands.

## Materials and methods

### Study area

The study was carried out in the Diemel Valley (100–600 m a.s.l.; Central Germany), which has an area of about 460 km$^2$ along the border between the federal states of North Rhine-Westphalia and Hesse (51° 22′ N/8° 38′ E and 51° 38′ N/9° 25′ E; Fig. 1). The study area covers ~ 750 ha of calcareous and ~ 250 ha of mesic grasslands (Fartmann 2004). The climate is suboceanic (Müller-Wille 1981). The surrounding matrix of these semi-natural grasslands is dominated by a patchwork of woodland, improved grassland and arable fields (Poniatowski and Fartmann 2010). In accordance with the elevation gradient in the study area, annual precipitation increases with elevation from 732 to 948 mm, while annual temperature decreases from 8.8 to 7.9 °C (long-term mean: 1981–2010; weather station Warburg and Brilon, respectively; German Meteorological Service 2021). To account for possible spatial autocorrelation, the study area was divided into seven subareas according to the landscape configuration (Fig. 1).

## Sampling design

### Plots

We studied two types of semi-natural grasslands with low land-use intensity: (i) calcareous and (ii) mesic grasslands (Fig. 2). For each grassland type, we randomly selected 27 square-shaped plots with a size of 5 ha and a cover of the focal grassland type of at least 50% within the plot (cf. Fartmann et al. 2018) across the elevation (climate) gradient of the study area ($N = 54$).

## Environmental conditions

We used digital elevation models with a spatial resolution of 4 ha to calculate the mean elevation of the plots (Geobasis 2021). Climate data were derived from grid maps with a spatial resolution of 1 km$^2$ containing information on long-term averages of temperature and precipitation (period 1981–2010, German Meteorological Service 2021). For further analyses, we considered both mean annual values and mean values for the breeding season (March–August).

For each plot, we recorded the habitat composition in the field according to the German habitat classification scheme (scale: 1:1000; 15 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 (Fartmann et al. 2018; Schwarz et al. 2018):

$$H' = -\sum_i p_i \ln p_i,$$

**Table 1** Overview of sampled predictor variables (mean ± standard error [SE]; $N = 54$)

| Parameter | Grassland type | | $P$ |
|---|---|---|---|
| | Calcareous | Mesic | |
| (a) Climate | | | |
| Elevation a.s.l. (m) | 271 ± 15 | 286 ± 21 | n.s. |
| Precipitation (mm) | | | |
| Annual | 791 ± 14 | 830 ± 20 | n.s. |
| March–August (breeding season) | 392 ± 5 | 407 ± 8 | n.s. |
| Temperature (°C) | | | |
| Annual | 8.7 ± 0.1 | 8.5 ± 0.1 | n.s. |
| March–August (breeding season) | 12.4 ± 0.1 | 12.2 ± 0.1 | n.s. |
| (b) Habitat composition (ha)[1] | | | |
| Arable land | 0.33 ± 0.10 | 0.26 ± 0.10 | n.s. |
| Improved grassland | | | |
| Meadow | 0.20 ± 0.09 | 0.31 ± 0.15 | n.s. |
| Pasture | 0.02 ± 0.02 | 0.12 ± 0.06 | n.s. |
| Semi-natural mesic grassland | | | |
| Meadow | **0.17 ± 0.07** | **0.85 ± 0.24** | ** |
| Pasture | **0.23 ± 0.07** | **1.73 ± 0.29** | *** |
| Semi-natural calcareous grassland | | | |
| Open | **0.82 ± 0.24** | **0.03 ± 0.02** | *** |
| Blackthorn-rich | **0.66 ± 0.18** | **0.07 ± 0.04** | *** |
| Juniper-rich | **0.98 ± 0.28** | **0.03 ± 0.03** | *** |
| Overgrown | 0.08 ± 0.04 | 0.04 ± 0.03 | n.s. |
| Shrubbery | 0.19 ± 0.04 | 0.12 ± 0.03 | n.s. |
| Hedge and copse | **0.20 ± 0.05** | **0.47 ± 0.08** | ** |
| Pioneer forest | 0.37 ± 0.09 | 0.29 ± 0.11 | n.s. |
| Coniferous forest | **0.44 ± 0.13** | **0.08 ± 0.03** | ** |
| Broad-leaved forest | **0.22 ± 0.12** | **0.49 ± 0.12** | * |
| Small-scale habitats[2] | 0.10 ± 0.04 | 0.10 ± 0.04 | n.s. |
| Shannon habitat diversity ($H'$) | 1.32 ± 0.09 | 1.19 ± 0.10 | n.s. |

Differences between the two grassland types were analysed using GLMM (negative binomial error structure) with 'subarea' as a random factor (cf. "Materials and methods" section). Significant differences are indicated by bold type . *$P < 0.05$, **$P < 0.01$, ***$P < 0.001$

*n.s.* not significant

[1]Units habitat-composition variables: ha; except Shannon habitat diversity ($H'$): unitless

[2]Building, clearcut, quarry, road, wetland

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

## Breeding-bird surveys

We mapped breeding-bird territories in all plots from the beginning of April to July 2019 (Fischer et al. 2005). Territory mapping is among the most accurate methods for estimating species richness and density of breeding birds (Bibby

et al. 2000). Altogether, we performed five surveys early in the morning with an interval of at least 10 days between each visit (Fartmann et al. 2018; Schwarz et al. 2018). During every survey, we followed a non-linear route covering the whole plot and noted all signs of territorial behaviour, such as singing, on a map (scale 1:1000) (Bibby et al. 2000). Breeding was assumed if a bird showed territorial behaviour twice within a period of 10 days between each visit (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). Prior to further analyses, we classified breeding-bird species as threatened (including near-threatened species) according to the red-data books of breeding birds in North Rhine-Westphalia (Grüneberg et al. 2017) and Hesse (Wolf and Widdig 2016).

