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Research article

Encroachment of the Upright brome (*Bromus erectus*) in calcareous grasslands – Assessment of the drivers and effects on plant species assemblages

Thomas Fartmann [a,b,*], Merle Streitberger [a], Dominik Poniatowski [a], Marcel Kettermann [a], Carsten Schmidt [c], Lisa Holtmann [a]

[a] Department of Biodiversity and Landscape Ecology, Osnabrück University, Barbarastraße 11, 49076, Osnabrück, Germany
[b] Institute of Biodiversity and Landscape Ecology (IBL), An der Kleimannbrücke 98, 48157, Münster, Germany
[c] Sudmühlenstraße 88, 48157, Münster, Germany

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ABSTRACT

Calcareous grasslands have an outstanding value for biodiversity conservation. However, they are threatened across Europe. The Upright brome (*Bromus erectus*) is a tall perennial tussock grass, which has increasingly become dominant in calcareous grasslands. Today, its expansion is a major challenge for nature conservation. Here, we studied the drivers and effects of *B. erectus* encroachment on plant species assemblages across a productivity gradient in semi-dry calcareous grasslands in Germany. Our study revealed, that despite intensified conservation management, the cover of *B. erectus* increased from 1978–'81 to 2020 in the two most productive types of grasslands (*Onobrychido-Brometum typicum* and *primuletosum*) by the factor 1.6 and 2.0, respectively. Across the environmental gradient, *B. erectus* had its highest cover (mean: 53 %) in plots of the *Onobrychido-Brometum typicum*, which exhibited an intermediate productivity. Overall, the encroachment of *B. erectus* has led to a structural and floristic homogenisation. We explain the expansion during the last 40 years particularly by climate change (i.e., milder winters and drier summers) but also nitrogen deposition. The capacity of *B. erectus* to exploit its habitats even during cool periods of the year is a strong advantage against competitors. This is especially true for deep soils that are enriched in nitrogen due to atmospheric deposition. Summer drought also favours the species. Overall, a higher management frequency is needed to counteract the encroachment of *B. erectus*. Particularly, grazing in winter and early spring, but also mowing and prescribed burning during that period, are suitable tools.

1. Introduction

Temperate, semi-natural grasslands are hotspots of biodiversity (Bonari et al., 2017; Feurdean et al., 2018; Fartmann, 2024). Over many centuries, traditional land management (i.e., grazing, mowing or burning) has created and maintained these species-rich ecosystems (Pärtel et al., 2005; Bonari et al., 2017; Feurdean et al., 2018; Fartmann, 2024). However, with ongoing intensification of agriculture, particularly from the second half of the 20th century onwards, the area of semi-natural grasslands has dramatically decreased. Land use intensification, abandonment with subsequent succession and afforestation have mainly contributed to this (Squires et al., 2018; Fartmann, 2024). Today, the remnants of semi-natural grasslands often suffer from a deteriorating habitat quality due to inappropriate management (Poniatowski et al., 2018a; Fartmann, 2024), eutrophication as a result of airborne nitrogen deposition (WallisDeVries and Bobbink, 2017; Vogels et al., 2023) or climate change (Díaz et al., 2019; Harvey et al., 2023).

Calcareous grasslands are among the most species-rich semi-natural grasslands throughout Europe (Fartmann, 2024). They have an

* Corresponding author. Department of Biodiversity and Landscape Ecology, Osnabrück University, Barbarastraße 11, 49076, Osnabrück, Germany.
E-mail address: t.fartmann@uos.de (T. Fartmann).

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outstanding value for biodiversity conservation due to their highly diverse flora and insect fauna, but also bird assemblages (Poschlod and WallisDeVries, 2002; WallisDeVries et al., 2002; Köhler et al., 2016; Poniatowski et al., 2018a; Brüggeshemke et al., 2022). Moreover, calcareous grasslands supply many providing, regulating, and cultural ecosystem services (Hallikma et al., 2023). Semi-dry calcareous grasslands are considered vulnerable at the EU level (Janssen et al., 2016) and even endangered to critically endangered in Germany (Finck et al., 2017). Due to their importance for biodiversity conservation and high threat status, they are legally protected by the EU Habitats Directive (EC, 2013).

The Upright brome (*Bromus erectus* Huds.) is a tall perennial tussock grass, which is typical of calcareous grasslands in western and south-western Europe (Royer, 1991; Sutkowska et al., 2013). By contrast, in Central Europe, it was absent until the modern age (Poschlod and WallisDeVries, 2002). The northern parts of its Central European range have mostly been colonised since the 20th century and the expansion is still ongoing (Bornkamm, 2008; Poniatowski et al., 2018b). Moreover, particularly from the 1990s onwards and in contrast to its more mesophytic antagonist, *Brachypodium pinnatum* (Corcket et al., 2003; Kahlert et al., 2005), *B. erectus* has increasingly become dominant in calcareous grasslands (Fig. 1; Poniatowski et al., 2018b; Mazalla et al., 2022; Meier et al., 2022). This is especially true for all those regions that, today, are characterised by mild winters and where periods of summer drought regularly occur (Poniatowski et al., 2018b; Meier et al., 2022, 2024; own observation). Accordingly, there is growing evidence that climate change (i.e., drier summers and milder winters) has mainly favoured the population growth and, hence, the dominance of the grass (Poniatowski et al., 2018b; Lemmer et al., 2021; Meier et al., 2022). However, airborne nitrogen deposition has likely been an additional driver (Meier et al., 2022). It has been shown that the dominance of *B. erectus* leads to taller, denser swards, a higher cover of litter and declines in plant species richness (Poniatowski et al., 2018b; Meier et al., 2022). Due to structural and floristic homogenisation as well as a cooler microclimate the diversity of insect species is also known to suffer (Poniatowski et al., 2018b). However, species-rich grasslands are generally more resistant and resilient against the effects of global warming (De Keersmaecker et al., 2016; Vogel et al., 2012). As a result, the already large extent of calcareous grasslands with encroachment of *B. erectus* is a major challenge for biodiversity conservation in Central Europe.

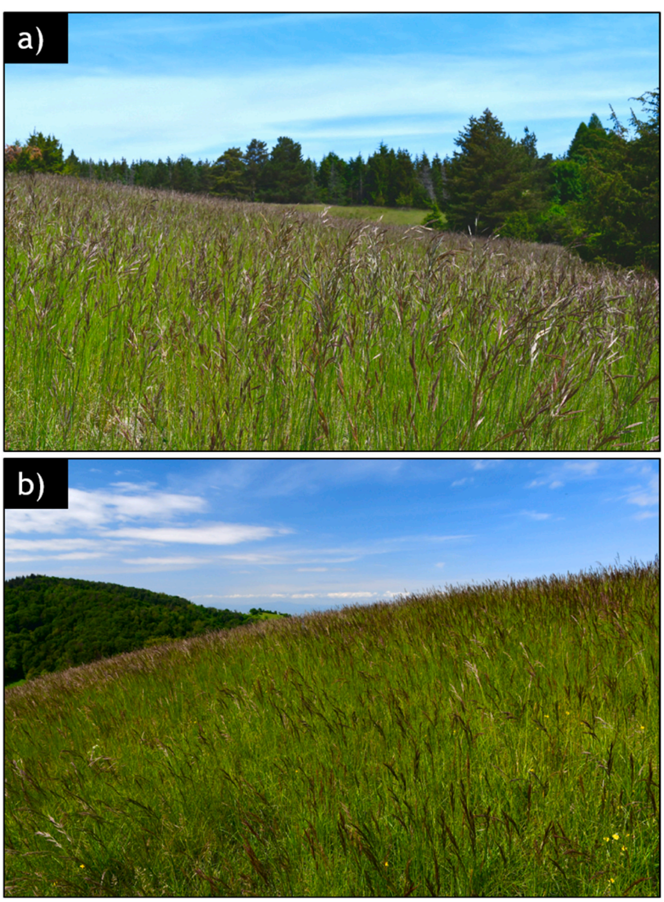

Fig. 1. Examples of calcareous grasslands with encroachment of the Upright brome (*Bromus erectus*) in Central Europe: a) Hohe Geba (Central Germany: Thuringia) and b) Kaiserstuhl (study area, SW Germany: Baden-Württemberg). Photographs: T. Fartmann.

The aim of the study was to identify the drivers and effects of *B. erectus* encroachment on plant species assemblages across a productivity gradient in semi-dry calcareous grasslands. It was conducted in the Kaiserstuhl in the south-west of the German federal state of Baden-Württemberg (SW Germany; Figs. 2 and 3). We selected this study area, (i) since *B. erectus* was already widespread in the calcareous grasslands in former times (von Rochow, 1951), (ii) historic data (1978–'81) on the cover of the grass species were available (Bürger, 1983) and (iii) the grasslands are nationally famous for their high plant species richness (Wilmanns, 2011). Moreover, particularly during the past 20 years, a sophisticated management has been introduced in the calcareous grasslands (Meineke et al., 2011). Accordingly, we were able to assess changes in the cover of *B. erectus* over a time period of 40 years and to evaluate both the effects of abiotic drivers and land use on the population growth of the species in the grasslands. In detail, we studied three different vegetation types each with three management treatments, across an environmental gradient from more xerophytic to more mesophytic calcareous grasslands, because soil productivity may affect *B. erectus* encroachment. Per treatment we randomly selected six plots ($N = 54$) that had been managed consistently in the same way for at least seven years. Per plot, we sampled abiotic parameters (mesoclimate, Ellenberg indicator values), plant species and their cover as well as the cover of litter and the grass/herb ratio. Based on our findings, we made recommendations for the management of species-rich calcareous grasslands in times of global change. In particular, we address the following research questions.

(i) Has the cover of *B. erectus* changed in the semi-dry calcareous grasslands of the study area during the last 40 years?
(ii) How does the encroachment of *B. erectus* affect plant species assemblages?
(iii) What are the drivers of *B. erectus* cover?
(iv) What are the recommendations for the management of species-rich calcareous grasslands in times of global change?

