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RESEARCH ARTICLE

Microclimate shapes vegetation response to drought in calcareous grasslands

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Abstract

Questions: Semi-natural grasslands have been shown to be relatively resilient to drought events, but there seems to be no uniform response of different grassland types or across species. The typical vegetation of calcareous grasslands, which are biodiversity hotspots in Europe, reportedly even profits from droughts. What was the response of their vegetation, considering different species groups, to the recent periods of intense summer droughts? How did differences in microclimate, such as between steep, south-facing slopes (SSF) and flat or north-facing slopes (FNF), affect species composition and drought response?

Location: Semi-arid calcareous grasslands (*Mesobromion*) in northwest Germany.

Methods: In 2019, we resurveyed 112 vegetation plots from 25 sites first established in 2008, after 11 exceptionally dry years. Species identities and cover were assessed in plots of 1 m^2. We used linear mixed models to determine the effect of microclimate on species composition and drought response. Vegetation changes were visualised by non-metric multidimensional scaling (NMDS).

Results: In the initial survey in 2008, the species composition was significantly influenced by the microclimate, with positive effects of dry and warm conditions on SSF on character species. Phosphorus availability played an equally important, albeit contrasting, role. Vegetation change between 2008 and 2019 showed strong signs of the severe droughts. On SSF slopes, total species richness decreased, with negative trends for all species groups except ruderal species. Remarkably, this also affected the character species of dry grasslands. By contrast, dry conditions on FNF favoured an increase in total species richness and character species. However, eutrophication indicators increased here as well.

Conclusions: We conclude that sites with a dry and warm microclimate have to date had a positive, stabilising effect on the typical vegetation of calcareous grasslands. However, increasing droughts due to climate change pose a potential threat to the characteristic species composition, especially at sites with hot and dry microclimates.

1 | INTRODUCTION

Climate change as a driver of weather extremes is expected to become an increasingly important factor for biodiversity (Thuiller et al., 2005; Behrens et al., 2009; Pompe et al., 2011). Periods of drought will most likely increase in frequency and intensity worldwide (IPCC, 2014) and regionally (DWD, 2018). Between 2015 and the present, Europe has experienced the most severe summer droughts in over 2,000 years (Büntgen et al., 2021). Although a direct causal link between single extreme weather events and anthropogenic climate change is impossible to prove, a recent review found numerous examples of detrimental effects of climate change on biodiversity (Pecl et al., 2017).

To date, there is no general agreement on the reaction of semi-natural grasslands to climate change. In experimental studies, they have proven relatively resilient to drought, both in terms of ecosystem processes and species composition (Grime et al., 2008; Bloor et al., 2010; Maalouf et al., 2012; Dengler et al., 2014; Fry et al., 2014). Although productivity was commonly observed to decrease in response to drought, it recovered quickly after the end of the drought (Sternberg et al., 1999; Morecroft et al., 2004; Evans et al., 2011; Hoover et al., 2014). There appears to be no uniform response of different grassland types, or of different functional groups and individual (dominant) species, to the same treatment (Grime et al., 2000; Maalouf et al., 2012; Hoover et al., 2014).

We here conducted a resurvey study of semi-arid calcareous grasslands in northwest Germany after a decade of exceptional drought. Calcareous grasslands are hotspots of biodiversity in Europe and show a record-breaking plant species density (Wilson et al., 2012). Furthermore, a large proportion of the total German species pool (ca. 15%) is restricted to calcareous grasslands (WallisDeVries et al., 2002; Dengler et al., 2014). Even though their great importance for biodiversity and dependence on permanent anthropogenic management bring then within the focus of conservation planning (Poschlod & WallisDeVries, 2002), calcareous grasslands are threatened in many ways. At present, area losses as a result of land-use change are considered the greatest threat to these grasslands and their species (Sala et al., 2000; WallisDeVries et al., 2002; Pompe et al., 2011). In addition, they are negatively affected by habitat degradation due to eutrophication and a lack of management (Bobbink & Willems, 1987; Bennie et al., 2006; Diekmann et al., 2014; Bauer & Albrecht, 2020; Ridding et al., 2020).