## Statistical analysis

We performed all statistical analyses using R 3.6.1 (R Core Team 2021). For detecting significant differences in environmental parameters (Table 1) as well as in species richness and territory density between the grassland types (Fig. 3), we applied univariable generalised linear mixed-effects models (GLMM) (R packages lme4, Bates et al. 2020) with 'subarea' as a random factor (Crawley 2007). Grassland type served as a nominal fixed factor, and we used the analysed parameters as dependent variables. We conducted negative binomial GLMMs for reducing overdispersion. We analysed the overall effect of grassland type on the environmental parameters by comparing the full models with reduced models without 'grassland type' as the fixed factor (intercept-only models) and applying likelihood-ratio tests.

We calculated multivariable GLMMs (negative binomial error structure) to detect environmental parameters that explain the species richness and territory density of breeding-bird assemblages, separately for all and threatened species, in the two grassland types. To avoid model over-fitting, we excluded intercorrelated ($|r_s| > 0.5$) variables and we used only the ecologically most meaningful variable in GLMMs (Tables A1 and A2) (cf. Löffler and Fartmann 2017). Therefore, for the plots of calcareous grasslands, we excluded elevation, annual precipitation and temperature, open and blackthorn-rich calcareous grasslands, shrubberies and broad-leaved forests from the GLMM analyses. For

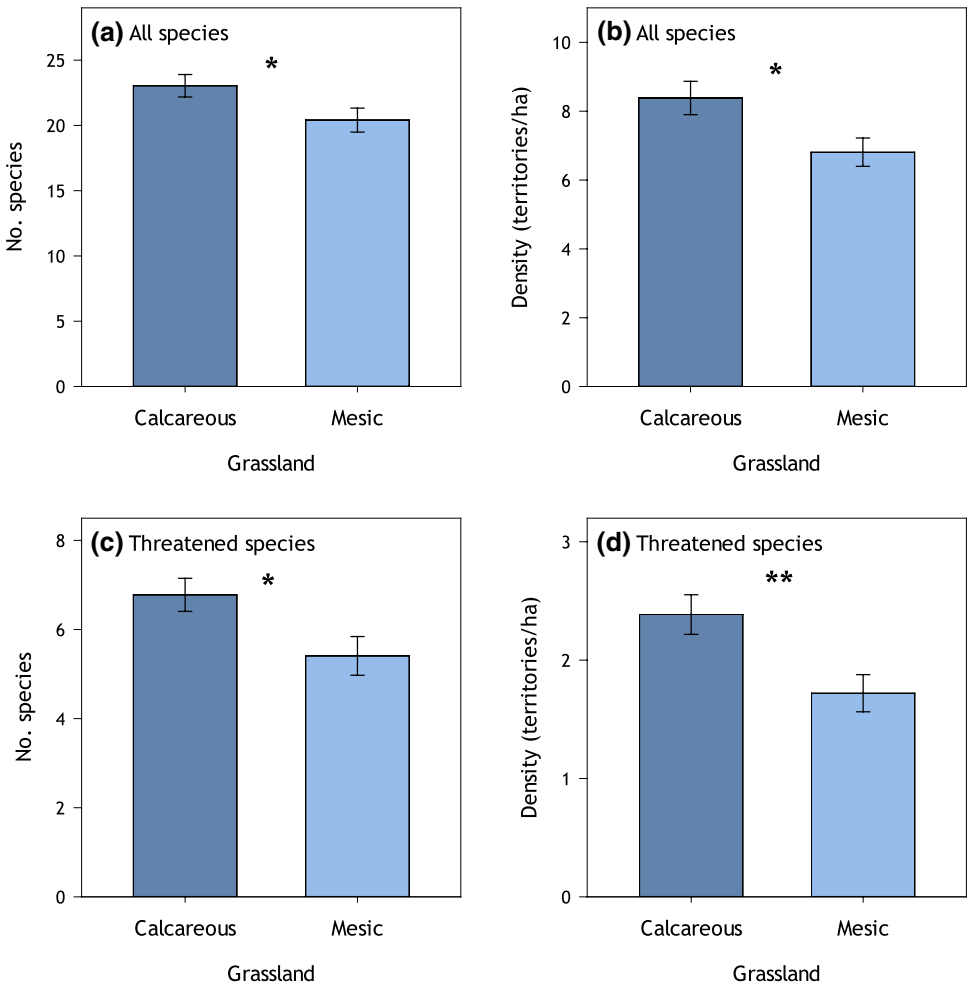


**Fig. 3** Mean values (±SE) of species richness and density of all (**a**, **b**) and threatened (**c**, **d**) breeding-bird species in plots of calcareous and mesic grasslands ($N = 54$). Differences between the two grassland types were analysed using GLMM with 'subarea' as a random factor. **a** $Z = -1.891$, $P < 0.05$, **b** $Z = -2.013$, $P < 0.05$, **c** $Z = -1.951$, $P < 0.05$, **d** $Z = -2.506$, $P < 0.01$. *$P < 0.05$; **$P < 0.01$

the plots of mesic grasslands, we eliminated elevation, precipitation (annual and breeding season), annual temperature, arable land, improved meadows and hedges/copses. For all GLMMs, the variable 'subarea' was used as a random factor (Crawley 2007). To increase model robustness and identify the most important environmental parameters, we conducted model averaging based on an information-theoretic approach (Burnham and Anderson 2002; Grueber et al. 2011). Model averaging was conducted using the dredge function (R package MuMIn, Bartón 2020) and included only top-ranked models within $\Delta AIC_C < 3$ (Grueber et al. 2011). The model-averaged regression coefficients were calculated from a range of top-ranked submodels within $\Delta AIC_C < 3$. This means that the averaged coefficients represent a 'weighted average' (based on AICc weights) across all submodels. For more details on the calculation see Burnham and Anderson (2002; Eq. 4.7). Non-significant predictors were also included in some of the top-ranked submodels as they can increase model accuracy. Therefore, they were also retained in the averaged models.