2. Materials and methods

2.1. Study area

The study area comprises the central part of the Kaiserstuhl in the south-west of the German federal state of Baden-Württemberg (SW Germany, 48°6"N, 7°41"E; Figs. 2 and 3). The Kaiserstuhl is a 92 km^2 large volcanic mountain remain rising about 350 m above the southern Upper Rhine Valley between Freiburg and the river Rhine (Wilmanns et al., 1974). The volcanic bedrock is covered by calcareous loess with a thickness of up to 30 m. Due to its geographic location, the Kaiserstuhl benefits from the invasion of warm air masses from southwest through the Belfort Gap and from rain shadow effects and foehn wind from the Vosges in the west (Möllenbeck et al., 2009). As a result, the study area is characterised by an exceptionally warm and dry climate with an average annual temperature of 11.2 °C and a mean annual precipitation of 666 mm (long-term mean: 1991–2020, Vogtsburg-Oberrotweil, 223 m a.s.l.;

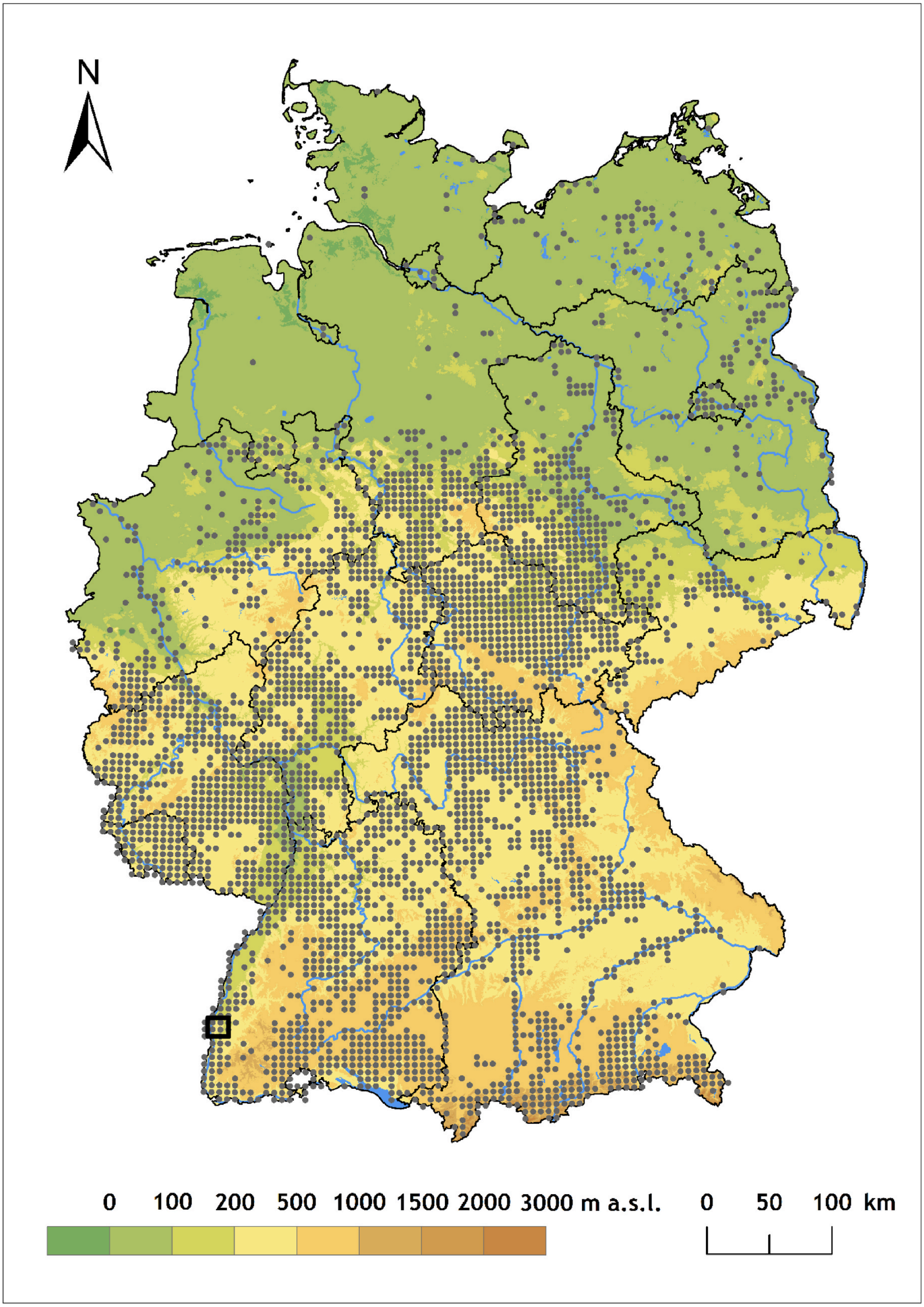

Fig. 2. Distribution of the Upright brome (*Bromus erectus*) in Germany. The study area (Kaiserstuhl) in southwestern Germany is outlined by a black frame. Source of the distribution data of *B. erectus*: Federal Agency for Nature Conservation (2024).

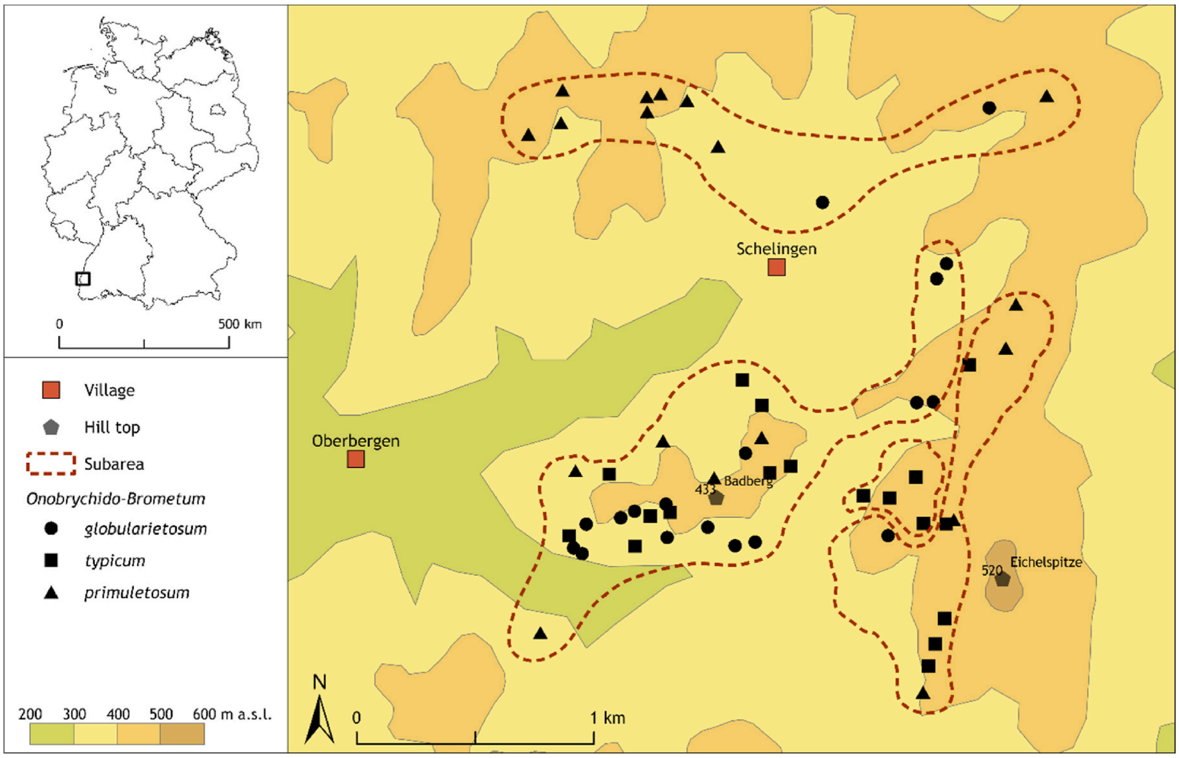

Fig. 3. Location of the study area (Kaiserstuhl), the four subareas and plots in southwestern Germany.

DWD, 2024).

From 1980 to 2020, mean annual temperature increased by 0.8 °C (linear regression: $R^2 = 0.12$, $P < 0.05$, $y = -29.03 + (0.0199 \times year)$), whereas annual precipitation decreased by 117 mm ($R^2 = 0.08$, $P < 0.05$, $y = 6515.326 - (2.913 \times year)$) (Fig. A.1; 1980–2003: Vogtsburg-Oberrotweil, 223 m a.s.l., DWD, 2024; 2004–2020: Rotweil, 179 m a.s.l., Agrarmeteorologie BW, 2024). Accordingly, periods of summer drought have occurred more frequently from the 1990s onwards (Boergens et al., 2020; European Drought Observatory, 2024; UFZ, 2024). Particularly, the summers 2003, 2018 and 2020 were characterised by severe drought (UFZ, 2024). Prior to the study in the growing season of 2020, meteorological spring was drier (−57 mm) and warmer (+1.3 °C) than usual (compared to the long-term mean (1991–2020), Rotweil, 179 m a.s.l., Agrarmeteorologie BW, 2024). By contrast, spring before the second study period in the summer of 2023 was a very typical one (difference to long-term mean: −8 mm, +0.1 °C).