In calcareous grasslands, drought events are commonly considered to have mostly positive effects, although Petermann et al. (2007) attested they have high sensitivity to climate change because their situation is already precarious owing to the above-mentioned threats and low regeneration potential. Calcareous grassland species are the best adapted to drought and heat in the Central European landscape, and therefore likely to benefit from a warming climate through an increase in potential habitat area (Behrens et al., 2009; Pompe et al., 2011). Dry spells presumably contribute to the long-term stability of the typical species assemblage because more competitive species, which are not adapted to these stressful conditions, are regularly "sorted out" (Bennie et al., 2006; Leuschner & Ellenberg, 2017b; Fischer et al., 2020). Droughts may also mitigate the effects of eutrophication by limiting water availability and thus the competitive power of potentially invading species (Bennie et al., 2006). These positive effects can be extended to dry conditions that are not caused by weather but by microclimatic conditions. Perring (1959) showed that topography-controlled wetness is an important factor for species composition in calcareous grasslands, with SSW exposed slopes being the driest, and NNE exposed slopes being the wettest. The impact of topography on local climatic conditions was also demonstrated by Suggitt et al. (2011), showing differences in maximum temperature of 7°C, and occasionally up to 20°C, between north- and south-facing slopes in heather moorland. By contrast, experimental studies in semi-arid calcareous grasslands found only minor effects of drought on species composition, despite a strong reduction in productivity (−35%) and a significant decrease in species numbers (Grime et al., 2008). Maalouf et al. (2012) found no effects of a 2-year spring drought simulation on species richness or Shannon diversity in a mesic calcareous grassland, but significant reductions in a xeric grassland.

In the current resurvey, we investigated the effects of extreme drought on the species composition and richness of calcareous grasslands in northwest Germany. In doing so, we focused on differences not only between species groups with varying habitat requirements, but also between sites with different microclimatic conditions.

Our main hypotheses were as follows:

H1. Particularly warm and dry microclimates generally have a positive effect on the characteristic species composition of dry grasslands. To test this hypothesis, we used the data of the initial survey in 2008.

H2. The species composition of semi-arid calcareous grasslands is generally robust to the exceptional droughts of the past decade.

H3. Changes in species composition and richness between the two surveys as induced by drought depend on the microclimatic conditions of the site and differ between species groups.

2 | METHODS

2.1 | Study area

The 25 study sites are located in Lower Saxony, Germany, between the latitudes of 51.507 and 52.152 and the longitudes of 9.570 and 10.044, except for one isolated site close to Osnabrück (52.209,

7.955), ca. 100 km further west. A map showing the locations of the study sites is given in Appendix S1. Sites were limited to areas with a suboceanic climate with mean temperatures of around 8.8°C and mean yearly precipitation of ca. 700 mm (DWD, 2021). The sites were selected as to represent the typical calcareous grassland vegetation in northwest Germany, being assigned to the alliance *Bromion erecti* Koch 1926 in the class *Festuco-Brometea* Br.-Bl. Et Tx. In Br.-Bl. (1949). Soils are shallow with a median depth of 10 cm (minimum 4 cm, maximum 35 cm), whereas pH values range from 6.1 to 7.3, with a median of 7.1. According to model data from the study region, nitrogen deposition varied between 13 and 17 kg N ha^{-1} year^{-1}, with one outlier of 23 kg N ha^{-1} year^{-1} at one site (data from 2013–2015, UBA, 2021). The environmental conditions would naturally support forest, mainly mull beech forests (*Galio odorati-Fagenion* Tx. 1955) on base-rich soils, some tending to mesic limestone beech forests (*Hordelymo-Fagetum* Kuhn 1937), some to moder beech forests on more acid soils (*Luzulo-Fagetum* Meusel 1937) (Suck et al., 2013; Leuschner & Ellenberg, 2017a). The grasslands are kept open by human intervention. All sites represent nature reserves, 21 of them are also registered as Natura 2000 areas. In 2008, ten of the sites were mown, seven grazed and eight managed in a mixed form with grazing in summer and a regular additional cut in autumn or winter. In 2019, four of the mown sites had been converted to grazing (two) or a mixed mowing/grazing regime (two), with the management of all others remaining unchanged.