To identify indicator species for each grassland type an indicator-species analysis (ISA) (Dufrêne and Legendre 1997; Cáceres and Jansen 2016) was carried out. ISA uses the relative abundance and relative frequency of a species to estimate the strength of its association with the two grassland types. The more the indicator value (IV; scaled from 0 to 1) of a species increases, the more abundant is a species and the more frequently it occurs compared with other species in the focal grassland type. The statistical significance of this relationship is tested using a permutation test. This method is a common statistical tool in community ecology and is frequently used to identify characteristic species of certain habitat types (e.g. Thorn et al. 2016; Fartmann et al. 2018).

## Results

### Environmental conditions

In contrast to climatic conditions, habitat composition differed between plots of calcareous and mesic grasslands (Table 1). Each grassland type was dominated by its respective eponymous grassland (open, blackthorn-rich and juniper-rich calcareous grasslands vs. mesic meadows and pastures). Additionally, plots of calcareous grasslands had a larger area of coniferous forests than plots of mesic grasslands. By contrast, the area of hedges/copses and broad-leaved forests were larger in plots of mesic grasslands. All other habitat parameters did not differ.

### Breeding-bird assemblages

Altogether, we detected 67 breeding bird species on the 54 plots (Table A3). Among them were 23 threatened species. The most common species (i.e., > 100 territories on all plots), in decreasing order, were Yellowhammer (*Emberiza citrinella*), Eurasian Blackcap (*Sylvia atricapilla*), Chiffchaff (*Phylloscopus collybita*), Great Tit (*Parus major*), Blackbird (*Turdus merula*), Whitethroat (*Sylvia communis*), Chaffinch (*Fringilla coelebs*) and Robin (*Erithacus rubecula*). The most common threatened species (i.e., > 30 territories on all plots) were Yellowhammer, Willow Warbler (*Phylloscopus trochilus*), Lesser Whitethroat (*Sylvia curruca*), Linnet (*Carduelis cannabina*), Red-backed Shrike (*Lanius collurio*) and Tree Pipit (*Anthus trivialis*).

### Relationship between breeding-bird assemblages and environmental conditions

Both the number and density of all and threatened species were higher in plots of calcareous grasslands than in those of mesic grasslands (Fig. 3). Altogether, we identified eight indicator species of calcareous grasslands; three of them, Linnet, Tree Pipit and Willow Warbler, were considered threatened (Table 2). A least four of the indicator species regularly used juniper for breeding: Bullfinch (*Pyrrhula pyrrhula*), Linnet, Long-tailed Tit (*Aegithalos caudatus*) and Song Thrush (*Turdus philomelos*) (own observation). By contrast, mesic grasslands had no indicator species.

**Table 2** Results of indicator species analysis (ISA) (De Cáceres and Jansen, 2016; Dufrêne and Legendre 1997) for plots of calcareous and mesic grasslands based on territory densities ($N_{plots} = 54$)

| Species | IV | *P* | Grassland type | |
|---|---|---|---|---|
| | | | Calcareous | Mesic |
| Bullfinch (*Pyrrhula pyrrhula*) | 39.1 | *** | 81/48 | 19/11 |
| Chiffchaff (*Phylloscopus collybita*) | 55.9 | * | 53/100 | 47/100 |
| Eurasian Blackcap (*Sylvia atricapilla*) | 56.4 | * | 56/100 | 44/100 |
| Linnet (*Carduelis cannabina*) | **55.2** | *** | **71/78** | **29/41** |
| Long-tailed Tit (*Aegithalos caudatus*) | 53.1 | *** | 96/56 | 4/4 |
| Song Thrush (*Turdus philomelos*) | 56.3 | * | 61/93 | 39/78 |
| Tree Pipit (*Anthus trivialis*) | **49.5** | ** | **74/67** | **26/33** |
| Willow Warbler (*Phylloscopus trochilus*) | **58.7** | *** | **63/93** | **37/56** |

IV = indicator value; relative abundance comparing the two grassland types/relative frequency (percentage of plots within each grassland type with occurrence of the species). Grey-hatched: species are indicator species for this grassland type; bold-type values: species are threatened (Wolf and Widdig 2016; Grüneberg et al. 2017)

*$P < 0.05$; **$P < 0.01$; ***$P < 0.001$

**Table 3** Model-averaging results (GLMM, negative binomial error structure): relationship between species richness (a, c) and density (b, d) of all and threatened breeding-bird species, respectively, and environmental parameters on plots of calcareous grasslands ($N = 27$)

| Parameter | Estimate | SE | $Z$ | $P$ |
|---|---|---|---|---|
| (a) No. of all species ($R^2 = 0.22$–$0.40$) | | | | |
| (Intercept) | 2.73 | 0.19 | 13.63 | *** |
| Calcareous grassland (juniper-rich) | 0.11 | 0.03 | 3.13 | ** |
| Shannon habitat diversity *(H′)* | 0.25 | 0.10 | 2.42 | * |
| Semi-natural pasture | − 0.07 | 0.12 | 0.58 | n.s. |
| Coniferous forest | 0.09 | 0.06 | 1.47 | n.s. |
| (b) Density of all species ($R^2 = 0.27$–$0.35$) | | | | |
| (Intercept) | 1.75 | 0.28 | 6.02 | *** |
| Calcareous grassland (juniper-rich) | 0.16 | 0.05 | 3.11 | ** |
| Shannon habitat diversity *(H′)* | 0.30 | 0.14 | 1.99 | * |
| (c) No. of threatened species ($R^2 = 0.03$–$0.17$) | | | | |
| (Intercept) | 1.08 | 1.40 | 0.76 | n.s. |
| Arable land | 0.26 | 0.13 | 1.89 | n.s. |
| Breeding-season temperature | 0.22 | 0.11 | 1.98 | * |
| Calcareous grassland (juniper-rich) | 0.06 | 0.05 | 1.02 | n.s. |
| (d) Density of threatened species ($R^2 = 0.16$) | | | | |
| (Intercept) | 0.05 | 1.61 | 0.03 | n.s. |
| Calcareous grassland (juniper-rich) | 0.15 | 0.08 | 1.80 | n.s. |
| Breeding-season temperature | 0.33 | 0.10 | 3.17 | ** |
| Semi-natural pasture | 0.31 | 0.30 | 0.97 | n.s. |
| Hedge and copse | 0.47 | 0.47 | 0.94 | n.s. |
| Coniferous forest | − 0.15 | 0.20 | 0.74 | n.s. |