The special geographic location and climatic conditions have resulted in a flora rich in Mediterranean/sub-Mediterranean but also Continental species (Wilmanns, 2011). In former times, semi-dry calcareous grasslands, which were grazed in winter and mown once per year from July onwards, covered large parts of the study area (von Rochow, 1951; Bürger, 1983; Wilmanns, 1989; Treiber, 2019). These species-rich grasslands belong to the association *Onobrychido viciifoliae-Brometum erecti* (Bürger, 1983; nomenclature of the associations follows Bergmeier, 2020). Due to the water balance and, hence, nutrient availability of the soils, the grasslands can be differentiated into the following three subassociations (hereinafter referred to as ‘vegetation type’) (Bürger, 1983): Stands of the *Onobrychido-Brometum globularietosum* grow on steeper and shallow south-facing slopes and form transitions to the more xerophytic grasslands of the *Xerobrometum*. Besides some species of the *Xerobrometum*, such as *Allium sphaerocephalon*, *Galatella linosyris* or *Globularia bisnagarica*, plants of thermophilous fringes regularly occur in this vegetation type. Overall, the stands are characterised by a high share of threatened plant species. Due to the very low nutrient availability on the dry soils and, therefore, a very low productivity, mowing was often conducted only irregularly (Wilmanns, 1989). By contrast, stands of the *Onobrychido-Brometum primuletosum* grow on fresher soils, particularly on western, northern and eastern slopes (Bürger, 1983). They are transitions to mesic meadows of the *Arrhenatheretum* and are characterised by the highest plant species richness among the three vegetation types. Indicative species are *Betonica officinalis*, *Briza media*, *Primula veris*, *Prunella grandiflora*, and *Ranunculus nemorosus*. Environmental conditions of the soils colonised by stands of the *Onobrychido-Brometum typicum* are between those of the two other vegetation types. The *Onobrychido-Brometum typicum* has no indicative species.

Until the mid-1950s, most of the calcareous grasslands became abandoned (Bürger, 1983; Wilmanns, 2011). Long-term abandonment had resulted in: (i) a lower cover of many characteristic species of calcareous grasslands, (ii) an establishment of dominant stands of the rhizomatous Tor grass (*Brachypodium pinnatum*) and (iii) an encroachment of fringe (e.g. *Geranium sanguineum* or *Origanum vulgare*) and woody species (e.g. *Prunus spinosa* or *Robinia pseudoacacia*). Starting at the end of the 1980s and particularly during the last 20 years, a sophisticated management has been introduced to the vast majority of the remaining patches of calcareous grasslands to maintain grassland biodiversity (Meineke et al., 2011). In the study area, the current deposition rates of airborne nitrogen are 10–15 kg ha^{-1} y^{-1} (LUBW, 2022) and, hence, are already at the critical loads for calcareous grasslands, which are 10–20 kg ha^{-1} y^{-1} (Bobbink et al., 2022).

For the research, those four subareas that contained the largest calcareous grasslands within the study area were chosen (Fig. 3). They differed in environmental conditions, particularly in type of bedrock under the loess layer (cf. Walter et al., 2018), and had a total size of 235 ha of which 57 % (135 ha) was covered by calcareous grasslands. The elevation of the subareas varied from 280 to 480 m a.s.l.

2.2. Current conservation management in the calcareous grasslands

Conservation management in the plots (see below) has been conducted consistently in the same way for at least seven years (between 2017 and 2023). For each of the three vegetation types, three different management regimes were applied (hereinafter referred to as 'treatment'). Overall, management intensity was adjusted to moisture and nutrient availability, hence productivity across the vegetation types. Accordingly, it increases from the *Onobrychido-Brometum globularietosum*, over the *Onobrychido-Brometum typicum* to the *Onobrychido-Brometum primuletosum* (see above). For the *Onobrychido-Brometum globularietosum*, the following treatments were applied: (i) abandonment (ABA), (ii) rotational grazing by goats in summer (PAS_G) and (iii) mowing in autumn (mostly in September) (MEA_9). By contrast, all plots of the *Onobrychido-Brometum typicum* were used as meadows. The treatments included: (i) meadows that were mown in late summer (usually August) but were additionally grazed by sheep in early spring (usually March) (MEA_S3_8), (ii) meadows that were mown twice, once in spring (usually April) and once in late summer (usually August) (MEA_4_8) and (iii) meadows that were mown in summer (usually second half of July) and partly grazed in late autumn by sheep (MEA_7). For the *Onobrychido-Brometum primuletosum*, two meadow treatments and one pasture treatment had been established: (i) meadows that were mown in late summer (usually August) (MEA_8), (ii) meadows that were mown in summer (usually second half of July) and partly grazed in late autumn by sheep (MEA_7) and (iii) year-round pastures (cattle, horses and sheep (PAS_Y). In all mowing regimes, the hay was removed from the grasslands. The only exception was the treatment that included two mowing events. Here, during the first annual mowing the cut vegetation was not removed from the plot and between 2020 and 2022 this mowing event was even completely suspended.

2.3. Study design

Within the four subareas, we randomly selected six plots of 4 m × 4 m (16 m^2) for each of the nine combinations of vegetation types × treatments mentioned before using the 'create random points' tool in ArcGIS 10.8 ($N = 54$). Plots were marked at their corners with tent pegs and magnets. Additionally, the geographic coordinates were gathered by using a GPS (Garmin GPSMAP 64S). In June/July 2020 we estimated the cover of each plant species (vascular plants and bryophytes) per plot according to the Wilmanns scale (Wilmanns, 1998). For statistical analyses, the categories of the scale were translated into percentage-cover values: r = 0.1 %, + = 0.5 %, 1 = 1 %, 2m = 2.5 %, 2a = 10 %, 2b = 20.5 %, 3 = 38 %, 4 = 63 %, and 5 = 88 % (Dierschke, 1994). We quantified the taxonomic richness and diversity of plants using Hill numbers, which provide a mathematically unified set of diversity indices in units of species (Hill, 1973; Jost, 2006; Chao et al., 2014). The sensitivity of these indices to species relative abundances is controlled by the order q (Chao et al., 2014). We considered Hill numbers at $q = 0$, which represents species richness, and at $q = 1$, which is equivalent to the exponential of Shannon entropy (hereinafter termed 'Shannon diversity'; Jost, 2006; Chao et al., 2014). Additionally, we calculated the share of plant species threatened either in Baden-Württemberg or in Germany per plot (including near threatened species) (for threatened species see Tab. A.2 and A.3). Information on the threat status was derived for vascular plants from Breunig and Demuth (2023) and Metzing et al. (2018), and for bryophytes from Sauer and Ahrens (2006) and Caspari et al. (2018).

Moreover, we estimated the cover of grasses, herbs and litter with an accuracy of 5 %. If values were above 95 % or below 5 %, we used steps of 2.5 % (Helbing et al., 2021). Since the vitality of *Bromus erectus* is known to vary due to weather conditions in spring (Bornkamm, 1961), the cover of *B. erectus* and the three other parameters (cover of grasses, herbs and litter) were sampled once again in June 2023 in all plots. A magnetic pickup (Schonstedt GA-52Cx) and a GPS (Garmin GPSMAP 64S) were used to locate the permanent plots.

To characterise soil conditions, we calculated Ellenberg's indicator values for nitrogen, moisture, soil reaction and light (Ellenberg and Leuschner, 2010; nitrogen indicator values for mosses were derived from Simmel et al., 2020). Moreover, we assessed aspect and slope by using a compass with inclinometer. For further analysis, we converted aspect by sine and cosine into 'eastness' and 'northness' (for instance eastness = 0 and northness = 1 meaning 360°, eastness = 1 and northness = 0 meaning 90°). Additionally, aspect, inclination and latitude were used to calculate the heat load index according to McCune and Keon (2002).

To ascertain changes in the cover of *B. erectus* in stands of the three subassociations of the *Onobrychido-Brometum* during recent decades, we compared mean cover of *B. erectus* in relevés conducted by Bürger (1983) in 1978–1981 in the same study area. The translation of the cover categories followed the rules mentioned above. Samples of dominance stands of *Brachypodium pinnatum* within the *Onobrychido--Brometum* due to long-term abandonment were excluded from the analysis. Overall, 30 samples of the *Onobrychido-Brometum globularietosum*, 7 of the *Onobrychido-Brometum typicum* and 29 of the *Onobrychido-Brometum primuletosum* were available for the comparison.

2.4. Statistical analysis

All statistical analyses were performed by using R 4.3.1 (R Development Core Team, 2024). Differences in environmental parameters, species richness, Shannon diversity (see below) and proportion of threatened species (response variables) between vegetation types and treatments (explanatory variables) were analysed by generalised linear mixed-effects models (GLMMs) with Poisson (count data) or proportional binomial error (proportional/cover data) structure. The GLMMs were followed by Tukey contrasts for pairwise comparisons (glht function, R package multcomp; Hothorn et al., 2024).

To assess the abiotic drivers (explanatory variables) of *B. erectus* cover (response variable), we fitted multivariable proportional binomial GLMMs. Predictors were standardised (centred and scaled) to make their effect size comparable (cf. Kämpfer et al., 2023). To avoid model overfitting, we checked all abiotic parameters (Ellenberg indicator values, northness, eastness, heat load index) for intercorrelations using Spearman's rank correlation (r_s). Due to intercorrelations ($|r_s| > 0.5$), eastness and northness as well as light, moisture, and soil reaction indicator value were excluded from further analysis (see Table A.1). If graphical inspections of the data suggested unimodal rather than linear relationships between the response variable and predictor variables, centred and squared values of the predictors were entered into the full model in addition to the untransformed values (cf. Kämpfer et al., 2023). As a result, we included the four following variables: (i) nitrogen indicator value, (ii) centred and squared nitrogen indicator value, (iii) heat load index and (iv) centred and squared heat load index in the model. Due to overdispersion in the model, we included observation level random effects to reduce overdispersion (Harrison, 2014, 2015). To identify the most important predictors, model averaging based on an

Table 1
Mean values (±SE) of environmental parameters of the studied vegetation types and treatments. Vegetation type: *Onobrychido-Brometum globularietosum* (glob), *Onobrychido-Brometum typicum* (typ) and *Onobrychido-Brometum primuletosum* (prim). Treatment: ABA = abandoned grassland, PAS_G = rotational goat pasture, MEA_9 = meadow mown in autumn, MEA_S3_8 = meadow grazed by sheep in spring and mown in late summer, MEA_4_8 = meadow mown in spring and late summer, MEA_7 = meadow mown in mid-summer and partly grazed by sheep in late autumn, MEA_8 = meadow mown in late summer, PAS_Y = year-round cattle and horse pasture. Sample size: $n = 6$ per treatment; $N = 54$. Statistical differences were detected using GLMM with subarea as a random intercept. Significance of pairwise comparisons is indicated by different letters (Tukey contrasts; $P \leq 0.05$). For further information see section 2. Statistical significances are indicated as follows: n.s. $P > 0.05$, *$P \leq 0.05$, **$P \leq 0.01$, ***$P \leq 0.001$.