There were only 11 years between the initial and resurvey studies. However, these years were exceptionally dry: according to the soil moisture index (SMI), published by the drought monitor for Germany (Zink et al., 2016), none of these 11 years reached the long-term median of growing season SMI of all years between 1951 and 2008. The first survey in 2008 was done after a period of relatively stable growing season SMI following the middle of the 1990s, except for the drought year 2003 (Figure 1). The second survey year, 2019, was the seventh driest year on record and followed a period of significantly reduced SMI (Wilcoxon rank test of SMI in 2008–2019 against the years 1951–2007, $p = 0.002$).

2.2 | Data sampling

The resurvey is based on 125 plots of 1 m^2, five in each of the 25 sites, sampled from late May to July 2008 in the context of a European project on atmospheric nitrogen deposition and vegetation change (Duprè et al., 2010). The five plots per site were positioned in a stratified random approach, ensuring they capture the variation in environmental conditions, but at the same time randomly distributed in the different site types. In most cases, the plots were well spaced within a site, only rarely were plots located close to each other when the grassland site was small and environmental variation was strong on a small spatial scale. A full list of vascular plants and their cover was compiled. GPS data for the position of each plot was recorded. Eight of the original plots had obviously incorrect (e.g.
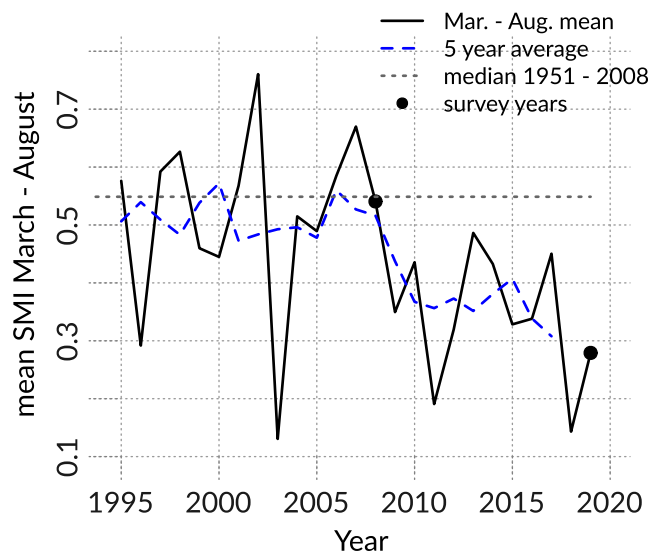
FIGURE 1 Mean soil moisture index (SMI) during the growing season (March–August) from 1995 to 2019.

located in adjacent arable fields) or missing GPS data. Owing to time or weather constraints, five other relevés could not be resurveyed. This left a total of 112 resampled relevés (from 15 sites with five plots each, 9 sites with four plots each and 1 site with two plots), surveyed in June and July of 2019. Because the GPS coordinates were not sufficiently exact to allow us a precise relocation, areas with small-scale heterogeneity or that were more overgrown with shrubs than average for the site were avoided in the resampling to obtain homogeneous plots. This corresponds to the methodology of plot selection in the original study. Species cover values were estimated with a modified Domin scale in both sampling periods. Soil and topographic data were collected for all plots in 2008. These variables included: soil depth (mean of five measurements done with a metal pin), inclination and aspect of the slope, C/N ratio, soil phosphorus concentration (Olsen extraction) and soil pH measured in CaCl$_2$ solution. Field capacity was extracted from soil maps (Landesamt für Bergbau, Energie und Geologie, 2021), representing the amount of water a soil is able to hold when it is saturated.