Model-averaged coefficients (conditional average) were derived from the top-ranked models ($\Delta AIC_C < 3$)

$R^2$ McFadden $R^2$, *n.s.* not significant

*$P < 0.05$; **$P < 0.01$; ***$P < 0.001$

In the multivariable GLMM analyses, the overall number and density of breeding bird species increased in plots of calcareous grasslands with the area of juniper-rich calcareous grasslands and Shannon habitat diversity (Table 3, Fig. 4). By contrast, the number and density of threatened species increased in calcareous and mesic grasslands with breeding-season temperature (Tables 3 and 4, Figs. 4 and 5). Additionally, in plots of mesic grasslands, the overall density increased with breeding-season temperature and overall species richness increased with the area of coniferous forest (Table 4, Fig. 5).

## Discussion

Our study revealed that both the number and the density of all and threatened species of breeding birds were higher in plots of calcareous grasslands than in those of mesic grasslands. Based on the multivariable GLMMs, the most important predictors of overall species richness and density of breeding birds in plots of calcareous grasslands were the area of juniper-rich calcareous grassland and Shannon habitat diversity. By contrast, the number and density of threatened species were in both grassland types mainly driven by breeding-season temperature.

Since diverse habitats offer more available niches, habitat heterogeneity is known to be an important driver of species richness and density in breeding-bird assemblages (Benton et al. 2003; Vickery and Arlettaz 2012; Farwell et al. 2020). Shannon habitat diversity based on habitat types is a rather coarse proxy for habitat heterogeneity, usually not reflecting the sometimes high three-dimensional structural diversity within a certain habitat type (cf. Cooper et al. 2020). Nevertheless, we detected a positive effect of Shannon habitat diversity on both overall species richness and density of breeding birds in plots of calcareous grasslands. Additionally, the area of juniper-rich calcareous grasslands was another important predictor of species richness and density of breeding birds in plots of this grassland type. While many plant and insect taxa of conservation concern prefer open habitat structures rich in bare ground (Bourn and Thomas 2002; Fartmann et al. 2012; Poniatowski et al. 2020), juniper-rich calcareous grasslands seem to be key habitats for bird assemblages with high species richness and density. In general, birds depend on (i) suitable foraging habitats with high prey accessibility and (ii) breeding habitats that provide shelter from potential nest predators (Benton et al. 2003; Moorcroft et al. 2002; Fartmann et al. 2018). Prey accessibility in grassland birds is granted by patches of low-growing vegetation and bare ground (Tagmann-Ioset et al. 2012; Kämpfer and Fartmann 2019; Fumy and Fartmann 2021). Taller vegetation is thought to reduce the predation risk of eggs and chicks in ground nests (Baines 1990; Schwarz et al. 2018). Dense and especially evergreen shrubs, such as the juniper (Fig. 2), offer sheltered nesting sites for shrub-breeding birds, exposed song posts and hunting perches (Gatter 2000; Schwarz et al. 2018). The calcareous grasslands in the study area are characterised by an extraordinarily high three-dimensional structural diversity (Poniatowski and Fartmann 2008; Poniatowski et al. 2018) (cf. Fig. 2). This is especially true for the juniper-rich ones. They consist of small-scale mosaics of sparsely-vegetated swards, taller vegetation and interspersed juniper shrubs (Fartmann 2004) (Fig. 2) that provide all the vital microhabitats for birds mentioned before (cf. Berg and Part 1994; Kujawa and Tryjanowski 2000).