Parameter	*Onobrychido-Brometum globularietosum*			*P*	*Onobrychido-Brometum typicum*			*P*	*Onobrychido-Brometum primuletosum*			*P*	*Onobrychido-Brometum*			*P*
	ABA	PAS_G	MEA_9		MEA_S3_8	MEA_4_8	MEA_7		MEA_8	MEA_7	PAS_Y		glob	typ	prim	
Mesoclimate																
Heat load index	0.9 ± 0.0	0.8 ± 0.0	0.9 ± 0.0	n.s.	0.8 ± 0.1^{a}	0.9 ± 0.0^{b}	0.8 ± 0.1^{a}	*	0.8 ± 0.1	0.8 ± 0.0	0.8 ± 0.1	n.s.	0.8 ± 0.0	0.8 ± 0.0	0.8 ± 0.0	n.s.
Eastness	0.2 ± 0.1	0.3 ± 0.1	−0.3 ± 0.3	n.s.	0.0 ± 0.4^{a}	−0.9 ± 0.0^{b}	−0.2 ± 0.3^{a}	**	−0.4 ± 0.3	−0.6 ± 0.2	0.1 ± 0.5	n.s.	0.1 ± 0.1	−0.3 ± 0.2	−0.4 ± 0.2	n.s.
Northness	−0.9 ± 0.0	−0.9 ± 0.1	−0.5 ± 0.2	n.s.	0.0 ± 0.3	−0.1 ± 0.2	0.4 ± 0.2	n.s.	0.0 ± 0.3	0.5 ± 0.2	−0.4 ± 0.2	n.s.	−0.8 ± 0.1^{a}	0.1 ± 0.1^{b}	0.1 ± 0.2^{b}	***
Indicator value																
Light	7.7 ± 0.1^{ab}	7.8 ± 0.1^{a}	7.5 ± 0.0^{b}	*	7.3 ± 0.1^{a}	7.2 ± 0.1^{ab}	7.1 ± 0.1^{b}	*	7.1 ± 0.1^{a}	7.1 ± 0.1^{a}	7.4 ± 0.0^{b}	*	7.6 ± 0.1^{a}	7.2 ± 0.1^{b}	7.2 ± 0.1^{b}	***
Moisture	3.1 ± 0.1	3.2 ± 0.0	3.3 ± 0.1	n.s.	3.5 ± 0.2^{a}	3.7 ± 0.1^{ab}	4.0 ± 0.2^{b}	*	3.9 ± 0.1	4.0 ± 0.1	3.8 ± 0.1	n.s.	3.1 ± 0.1^{a}	3.6 ± 0.1^{b}	4.0 ± 0.1^{c}	***
Nitrogen	2.9 ± 0.1	2.9 ± 0.1	2.9 ± 0.1	n.s.	3.2 ± 0.3^{a}	3.4 ± 0.1^{ab}	3.9 ± 0.2^{b}	*	3.4 ± 0.1	3.6 ± 0.2	3.6 ± 0.1	n.s.	2.9 ± 0.1^{a}	3.3 ± 0.1^{b}	3.6 ± 0.1^{c}	***
Soil reaction	7.7 ± 0.0	7.7 ± 0.1	7.5 ± 0.1	n.s.	7.3 ± 0.2	7.3 ± 0.1	6.9 ± 0.2	n.s.	7.2 ± 0.2	6.9 ± 0.2	7.2 ± 0.1	n.s.	7.7 ± 0.0^{a}	7.2 ± 0.1^{b}	7.1 ± 0.1^{b}	***

information-theoretic approach using the 'dredge' function (R package MuMIn; Barton, 2020) was conducted (Burnham and Anderson, 2002; Grueber et al., 2011). Only the top-ranked models within $\Delta AIC_C < 3$ were included (Grueber et al., 2011). In all GLMMs subarea was used as a random intercept. Since these random effects inflate conditional R^2 despite having little ecological importance, we only displayed marginal R^2 in our models (Harrison, 2014; Nakagawa et al., 2017).

Differences in the cover of *B. erectus* between 1978–'81 and 2020 were analysed by using a *t*-test. By contrast, differences in the cover of *B. erectus* and litter as well as in the grass/herb ratio between 2020 and 2023 were assessed by paired *t*-test.

3. Results

3.1. Environmental conditions

Environmental conditions clearly differed between the vegetation types, particularly between plots of the *Onobrychido-Brometum globularietosum* and those of the two other vegetation types (Table 1). The prior was characterised by more southern aspects (= negative northness figures) as well as higher light and soil reaction indicator values. Moisture and nitrogen indicator values increased along the studied productivity gradient of calcareous grasslands in the following order: plots of the *Onobrychido-Brometum globularietosum*, *typicum* and *primuletosum.* By contrast, differences in mesoclimate and indicator values between the treatments within one of the vegetation types were usually low. The only exception was the *Onobrychido-Brometum typicum*. Meadows mown twice were characterised by more western aspects (= negative eastness figures) and a higher heat load index than plots of the two other treatments. Moreover, light indicator values decreased, while moisture as well as nitrogen indicator values increased in the following order: meadows that were also grazed in spring, meadows mown twice and meadows mown once. In the two other vegetation types, only the light indicator values differed between the treatments. In plots of the *Onobrychido-Brometum globularietosum*, they were highest in the goat pastures and lowest in the meadows mown in autumn. In plots of the *Onobrychido-Brometum primuletosum*, the light indicator values were higher in the year-round pastures than in those of the two other treatments.

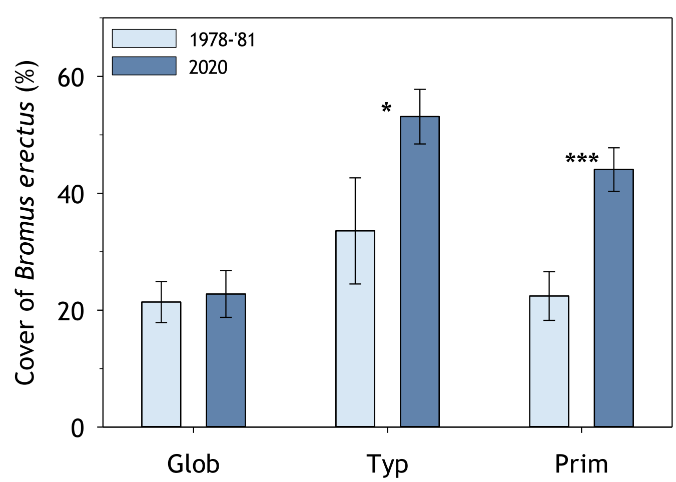

Fig. 4. Mean (±SE) changes in the cover of *Bromus erectus* in the study area from 1978–'81 to 2000 in the three vegetation types. Vegetation type: *Onobrychido-Brometum globularietosum* (Glob), *Onobrychido-Brometum typicum* (Typ) and *Onobrychido-Brometum primuletosum* (Prim). Sample size: Glob – 30 vs. 18, Typ – 7 vs. 18, Prim – 29 vs. 18. Statistical differences between years were analysed by *t*-test. For further information see section 2. Statistical significances are indicated as follows: *$P \leq 0.05$, ***$P \leq 0.001$.

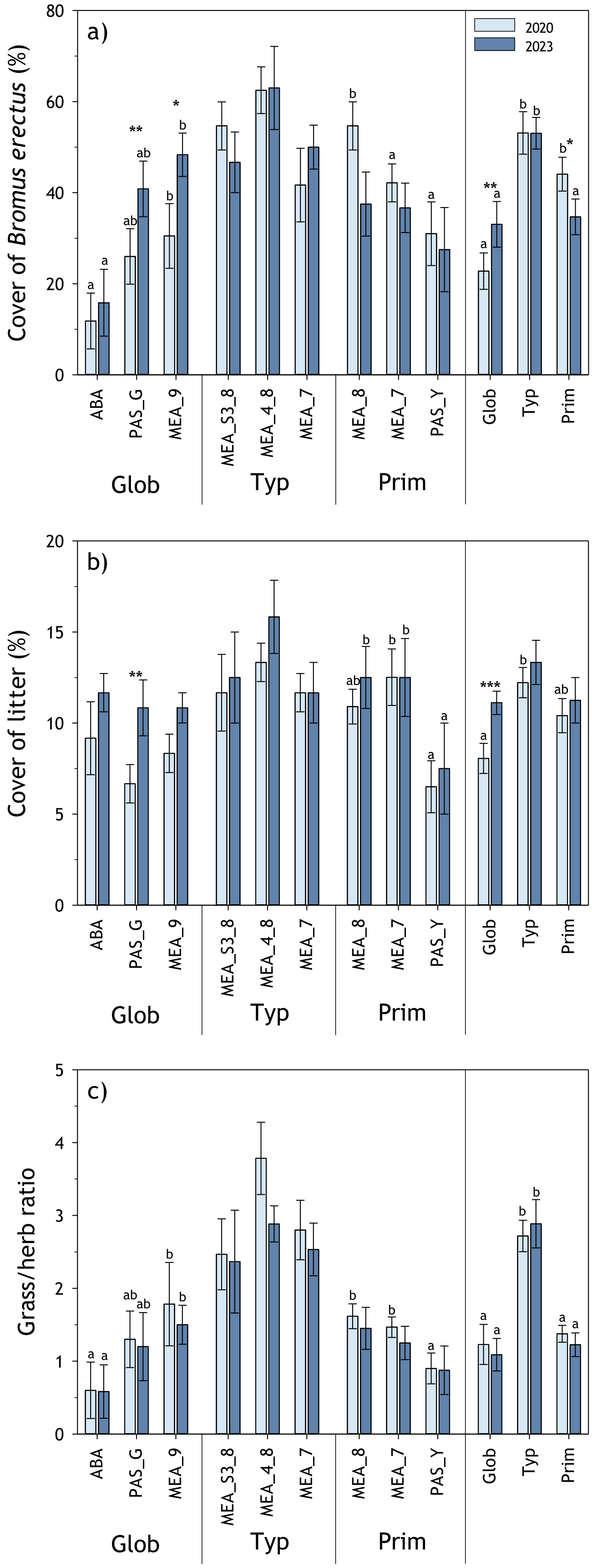

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Fig. 5. Mean (±SE) changes in the cover of *Bromus erectus* and litter as well as in the grass/herb cover ratio from 2020 to 2023 between the vegetation types and treatments. Vegetation type: *Onobrychido-Brometum globularietosum* (Glob), *Onobrychido-Brometum typicum* (Typ) and *Onobrychido-Brometum primuletosum* (Prim). For treatments see Table 1. Sample size: $n = 6$ per treatment; $N = 54$. Statistical differences within vegetation types were detected using GLMM with subarea as a random intercept. Significance of pairwise comparisons is indicated by different letters (Tukey contrasts; $P \leq 0.05$). Statistical differences between years were analysed by paired *t*-test. For further information see section 2. Statistical significances are indicated as follows: n.s. $P > 0.05$, $^{*}P \leq 0.05$, $^{**}P \leq 0.01$, $^{***}P \leq 0.001$.