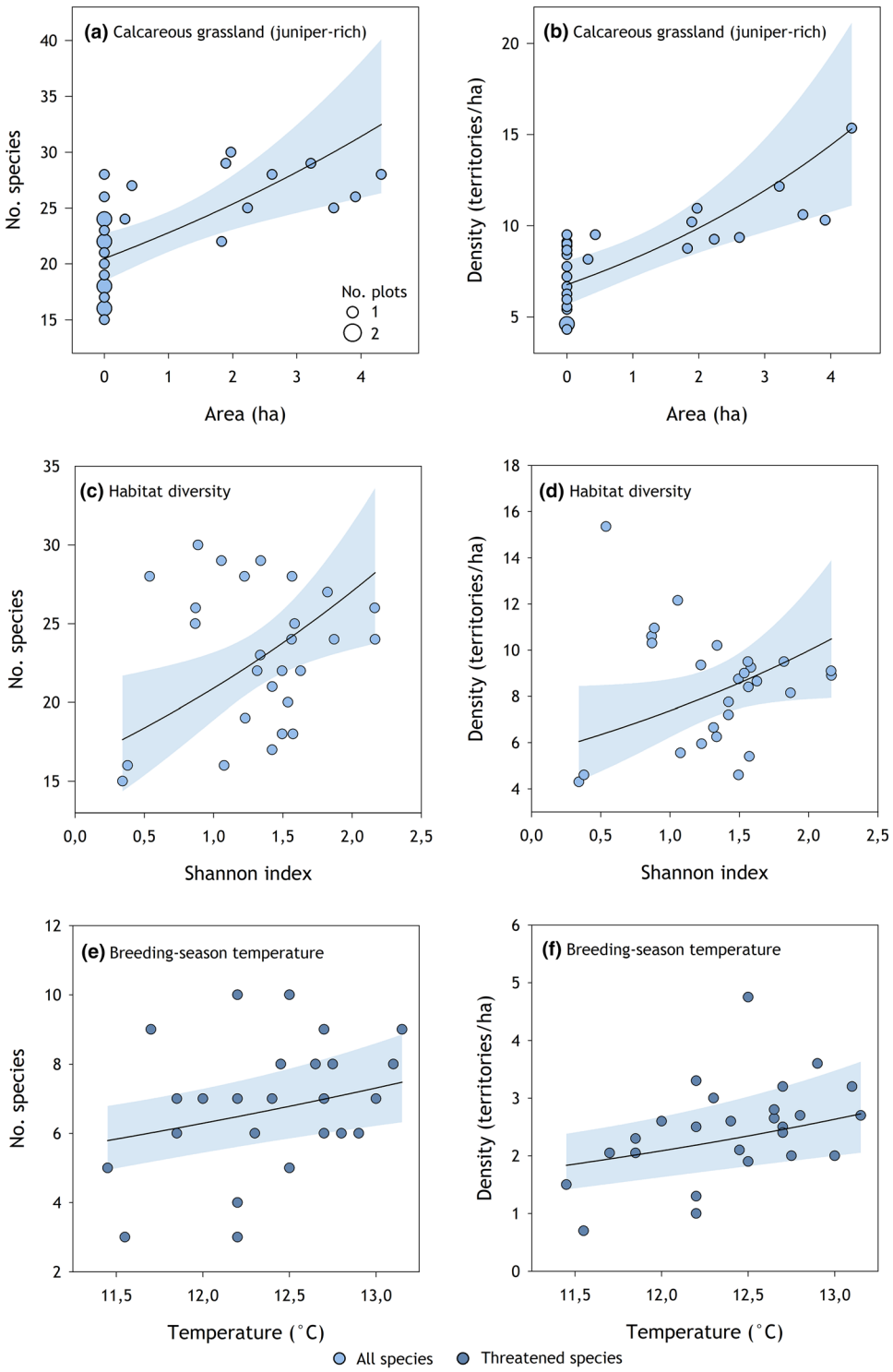


**Fig. 4** Relationship between species richness and density of all and threatened breeding bird species, respectively, and the significant environmental parameters of averaged models for plots of calcareous grasslands ($N = 27$) (see Table 3). The regression slopes (including 95% confidence intervals) were fitted using a single predictor GLMM (negative binomial error structure)

By contrast, mesic grasslands were usually characterised by rather homogeneous swards (especially in meadows; own observation), although land-use intensity was low. Plots of mesic grasslands included larger areas of hedges and copses (cf. also Fig. 2), which also offer potential nesting sites, song posts or hunting perches. However, these habitat elements were mostly restricted to the edges of the grassland patches limiting the number of territories of breeding birds.

In particular, specialised bird species depend on habitat heterogeneity (Fuhlendorf et al. 2006; Reif et al. 2008; Correll et al. 2019). Hence, the high number of indicator species in plots of calcareous grasslands can likely also be attributed to the higher habitat heterogeneity of calcareous,

**Table 4** Model-averaging results (GLMM, negative binomial error structure): relationship between species richness (a, c) and density (b, d) of all and threatened breeding-bird species, respectively, and environmental parameters on plots of mesic grasslands ($N = 27$)

| Parameter | Estimate | SE | $Z$ | $P$ |
|---|---|---|---|---|
| (a) No. of all species ($R^2 = 0.27–0.38$) | | | | |
| (Intercept) | 2.20 | 1.17 | 1.84 | n.s. |
| Breeding-season temperature | 0.16 | 0.09 | 1.74 | n.s. |
| Coniferous forest | 0.58 | 0.26 | 2.13 | * |
| Broad-leaved forest | 0.13 | 0.07 | 1.59 | n.s. |
| (b) Density of all species ($R^2 = 0.16–0.23$) | | | | |
| (Intercept) | 0.54 | 1.54 | 0.35 | n.s. |
| Breeding-season temperature | 0.25 | 0.05 | 4.69 | *** |
| Coniferous forest | 0.43 | 0.34 | 1.19 | n.s. |
| (c) No. of threatened species ($R^2 = 0.01–0.21$) | | | | |
| (Intercept) | − 0.78 | 1.91 | 0.40 | n.s. |
| Breeding-season temperature | 0.27 | 0.12 | 2.14 | * |
| Coniferous forest | 0.54 | 0.43 | 1.19 | n.s. |
| Shannon habitat diversity ($H'$) | 0.32 | 0.22 | 1.38 | n.s. |
| (d) Density of threatened species ($R^2 = 0.14$) | | | | |
| (Intercept) | − 2.15 | 2.78 | 0.77 | n.s. |
| Breeding-season temperature | 0.41 | 0.13 | 2.85 | ** |

Model-averaged coefficients (conditional average) were derived from the top-ranked models ($\Delta AIC_C < 3$)

$R^2$ McFadden $R^2$, *n.s.* not significant

$^*P < 0.05$; $^{**}P < 0.01$; $^{***}P < 0.001$

especially juniper-rich calcareous grasslands compared with mesic grasslands.

Apart from habitat heterogeneity, temperature is another important driver of bird species richness and density (Pearce-Higgins and Green 2014; Keller et al. 2020). In the rather homogeneous mesic grasslands of the study area it was even the most important one. Overall species richness and the number and density of threatened species increased in plots of mesic grasslands with breeding-season temperature (= lower elevations, cf. Table A2). The same was true for the number and density of threatened species in plots of calcareous grasslands. Several thermophilic bird species detected in our study reach their regional upper distribution limit in the Diemel Valley. For example, the main distribution of Cuckoo (*Cuculus canorus*), Eurasian Turtle Dove (*Streptopelia turtur*), Green Woodpecker (*Picus viridis*), Nightingale (*Luscinia megarhynchos*) and Wryneck (*Jynx torquilla*) are largely restricted to lower elevations in the study area (cf. Grüneberg et al. 2013). Except Green Woodpecker and Nightingale all are considered threatened (Table A3). Moreover, in plots of mesic grasslands breeding-season temperature was intercorrelated with the area of hedges and copses (Table A2). As a result, the observed relationship also reflects a higher availability of potential nesting sites, song posts or hunting perches due to more hedges and copses in plots of mesic grasslands characterised by higher temperatures and lower elevations.

The area of coniferous forests was a further predictor of overall species richness of breeding birds in plots of mesic grasslands. Among the detected breeding-bird species there were several species that strongly depend on coniferous forests, such as Coal Tit (*Periparus ater*), Crested Tit (*Lophophanes cristatus*), Firecrest (*Regulus ignicapilla*), Goldcrest (*Regulus regulus*), or Treecreeper (*Certhia familiaris*), explaining this pattern (Table A3; Gatter 2000; Fartmann et al. 2018). To exclude potential effects of other habitat types such as coniferous forest on bird species composition, further studies should use plots that only consist of one of the two considered grassland types.

In conclusion, (i) habitat heterogeneity and (ii) warmer climatic conditions fostered species richness and density of breeding-bird species in semi-natural grasslands along an elevation (climate) gradient. Plots of calcareous grasslands had a high species richness and density. Especially the heterogeneous, juniper-rich calcareous grasslands seem to be a key habitat for bird assemblages with high species richness and density. These grasslands usually consisted of small-scale habitat mosaics providing suitable nesting sites and foraging grounds in close proximity. By contrast, mesic grasslands had rather homogeneous swards and shrubs or trees were normally restricted to the edges of the grassland patches.

## Implications for conservation

Based on our study, increasing small-scale habitat heterogeneity within calcareous and mesic grasslands is the key to promoting richness and density of bird species. Calcareous grasslands are hotspots of plant and insect diversity (Wallis De Vries et al. 2002; Poniatowski and Fartmann 2008; Krämer et al. 2012). As our study showed, they are also an important habitat for birds. Much of the plant and insect diversity, especially of threatened species, is associated with early and mid-successional stages of calcareous grasslands (Bourn and Thomas 2002; Fartmann et al. 2012; Poniatowski et al. 2020). Consequently, conservation management in calcareous grasslands aims to stop succession and to retain open swards in favour of specialised plant and insect species (Dekoninck et al. 2007; Poniatowski et al. 2018). For future management, habitat preferences of threatened species of breeding birds should be considered as well. Especially in areas where a continuous management (usually grazing) cannot be sustained, the successional development towards semi-open juniper-rich calcareous grasslands should be supported in favour of threatened breeding birds. Such heterogeneous habitats have generally become scarce

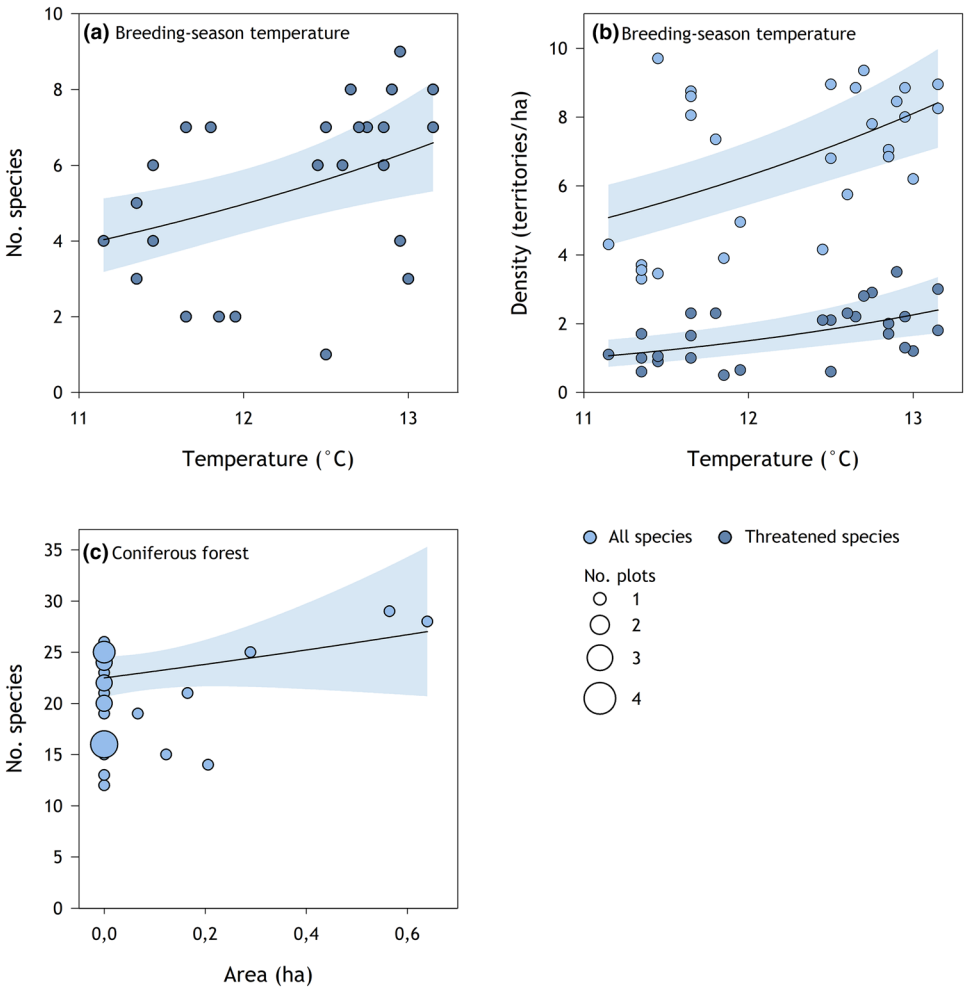


**Fig. 5** Relationship between species richness and density of all and threatened breeding-bird species, respectively, and the significant environmental parameters of averaged models for plots of mesic grasslands ($N = 27$) (see Table 4). The regression slopes (including 95% confidence intervals) were fitted using a single predictor GLMM (negative binomial error structure)

throughout Central European landscapes with negative effects on biodiversity at the landscape scale (Diacon-Bolli et al. 2012; Bonari et al. 2017; Poschlod and Braun-Reichert 2017). Additionally, juniper-rich calcareous grasslands are even legally protected under the EU Habitats Directive (EC 2007).