3.2. *Effects of encroachment of Bromus erectus on plant species assemblages*

Forty years ago, the mean cover of *Bromus erectus* varied between 21 % and 36 % in the three vegetation types (Fig. 4). However, despite intensified conservation management during recent decades, the cover of *B. erectus* had increased from 1978–'81 to 2020 in plots of the *Onobrychido-Brometum typicum* by a factor of 1.6 and in those of the *Onobrychido-Brometum primuletosum* by a factor of 2.0. By contrast, in plots of the more xerophytic *Onobrychido-Brometum globularietosum* the cover of the grass species had not changed.

Bromus erectus had its highest cover in plots of the *Onobrychido-Brometum typicum* (Figs. 1b, 4 and 5), hence on sites of intermediate productivity across the studied environmental gradient of calcareous grasslands. Here, on average *B. erectus* covered 53 % of the plots in 2020 and 2023 (Fig. 5). Moreover, the cover of litter (only 2020) and particularly the grass/herb ratio also peaked in this vegetation type.

Overall, in plots of the *Onobrychido-Brometum typicum*, the cover of *B. erectus* and litter as well as the grass/herb ratio did vary neither between the treatments nor between the two study years (Fig. 5). By contrast, at both ends of the studied environmental gradient in calcareous grasslands, in plots of the *Onobrychido-Brometum globularietosum* and *primuletosum*, there were differences in all three parameters across the treatments and years. Within plots of the *Onobrychido-Brometum globularietosum*, the cover of *B. erectus* and grass/herb cover ratio increased in both study years in the following order: abandoned plots, goat pastures and meadows mown in autumn. In plots of the *Onobrychido-Brometum primuletosum*, the cover of *B. erectus* was higher in meadows mown in late summer than in the other two treatments in 2020. By contrast, the cover of litter (both years) and the grass/herb ratio (only 2020) were lowest in year-round pastures.

Interannual fluctuations were observed for the cover of *B. erectus* and litter (Fig. 5). However, the observed changes were opposed in plots of the more xerophytic *Onobrychido-Brometum globularietosum* and those of the more mesophytic *Onobrychido-Brometum primuletosum*. In the prior, the cover of *B. erectus* and litter had overall and in some of the treatments (both parameters: goat pastures; cover of *B. erectus*: meadows mown in autumn) increased from 2020 (after a dry and warm spring) to 2023 (after a typical spring). By contrast, in plots of the *Onobrychido-Brometum primuletosum* the cover of *B. erectus* had decreased from 2020 to 2023.

Overall, we found 201 vascular plant species (among them 66 threatened ones, 33 %) and 48 bryophyte species (15 threatened ones, 31 %), in the 54 plots in 2020 (Table A.2 and A.3). *Bromus erectus* was the most widespread species, it occurred in all plots except one (Table A.2). Species richness increased along the productivity gradient in the following order: plots of the *Onobrychido-Brometum globularietosum*, *typicum* and *primuletosum* (Fig. 6). By contrast, Shannon diversity was higher in plots of the *Onobrychido-Brometum primuletosum* compared to those of the other two vegetation types. The proportion of threatened species peaked in plots of the *Onobrychido-Brometum globularietosum* and was lowest in the other two vegetation types. Among the

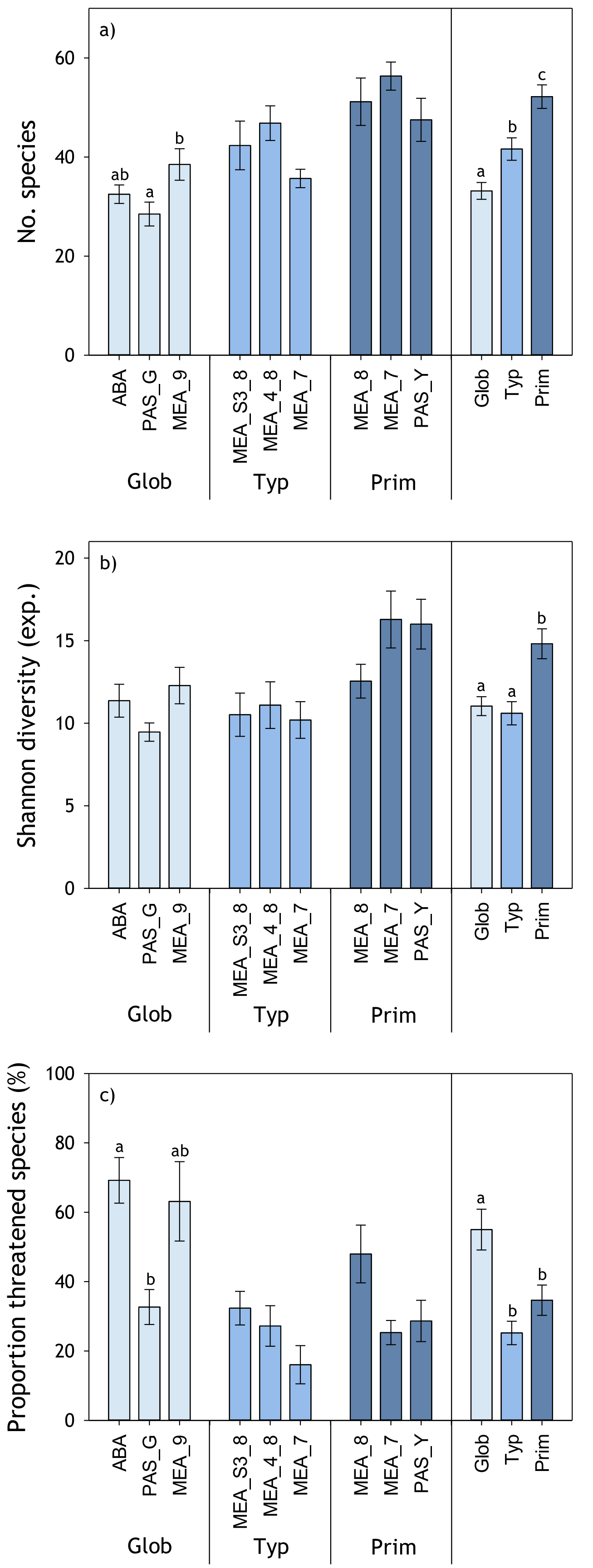

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Fig. 6. Mean (±SE) species richness, Shannon diversity and proportion of threatened species in the studied vegetation types and treatments. Vegetation type: *Onobrychido-Brometum globularietosum* (Glob), *Onobrychido-Brometum typicum* (Typ) and *Onobrychido-Brometum primuletosum* (Prim). For treatments see Table 1. Sample size: $n = 6$ per treatment; $N = 54$. Statistical differences between vegetation types and treatments were detected using GLMM with subarea as a random intercept. Significance of pairwise comparisons is indicated by different letters (Tukey contrasts; $P \leq 0.05$). For further information see section 2.

vegetation types, treatment had only an effect on species richness and the proportion of threatened species in plots of the *Onobrychido-Brometum globularietosum.* They were lowest in goat pastures and highest in meadows mown in autumn and abandoned plots, respectively.

3.3. Drivers of *Bromus erectus* cover

In the studied semi-dry calcareous grasslands, the cover of *Bromus erectus* was best predicted by intermediate nitrogen indicator values (Figs. 7 and 8). The nitrogen indicator value was positively correlated with northness and the moisture indicator value, but negatively with the light and soil reaction indicator value (Table A.1). Accordingly, a high cover of *B. erectus* was not only characteristic for calcareous grasslands that exhibited an intermediate nutrient supply but also that were characterised by neither northern nor southern aspects as well as intermediate moisture, soil reaction and light conditions.

4. Discussion

Our study revealed that despite intensified conservation management, the cover of *Bromus erectus* increased from 1978–'81 to 2020 in the two most productive types of semi-dry calcareous grasslands (*Onobrychido-Brometum typicum* and *primuletosum*) by the factor 1.6 and 2.0, respectively. Across the studied environmental gradient of calcareous grasslands, *B. erectus* had its highest cover (mean: 53 % in 2020 and 2023) in plots of the *Onobrychido-Brometum typicum*, which were characterised by an intermediate productivity. Moreover, the GLMM analyses revealed that intermediate nitrogen indicator values, which were a proxy for an intermediate productivity, fostered the cover of *B. erectus*.