In mesic grasslands, habitat heterogeneity should be increased (Bonari et al. 2017). In particular, management should aim to promote stands consisting of mosaics with varying sward heights, interspersed shrubs and some solitary trees (cf. Hartel and Plieninger 2014; Plieninger et al. 2015; Jakobsson et al. 2020; Tschumi et al. 2020). Both low-intensity rough grazing and year-round grazing systems with low stocking rates seem to be suitable tools to increase the heterogeneity in mesic grasslands and, thus, should generally be preferred against regular mowing (Olff et al. 1999; Fraser et al. 2014; Köhler et al. 2016; Kmecl and Denac 2018).

**Supplementary Information** The online version contains supplementary material available at https://doi.org/10.1007/s10336-022-01972-7.

**Acknowledgements** We are grateful to Matthias Tschumi and three anonymous reviewers for valuable comments on an earlier version of the manuscript. The study was funded by the Stöckmann Foundation for Environment and Nature Conservation (Grant: S0393/10017/2019).

**Funding** Open Access funding enabled and organized by Projekt DEAL. This work was funded by Stöckmann Foundation for Environment and Nature Conservation (Grant no: S0393/10017/2019).

## Declarations

**Conflict of interest** The authors have no conflicts of interest to declare that are relevant to the content of this article.

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# Electronic Supplementary Material

# Effects of local climate and habitat heterogeneity on breeding-bird assemblages of semi-natural grasslands

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**Table A1:** Results of Spearman rank correlations ($r_s$) of environmental variables on plots of calcareous grasslands. Only intercorrelated variables are displayed. Variables with intercorrelations ($|r_s| \geq 0.5$) are highlighted by bold type. Precip. = precipitation, Temp. = temperature, Impr. mead. = improved meadow, Calca. = calcareous grassland, Forest bro. = broad-leaved forest, Small-scale = small-scale habitats, an. = annual, BS = breeding season, black = blackthorn-rich, junp. = juniper-rich. n.s. = not significant; * $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$.

| Parameter | Preci. (an.) | Preci. (BS) | Temp. (an.) | Temp. (BS) | Impr. mead. | Calca. open | Calca. black | Calca. junp. | Shrub-bery | Forest broad. | Small-scale |
|---|---|---|---|---|---|---|---|---|---|---|---|
| Elevation | 0.40* | 0.30n.s. | **–0.92*****| **–0.92***** | 0.19n.s. | 0.17n.s. | 0.21n.s. | **–0.53**** | 0.46* | **0.69***** | **0.73***** |
| Precip. (an.) | / | **0.97***** | –0.46* | **–0.52**** | 0.03n.s. | 0.35n.s. | –0.27n.s. | –0.21n.s. | 0.12n.s. | 0.37n.s. | 0.27n.s. |
| Precip. (BS) | . | / | –0.40* | –0.44* | 0.03n.s. | 0.27n.s. | –0.34n.s. | –0.07n.s. | –0.02n.s. | 0.34n.s. | 0.23n.s. |
| Temp (an.) | . | . | / | **0.98***** | –0.30n.s. | –0.03n.s. | –0.26n.s. | 0.42* | –0.35n.s. | **–0.69***** | **–0.68***** |
| Temp. (BS) | . | . | . | / | –0.26n.s. | –0.11n.s. | –0.17n.s. | 0.44* | –0.42* | **–0.69***** | **–0.68***** |
| Impr. mead. | . | . | . | . | / | **–0.53**** | 0.26n.s. | –0.06n.s. | 0.26n.s. | 0.30n.s. | –0.04n.s. |
| Calca. open | . | . | . | . | . | / | –0.07n.s. | **–0.52**** | 0.23n.s. | 0.16n.s. | 0.22n.s. |
| Calca. black | . | . | . | . | . | . | / | **–0.55**** | 0.19n.s. | 0.19n.s. | 0.06n.s. |
| Calca. junp. | . | . | . | . | . | . | . | / | **–0.51**** | –0.48* | –0.34n.s. |
| Shrubbery | . | . | . | . | . | . | . | . | / | 0.35n.s. | 0.30n.s. |
| Forest broad. | . | . | . | . | . | . | . | . | . | / | **0.65***** |

**Table A2:** Results of Spearman rank correlations ($r_s$) of environmental variables on plots of mesic grasslands. Only intercorrelated variables are displayed. Variables with intercorrelations ($|r_s| \geq 0.5$) are highlighted by bold type. Precip. = precipitation, Temp. = temperature, Impr. = improved, Hedge = hedges and copses, an. = annual, BS = breeding season, mead. = meadow, past. = pasture. n.s. = not significant; * $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$.

| Parameter | Precip. (an.) | Precip. (BS) | Temp. (an.) | Temp. (BS) | Arable land | Impr. mead. | Impr. past. | Hedge |
|---|---|---|---|---|---|---|---|---|
| Elevation | **0.78***** | **0.70***** | **–0.93***** | **–0.93***** | **–0.53***** | 0.12n.s. | 0.06n.s. | **–0.61***** |
| Precip. (an.) | / | **0.98***** | **–0.88***** | **–0.88**** | **–0.66**** | 0.27n.s. | 0.15n.s. | –0.36n.s. |
| Precip. (BS) | . | / | **–0.83***** | **–0.82*** | **–0.64**** | 0.27n.s. | 0.15n.s. | –0.34n.s. |
| Temp (an.) | . | . | / | **0.99***** | **0.58***** | –0.13n.s. | –0.02n.s. | **0.58**** |
| Temp. (BS) | . | . | . | / | **0.56***** | –0.29n.s. | –0.05n.s. | **0.56**** |
| Arable land | . | . | . | . | / | –0.33n.s. | –0.29n.s. | 0.16n.s. |
| Impr. mead. | . | . | . | . | . | / | **0.66***** | 0.29n.s. |
| Impr. past. | . | . | . | . | . | . | / | –0.17n.s. |