Experiments have shown that *B. erectus* grown under exclusion of competitors prefers fresh to moist, moderately nitrogen-rich soils (Ellenberg and Leuschner, 2010). By contrast, if other grasses (*Arrhenatherum elatius*, *Dactylis glomerata*, *Poa palustris*) were cultivated additionally as potential antagonists, *B. erectus* had its maximum growth under drier conditions. In line with this, *B. erectus* was—across the studied productivity gradient in semi-dry calcareous grasslands—most dominant in plots of the *Onobrychido-Brometum typicum* and an intermediate productivity was identified as the driver of *B. erectus* cover. By contrast, in plots of the *Onobrychido-Brometum globularietosum* on steep and shallow south-facing slopes, *B. erectus* had generally a low cover. Pérez-Ramos et al. (2013) also highlighted that *B. erectus* hardly becomes dominant on very shallow, dry soils. However, in our study, the grass species reached dominance within the investigated most productive semi-dry calcareous grasslands. In 2020, after a warm and dry spring, the cover of *B. erectus* in plots of the *Onobrychido-Brometum primuletosum* was comparable to those of the *Onobrychido-Brometum typicum*. We assume that the warm and dry spring weather reduced the competitive power of more mesophytic antagonists, such as *Brachypodium pinnatum*, which is known to have a low tolerance to water stress (Corcket et al., 2003; Kahlert et al., 2005). By contrast, *B. erectus* is relatively drought resistant, particularly on deep soils where it develops extensive root systems to tap deep soil water (Grime et al., 2007; Pérez-Ramos et al., 2013; Madaj et al., 2023). Consequently, we argue that the growth of *B. erectus* at the moist end of the studied

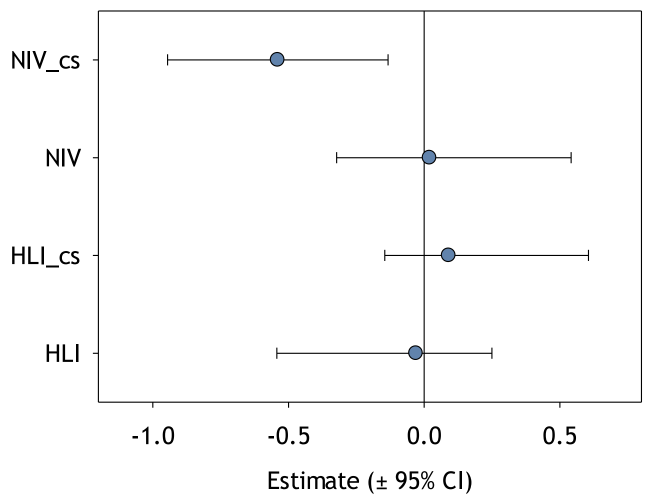

Fig. 7. Abiotic drivers of the cover of *Bromus erectus* in the studied calcareous grasslands in June/July 2020 ($N = 54$). Statistical relationships between the cover of *Bromus erectus* and environmental parameters were detected using proportional binomial GLMM with subarea as a random intercept and observation level random effect to avoid overdispersion. Averaged coefficients (standardised estimates ± 95 % confidence intervals = CI) are shown. Confidence intervals of significant predictors ($P < 0.05$) do not cross x = 0 (for more details see Table A.4). NIV_cs = centred and squared Ellenberg nitrogen indicator value, NIV = Ellenberg nitrogen indicator value, HLI_cs = centred and squared heat load index, HLI = heat load index.

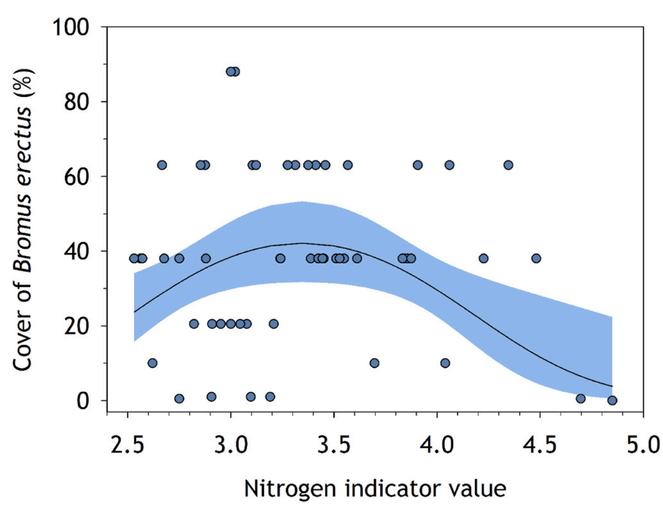

Fig. 8. Results of the GLMM analysis: Relationship between the significant abiotic predictor (Ellenberg nitrogen indicator value) and the cover of *Bromus erectus* in June/July 2020. The regression slope was fitted using the multivariable linear model (see Table A.4 for detailed model statistics). The blue band indicates 95 % confidence intervals.

environmental gradient was favoured by reduced competition of its antagonists due to drier conditions (cf. Corcket et al., 2003).

In the study area, from 1980 to 2020, annual temperatures have increased by 0.8 °C, annual precipitation has decreased by 117 mm and summer drought has occurred more frequently from the 1990s onwards as a result of climate change. Moreover, current nitrogen deposition rates of 10–15 kg ha^{-1} y^{-1} were already at the critical loads of calcareous grasslands. In the same period, the cover of *B. erectus* has strongly increased in the two most productive types of semi-dry calcareous grasslands (*Onobrychido-Brometum typicum* and *primuletosum*). Since conservation management has been intensified during that time period, we assume that particularly climate change but also nitrogen deposition have favoured the encroachment of the grass species (see also Poniatowski et al., 2018b; Lemmer et al., 2021; Meier et al., 2022). *Bromus erectus* is winter-green and can, in contrast to many other vascular plants, even grow during warmer winter days (Kahlert et al., 2005; Grime et al., 2007). However, it particularly exhibits a rapid extension growth in early spring during moist periods (Bornkamm, 1961). The capacity to exploit its habitats even during cool periods of the year is a strong advantage against its competitors such as *B. pinnatum*, which grows rather late in spring (Kahlert et al., 2005; Grime et al., 2007). This is especially true for deep soils that are enriched in nitrogen by atmospheric deposition. Due to the deep root system (see above) and usually moist soil conditions during winter, *B. erectus* can very effectively absorb water and nutrients across extensive parts of the soil. Thus, both warmer winters and increased soil nitrogen contents favour the growth of *B. erectus*. As a result, it can produce more biomass during the year and suppress other grassland plants (Moser et al., 2011). Additionally, *B. erectus* is favoured by summer drought. In contrast to *B. pinnatum*, for example, the species has a high drought tolerance, particularly on deeper soils (see above), and its leaf production even restarts after drought periods later in the season (Kahlert et al., 2005).

In the *Onobrychido-Brometum typicum*, the vegetation type where *B. erectus* was most dominant, the cover of the grass species did not vary between the two study years although spring weather conditions were quite different (2020: dry and warm; 2023: typical). By contrast, at both ends of the studied productivity gradient there was interannual variation in the cover of *B. erectus.* However, the observed changes were opposed in plots of the more xerophytic *Onobrychido-Brometum globularietosum* and those of the more mesophytic *Onobrychido-Brometum primuletosum*. From 2020 to 2023, in the prior vegetation type the cover increased and in the latter it decreased. Based on the aforementioned, we argue that on the least productive soils on which semi-dry calcareous grasslands can grow, a moist spring favours *B. erectus* without becoming dominant. By contrast, on the most productive soils across the environmental gradient a moist spring rather fosters its antagonists.

The high cover of *B. erectus* in plots of the *Onobrychido-Brometum typicum* resulted in a peak of litter accumulation in this vegetation type. Surprisingly, the number of plant species still increased across the environmental gradient from the least to the most productive sites, which is in line with observed patterns in historical times (Bürger, 1983). However, the grass/herb cover ratio was much wider in plots of the *Onobrychido-Brometum typicum* than in those of the other two. Consequently, although still many herb species were present in the plots, they had usually a low cover. Accordingly, Shannon diversity was low in plots of the *Onobrychido-Brometum typicum* and comparable to those of the *Ononbrychido-Brometum globularietosum*—the vegetation type with lowest species diversity. Moreover, the proportion of threatened plant species was even lowest in plots of the *Onobrychido-Brometum typicum*, although not differing from those of the *Onobrychido-Brometum primuletosum.* Therefore, our study corroborates previous work that showed that the encroachment of *B. erectus* leads to structural and floristic homogenisation in calcareous grasslands (Poniatowski et al., 2018b; Meier et al., 2022).

To sum up, we explain the encroachment of *B. erectus* during the last 40 years particularly by climate change (i.e., milder winters and drier summers) but also nitrogen deposition. The capacity to exploit its habitats even during cool periods of the year is a strong advantage against competitors such as *Brachypodium pinnatum*. This is especially true for deep soils that are enriched in nitrogen due to atmospheric deposition. As a consequence of the extensive root system and usually moist soil conditions during winter, *B. erectus* can very effectively absorb water and minerals across large parts of the soil. Summer drought also favours the species, since it has a high drought resistance, particularly on deeper soils, and its leaf production even restarts after drought later in the season. Our study showed that the encroachment of *B. erectus* leads to structural and floristic homogenisation of calcareous grasslands.

5. Implications for conservation

As our study revealed, the encroachment of *B. erectus* mainly occurs in semi-dry calcareous grasslands of intermediate productivity. However, after dry and warm springs also the more productive calcareous grasslands might be affected. Periods with such weather conditions become more likely due to climate change (Díaz et al., 2019). Accordingly, management activities that aim at repressing *B. erectus* in favour of overall biodiversity should focus on both types of calcareous grasslands.

Generally, the treatments applied in plots of the *Onobrychido-Brometum typicum* were insufficient to inhibit the dominance of *B. erectus* under current environmental conditions. They consisted of one mowing in mid- or late summer for hay making and usually a second management event in spring (grazing or mowing) or autumn (grazing). Consequently, we recommend a higher management frequency and shorter intervals between the management events in grasslands where *B. erectus* has become dominant and the communities currently have a low species richness (see Fig. 1). This is particularly true for the moist periods of the growing season (spring, but also late summer/autumn and winter), which favour the growth of *B. erectus* (Bornkamm, 1961; Kahlert et al., 2005). Therefore, the first management event should take place in spring, when the plants produce new tillers and leaves (Wedl and Meyer, 2003; Poniatowski et al., 2018b). During this growth period, the plants are very rich in nutrients and highly palatable for grazing animals (Ellenberg and Leuschner, 2010). However, grazing should occur before flowering and particularly fruiting of *B. erectus* since the plants are later increasingly avoided by grazing mammals such as sheep (own observation; for grasses in general: see also Bunzel-Drüke et al., 2008). The next grazing event should take place, when new tillers and leaves have emerged, which usually needs six to eight weeks if conditions are sufficiently moist (own observation). Mowing with biomass removal during these two growth periods might also be a possible solution. In most cases, we assume that an additional third management event (grazing or mowing) will be necessary. However, the effectiveness of the management regime described above has not been tested yet. Moreover, knowledge is lacking on the time needed to repress *B. erectus* sufficiently under the recommended management regime. When this has been achieved, a reduction in management intensity, particularly in summer, should take place to favour overall biodiversity.

By contrast, year-round horse grazing with low stocking rates has been shown to noticeably reduce the cover of *B. erectus* in calcareous grasslands (Köhler et al., 2015). In line with this, within plots of the *Onobrychido-Brometum primuletosum*, those that exhibited a year-round grazing system (cattle, horses, sheep) had the lowest cover of *B. erectus* and litter, and the narrowest grass/herb cover ratio in our study, too. Therefore, year-round grazing, particularly with genuine grazers (cattle or horses; Bunzel-Drüke et al., 2008) seems to be highly effective in preventing the dominance of *B. erectus*.

Moreover, although it was not a part of our study, winter burning is known to be very suitable in pushing back *B. erectus* (Moog et al., 2002; Kahlert et al., 2005; Grime et al., 2007). Kahlert et al. (2005) observed that the grass species completely disappeared from burnt plots. They explained this by the destruction of the living foliage above the ground and, thus, the loss of the plants' competitive advantage in early spring (see section 4). Hence, prescribed burning in winter can also be recommended as a measure to reduce the cover of *B. erectus*.

CRediT authorship contribution statement

Thomas Fartmann: Writing – original draft, Methodology, Funding acquisition, Formal analysis, Conceptualization. **Merle Streitberger:** Writing – review & editing, Investigation. **Dominik Poniatowski:** Writing – review & editing, Investigation. **Marcel Kettermann:** Visualization, Investigation. **Carsten Schmidt:** Investigation. **Lisa Holtmann:** Writing – review & editing, Investigation, Formal analysis.

Declaration of competing interest

The authors declare the following financial interests/personal relationships, which may be considered as potential competing interests: Thomas Fartmann reports financial support was provided by Stiftung Naturschutzfonds Baden-Württemberg. The other authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix

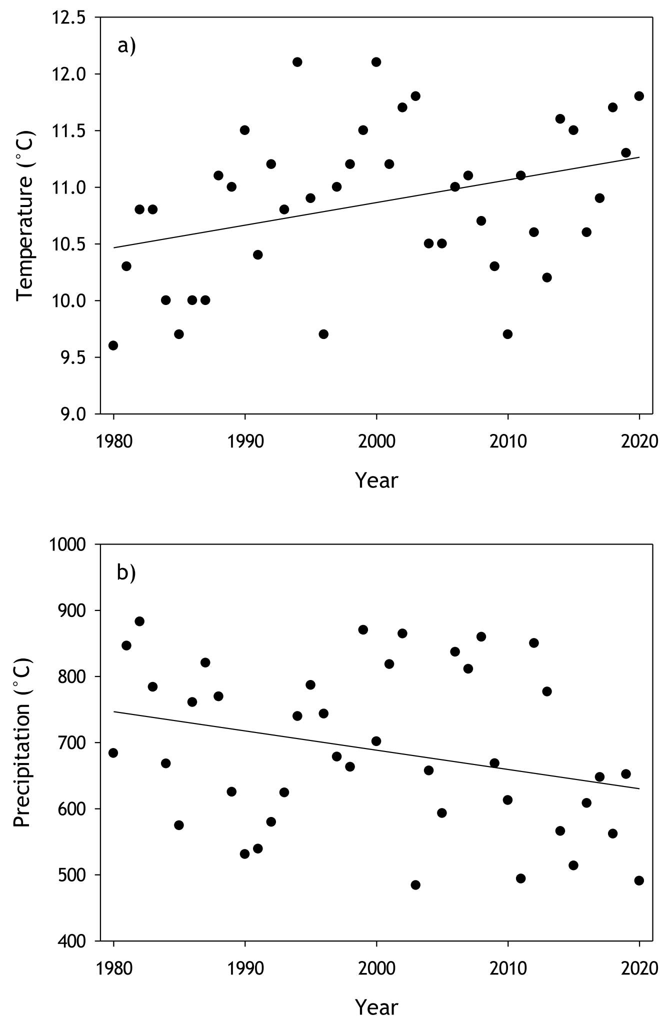

Fig. A.1. Changes in annual temperature (linear regression: $R^2 = 0.12$, $P < 0.05$, $y = -29.03 + (0.0199 \times \text{year})$) and annual precipitation ($R^2 = 0.08$, $P < 0.05$, $y = 6515.326 - (2.913 \times \text{year})$ from 1980 to 2020 in the study area (1980–2003: Vogtsburg-Oberrotweil, 223 m a.s.l., DWD, 2024; 2004–2020: Rotweil, 179 m a.s.l., Agrarmeteorologie BW, 2024).

Tab. A.1
Results of spearman rank correlations (r_s). Variables with strong intercorrelations ($|r_s| \geq 0.5$) are highlighted by bold type. HLI = Heat load index, IV = Ellenberg indicator value, react. = reaction. As a result, the variables eastness and northness as well as light, moisture and soil reaction indicator were excluded from the following analyses.

Parameter	HLI	Eastness	Northness	Light IV	Moisture IV	Nitrogen IV	Soil react. IV
HLI	/	**−0.64**	−0.48	0.15	−0.14	−0.07	0.09
Eastness	.	/	−0.24	0.28	−0.32	−0.30	0.38
Northness	.	.	/	**−0.68**	**0.71**	**0.56**	**−0.66**
Light IV	.	.	.	/	**−0.90**	**−0.83**	**0.80**
Moisture IV	.	.	.	.	/	**0.88**	**−0.87**
Nitrogen IV	.	.	.	.	.	/	**−0.79**

Tab. A.2
Frequency (%) of detected vascular plant species in the three vegetation types and their threat status (TS). Vegetation type ($n = 18$ per type): *Onobrychido-Brometum globularietosum* (glob), *Onobrychido-Brometum typicum* (typ) and *Onobrychido-Brometum primuletosum* (prim). Nomenclature: Metzing et al. (2018); Threat status: Breunig and Demuth (2023) and Metzing et al. (2018).

Species	TS	*Onobrychido-Brometum*		
		glob	typ	prim
Acer platanoides	.	.	.	6
Acer pseudoplatanus	.	.	.	6
Achillea millefolium	.	6	56	89
Acinos arvensis	x	17	6	6
Agrimonia eupatoria	.	.	.	33
Agrostis capillaris	.	.	11	22
Ajuga genevensis	x	.	.	17
Ajuga reptans	.	.	.	6
Allium sphaerocephalon	x	28	6	.
Alyssum alyssoides	x	28	6	.
Anemone nemorosa	.	.	.	6
Anthericum ramosum	x	6	11	17
Anthoxanthum odoratum	.	.	28	44
Anthyllis vulneraria	.	.	11	33
Aphanes arvensis	.	.	.	6
Arabis hirsuta	x	61	72	17
Arenaria serpyllifolia	.	72	61	50
Arrhenatherum elatius	.	6	56	50
Artemisia campestris	x	17	.	.
Asperula cynanchica	x	56	44	44
Aster amellus	x	.	6	11
Bellis perennis	.	.	.	6
Betonica officinalis	x	.	33	56
Betula pendula	.	.	.	6
Brachypodium pinnatum	.	17	61	78
Briza media	.	.	50	56
Bromus erectus	.	100	100	94
Bromus hordeaceus	.	.	.	11
Campanula glomerata	x	.	.	6
Campanula persicifolia	.	.	17	22
Campanula rapunculus	.	.	.	17
Campanula rotundifolia	.	.	6	.
Carex caryophyllea	x	28	50	61
Carex flacca	x	.	11	39
Carex humilis	x	94	33	17
Carex montana	.	.	22	22
Carex muricata agg.	.	.	.	17
Carlina vulgaris	.	.	.	11
Centaurea jacea	.	11	33	72
Centaurea scabiosa	.	50	61	39
Cerastium arvense	.	6	6	11
Cerastium holosteoides	.	.	17	22
Clinopodium vulgare	.	.	28	17
Coeloglossum viride	x	.	.	6
Colchicum autumnale	.	.	.	6
Convallaria majalis	.	.	.	6
Convolvulus arvensis	.	.	.	22
Cornus sanguinea	.	11	.	6
Corylus avellana	.	.	.	6
Crataegus monogyna	.	17	6	17
Cynosurus cristatus	.	.	6	17
Dactylis glomerata	.	67	83	78
Daucus carota	.	.	11	28
Dianthus carthusianorum	x	28	56	44
Echium vulgare	.	67	17	.
Erigeron annuus	.	.	6	17
Erigeron canadensis	.	.	.	6
Eryngium campestre	x	22	.	28
Euonymus europaeus	.	11	.	.
Euphorbia cyparissias	.	56	72	72
Euphorbia seguieriana	x	11	.	6
Festuca ovina agg.	.	67	83	83
Festuca pratensis	.	.	17	11
Festuca rubra agg.	.	17	39	50
Fragaria viridis	.	22	22	11
Galatella linosyris	x	56	6	.
Galium album	.	6	56	50
Galium glaucum	x	61	11	.
Galium pumilum	x	.	33	39
Galium verum	.	28	33	50

(*continued on next page*)

Tab. A.2 (*continued*)