**Table A3**: Breeding-bird species, threat status, and number of territories in the studied plots ($N$ = 54). Common name: Newton (2017); scientific name: Barthel and Helbig (2005). Threat status: North Rhine-Westphalia – Grüneberg et al. (2017); Hesse – Wolf and Widdig (2016); CR = critically endangered, EN = endangered, VU = vulnerable, NT = near threatened.

| Common name | Scientific name | Threat status | Territories |
|---|---|---|---|
| Yellowhammer | *Emberiza citrinella* | ./NT | 174 |
| Eurasian Blackcap | *Sylvia atricapilla* | ./. | 172 |
| Chiffchaff | *Phylloscopus collybita* | ./. | 161 |
| Great Tit | *Parus major* | ./. | 140 |
| Blackbird | *Turdus merula* | ./. | 133 |
| Whitethroat | *Sylvia communis* | ./. | 109 |
| Chaffinch | *Fringilla coelebs* | ./. | 102 |
| European Robin | *Erithacus rubecula* | ./. | 101 |
| Willow Warbler | *Phylloscopus trochilus* | NT/. | 93 |
| Blue Tit | *Cyanistes caeruleus* | ./. | 82 |
| Dunnock | *Prunella modularis* | ./. | 73 |
| Song Thrush | *Turdus philomelos* | ./. | 60 |
| Lesser Whitethroat | *Sylvia curruca* | NT/NT | 58 |
| Linnet | *Carduelis cannabina* | VU/VU | 55 |
| Garden Warbler | *Sylvia borin* | ./. | 51 |
| Red-backed Shrike | *Lanius collurio* | NT/NT | 37 |
| Tree Pipit | *Anthus trivialis* | EN/EN | 35 |
| Wood Pigeon | *Columba palumbus* | ./. | 33 |
| Greenfinch | *Carduelis chloris* | ./. | 27 |
| Tree Sparrow | *Passer montanus* | VU/NT | 27 |
| Wren | *Troglodytes troglodytes* | ./. | 25 |
| Green Woodpecker | *Picus viridis* | ./. | 23 |
| Long-tailed Tit | *Aegithalos caudatus* | ./. | 23 |
| Firecrest | *Regulus ignicapilla* | ./. | 17 |
| Great-spotted Woodpecker | *Dendrocopos major* | ./. | 16 |
| Bullfinch | *Pyrrhula pyrrhula* | ./. | 16 |
| Willow Tit | *Poecile montanus* | ./. | 16 |
| Jay | *Garrulus glandarius* | ./. | 14 |
| Skylark | *Alauda arvensis* | VU/NT | 13 |
| Marsh Tit | *Poecile palustris* | ./. | 13 |
| Wryneck | *Jynx torquilla* | CR/CR | 11 |
| Short-toed Treecreeper | *Certhia brachydactyla* | ./. | 10 |
| Magpie | *Pica pica* | ./. | 9 |
| Fieldfare | *Turdus pilaris* | NT/. | 9 |
| Goldcrest | *Regulus regulus* | ./. | 9 |
| Mistle Thrush | *Turdus viscivorus* | ./. | 8 |
| Carrion Crow | *Corvus corone* | ./. | 8 |
| Goldfinch | *Carduelis carduelis* | ./NT | 8 |
| Eurasian Nuthatch | *Sitta europaea* | ./. | 6 |
| Spotted Flycatcher | *Muscicapa striata* | ./. | 5 |
| Cuckoo | *Cuculus canorus* | EN/VU | 5 |
| Coal Tit | *Periparus ater* | ./. | 5 |

34 **Table A3 (continued)**

| Common name | Scientific name | Threat status | Territories |
|---|---|---|---|
| White Wagtail | *Motacilla alba* | NT/. | 4 |
| Crested Tit | *Lophophanes cristatus* | ./. | 4 |
| Hawfinch | *Coccothraustes coccothraustes* | ./. | 4 |
| Starling | *Sturnus vulgaris* | VU/. | 4 |
| European Turtle Dove | *Streptopelia turtur* | EN/EN | 4 |
| Wood Warbler | *Phylloscopus sibilatrix* | VU/VU | 4 |
| Common Buzzard | *Buteo buteo* | ./. | 4 |
| Woodlark | *Lullula arborea* | ./CR | 4 |
| Grey-headed Woodpecker | *Picus canus* | EN/EN | 4 |
| Black Redstart | *Phoenicurus ochrurus* | ./. | 3 |
| Stock Dove | *Columba oenas* | ./. | 3 |
| Nightingale | *Luscinia megarhynchos* | ./. | 3 |
| Black Woodpecker | *Dryocopus martius* | ./. | 3 |
| House Sparrow | *Passer domesticus* | NT/NT | 2 |
| Lesser Spotted Woodpecker | *Dryobates minor* | VU/NT | 2 |
| Marsh Warbler | *Acrocephalus palustris* | ./. | 2 |
| Treecreeper | *Certhia familiaris* | ./. | 2 |
| Common Grasshopper Warbler | *Locustella naevia* | VU/NT | 2 |
| Red Kite | *Milvus milvus* | ./. | 2 |
| Raven | *Corvus corax* | ./. | 2 |
| Grey Wagtail | *Motacilla cinerea* | ./. | 1 |
| Icterine Warbler | *Hippolais icterina* | ./VU | 1 |
| Hobby | *Falco subbuteo* | VU/NT | 1 |
| White-throated Dipper | *Cinclus cinclus* | ./. | 1 |
| Kestrel | *Falco tinnunculus* | ./. | 1 |

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