Species	TS	*Onobrychido-Brometum*		
		glob	typ	prim
Genista sagittalis	x	6	6	11
Genista tinctoria	x	50	50	56
Geranium columbinum	.	.	.	22
Geranium molle	.	.	.	11
Geranium pusillum	.	.	.	11
Geranium sanguineum	x	56	39	44
Glechoma hederacea	.	.	.	6
Globularia bisnagarica	x	39	11	6
Gymnadenia conopsea	x	.	.	11
Helianthemum nummularium subsp. *obscurum*	x	100	61	50
Helictotrichon pratense	x	.	.	28
Helictotrichon pubescens	.	.	17	11
Heracleum sphondylium	.	.	6	6
Hieracium cymosum	x	.	6	.
Hieracium pilosella	.	11	.	6
Himantoglossum hircinum	x	6	.	.
Hippocrepis comosa	x	50	72	39
Holcus lanatus	.	.	28	44
Hypericum montanum	x	.	.	6
Hypericum perforatum	.	44	28	28
Inula conyzae	.	.	6	.
Isatis tinctoria	.	44	.	6
Juglans regia	.	.	6	.
Knautia arvensis	.	17	33	72
Koeleria macrantha	x	44	39	28
Lathyrus pratensis	.	.	33	33
Leontodon hispidus	.	.	.	22
Leucanthemum vulgare agg.	.	.	17	44
Ligustrum vulgare	.	6	.	6
Lilium martagon	.	.	6	6
Linum catharticum	.	.	22	39
Linum tenuifolium	x	6	.	.
Listera ovata	.	.	.	6
Lolium perenne	.	.	.	17
Lotus corniculatus	.	17	33	72
Lupinus polyphyllus	.	.	6	.
Luzula campestris	.	.	11	28
Medicago falcata	.	39	28	11
Medicago lupulina	.	6	11	39
Medicago minima	x	11	.	6
Melilotus albus	.	6	.	.
Myosotis arvensis	.	.	6	6
Myosotis ramosissima	.	.	6	.
Onobrychis viciifolia	.	6	28	11
Ononis repens	.	6	6	11
Ononis spinosa	.	.	.	6
Orchis pyramidalis	x	.	.	17
Origanum vulgare	.	44	17	33
Orobanche elatior	x	.	6	17
Orobanche lutea	x	.	.	6
Peucedanum cervaria	x	6	.	6
Peucedanum oreoselinum	x	17	.	11
Phleum phleoides	x	11	11	6
Phleum pratense	.	.	.	6
Phyteuma orbiculare	x	.	6	11
Pimpinella saxifraga	.	11	28	44
Pinus sylvestris	.	.	.	6
Plantago lanceolata	.	17	94	100
Plantago media	.	.	11	44
Poa angustifolia	.	33	56	50
Poa annua	.	.	.	6
Poa pratensis	.	6	22	11
Polygala amarella	x	.	.	6
Polygala comosa	x	.	.	6
Polygonatum odoratum	x	6	.	6
Potentilla erecta	.	.	.	6
Potentilla heptaphylla	x	39	56	50
Potentilla reptans	.	.	.	6
Potentilla verna	.	11	11	22
Primula veris	x	11	44	44
Prunella grandiflora	x	.	.	50
Prunus spinosa	.	11	.	.
Pulsatilla vulgaris	x	.	6	.
Quercus petraea	.	.	.	6

(*continued on next page*)

Tab. A.2 (*continued*)

Species	TS	*Onobrychido-Brometum*		
		glob	typ	prim
Ranunculus bulbosus	.	11	.	33
Ranunculus polyanthemos agg.	x	.	6	6
Ranunculus polyanthemos subsp. *nemorosus*	x	.	28	56
Ranunculus polyanthemos subsp. *polyanthemos*	x	.	.	11
Reseda lutea	.	28	.	.
Rhinanthus alectorolophus	.	.	.	11
Rubus caesius	.	6	.	.
Rumex acetosa	.	.	50	39
Salvia pratensis	x	78	72	67
Sambucus nigra	.	.	.	6
Sanguisorba minor	.	28	94	72
Scabiosa canescens	x	6	.	.
Scabiosa columbaria	.	.	22	50
Scorzoneroides autumnalis	.	.	.	11
Securigera varia	.	67	56	28
Sedum album	.	11	.	.
Sedum sexangulare	.	.	6	6
Senecio jacobaea	.	6	33	11
Sherardia arvensis	x	.	.	6
Silene nutans	.	6	6	6
Silene vulgaris	.	28	11	.
Solidago gigantea	.	.	.	6
Solidago virgaurea	.	.	.	11
Sonchus asper	.	.	.	6
Stachys recta	x	72	50	22
Stellaria graminea	.	.	11	28
Stipa capillata	x	11	.	.
Tanacetum corymbosum	x	.	.	6
Taraxacum sect. *Ruderalia*	.	.	6	11
Teucrium chamaedrys	.	89	28	6
Teucrium montanum	x	33	.	.
Thalictrum minus	x	28	33	39
Thalictrum simplex	x	6	.	.
Thymus pulegioides subsp. *carniolicus*	x	33	17	33
Thymus pulegioides subsp. *pulegioides*	.	33	56	78
Torilis japonica	.	.	.	11
Tragopogon orientalis	x	11	6	22
Tragopogon pratensis	.	6	.	.
Trifolium alpestre	*x*	6	.	22
Trifolium arvense	.	.	11	.
Trifolium campestre	.	.	28	50
Trifolium dubium	.	.	.	6
Trifolium montanum	x	.	17	39
Trifolium pratense	.	.	11	61
Trifolium repens	.	.	.	17
Trisetum flavescens	.	.	72	83
Ulmus minor	.	11	.	.
Valeriana pratensis subsp. *angustifolia*	.	.	6	11
Verbascum lychnitis	.	17	.	.
Veronica arvensis	.	.	6	11
Veronica chamaedrys	.	.	33	44
Veronica teucrium	x	.	6	.
Vicia angustifolia	.	.	17	28
Vicia hirsuta	.	.	22	22
Vicia sepium	.	.	11	6
Vincetoxicum hirundinaria	.	33	33	6
Viola hirta	.	.	44	33
No. species	**66**	**92**	**119**	**170**

Tab. A.3
Frequency (%) of detected bryophyte species in the three vegetation types and their threat status (TS). Vegetation type ($n = 18$ per type): *Onobrychido-Brometum globularietosum* (glob), *Onobrychido-Brometum typicum* (typ) and *Onobrychido-Brometum primuletosum* (prim). Nomenclature: Caspari et al. (2018); Threat status: Sauer and Ahrens (2006) and Caspari et al. (2018).

Species	TS	*Onobrychido-Brometum*		
		glob	typ	prim
Abietinella abietinum	.	83	56	28
Barbula unguiculata	.	28	33	28
Brachythecium albicans	.	.	6	11
Brachythecium campestre	x	.	.	6
Brachythecium rutabulum	.	.	.	6
Bryum argenteum	.	33	6	.
Bryum bicolor	.	.	.	6
Bryum ruderale	x	22	17	17
Bryum violaceum	.	6	6	.
Calliergonella cuspidata	.	.	22	22
Campyliadelphus chrysophyllus	x	6	.	.
Didymodon acutus	x	11	.	.
Didymodon fallax	.	.	.	6
Didymodon luridus	.	.	6	.
Entodon concinnus	.	6	17	28
Eurhynchiastrum pulchellum/Oxyrrhynchium hians	x	.	.	6
Fissidens dubius	.	17	17	6
Fissidens taxifolius	.	.	22	11
Homalothecium lutescens	.	39	67	17
Hylocomium splendens	.	6	17	17
Hypnum cupressiforme var. *lacunosum*	.	11	28	6
Lophocolea bidentata	.	.	6	.
Microbryum curvicollum	x	17	.	.
Plagiomnium affine	.	.	56	33
Plagiomnium undulatum	.	.	.	17
Pleurozium schreberi	.	.	.	6
Pseudoscleropodium purum	.	22	83	67
Pterygoneurum lamellatum/ovatum	x	6	.	.
Ptychostomum capillare/torquescens	.	6	6	.
Ptychostomum rubens	.	22	17	6
Rhodobryum roseum	.	6	6	6
Rhynchostegium megapolitanum	x	6	28	11
Rhytidiadelphus squarrosus	.	.	28	33
Rhytidiadelphus triquetrus	.	6	6	22
Rhytidium rugosum	x	78	17	6
Syntrichia cf. *calcicola*	.	.	6	.
Thuidium assimile	.	.	33	39
Tortella inclinata	.	6	.	.
Tortella squarrosa	x	72	28	.
Tortula acaulon	.	11	6	17
Tortula caucasica	.	.	6	.
Tortula lanceola	x	.	11	6
Trichostomum crispulum	.	6	.	.
Weissia brachycarpa	x	11	17	6
Weissia condensa	x	6	.	.
Weissia controversa	.	33	17	6
Weissia fallax	x	11	.	.
Weissia longifolia	x	39	50	33
No. species	**15**	**30**	**33**	**32**

Tab. A.4
Detailed results of the GLMM analysis: Relationship between the abiotic predictors and the cover of *Bromus erectus* in the studied calcareous grasslands. R^2_m = variance explained by fixed effects (Nakagawa et al., 2017). For further information see section 2. NIV_cs = centred and squared Ellenberg nitrogen indicator value, NIV = Ellenberg nitrogen indicator value, HLI_cs = centred and squared heat load index, HLI = heat load index. Statistical significances are indicated as follows: n.s. $P > 0.05$, ** $P < 0.01$, *** $P < 0.001$.

Parameter	Estimate	SE	Z	*P*
Intercept	−0.70	0.18	−3.78	***
NIV_cs	−0.54	0.20	−2.60	**
NIV	0.02	0.10	0.20	n.s.
HLI_cs	0.09	0.16	0.55	n.s.
HLI	−0.03	0.11	−0.30	n.s.
Range of R^2m = 0.14–0.17				

Data availability

The authors do not have permission to share data.

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