2.3 | Data analysis

All data were organised using Turboveg (Hennekens & Schaminée, 2001) and analyses were conducted with R (R Core Team, 2021) and RStudio (RStudio Team 2016), including the packages *exactRankTests* (Hothorn & Hornik, 2019), *ggeffects* (Lüdecke, 2018), *lmerTest* (Kuznetsova et al., 2017), *ncdf4* (Pierce, 2019), *r2glmm* (Jaeger, 2017), *reshape2* (Wickham, 2007), *scales* (Wickham & Seidel, 2019), *vegan* (Oksanen et al., 2019), *vegdata* (Jansen & Dengler, 2010), *viridis* (Garnier, 2018) and *zoo* (Zeileis & Grothendieck, 2005). Species names were harmonised according to the GermanSL1.3 (Jansen & Dengler, 2008).

To characterise the sites in terms of temperature and water availability, a heat index integrating the effects of slope inclination and aspect was calculated (Parker, 1988):

$$\text{heat index} = \cos(\text{acpect} - 225)^{*}\tan(\text{inclination}).$$

Steep slopes facing southwest obtain the highest scores, whereas steep slopes facing northeast have the lowest, negative, values. Plane sites by definition have a score of 0. Heat indices varied between −0.35 and 0.70 in our data set. Bennie et al. (2006) classified slopes into three categories, which we merged into two groups for presentation purposes. Steep, south-facing (SSF) slopes were accordingly defined to have an inclination of >15° and are facing SE to W, whereas flat or north-facing (FNF) slopes either have inclinations <15° or are facing NW to E. The category "steep and south-facing" corresponds to heat indices of 0.27 or more.

Mean weighted Ellenberg indicator values (Ellenberg et al., 1992) for light (mL), soil moisture (mF) and nutrients (mN) were calculated for each site, based on square root transformed species cover values. Evenness was calculated as a measure of the dominance structure of the stands (Pielou, 1966). We also computed pairwise Sørensen dissimilarities of all plots between 2008 and 2019 based on cover values of all species (Borcard et al., 2018). The grasses-to-forbs ratio was calculated by dividing the cumulative cover of all graminoid species (including *Poaceae*, *Cyperaceae* and *Juncaceae*) by the sum of cover of all non-graminoid herbaceous species (dicotyledons and monocotyledons).

All species were classified as belonging to one of six plant sociological groups, following Ellenberg et al. (1992): (a) dry grassland character species of *Festuco-Brometea* and *Koelerio-Corynephoretea* (*n* = 39); (b) other species of nutrient-poor grasslands, including character species of *Calluno-Ulicetea* and *Molinio-Arrhenatheretea* with Ellenberg *N* values ≤3 (*n* = 24); (c) agricultural grassland species – character species of *Molinio-Arrhenatheretea* with Ellenberg *N* values >3 (*n* = 31); (d) ruderal species – character species of *Sisymbrietea, Stellarietea mediae, Artemisietea vulgaris, Galio-Urticetea* and *Agrostietea stoloniferae* (*n* = 24); (e) fallow indicators – character species of coniferous and broad-leaved forests as well as of communities of forest edges and clearings (*n* = 55); and (f) indifferent species (*n* = 37).

To test which variables had an effect on the species composition in the first survey year (2008), linear mixed models for several vegetation indices were generated with automatic backwards selection. The 25 study sites were defined as a random factor to eliminate their individual differences before analyses and therefore account for the block design of the study. Dependent variables were total species number per plot, proportions of abundance and cover of the five species groups, mN, mF and mL, the grasses-to-forbs ratio and evenness. Predictor variables were soil chemical parameters (phosphorus, pH, C/N), topographic conditions (inclination, heat index, soil depth, field capacity) and management type (factor variable: mown, grazed, grazed/mown). Heat index and inclination were positively correlated ($p < 0.001$,

Kendall's $\tau = 0.51$), but still sufficiently independent to be used in the same model to test for independent effects of heat index and topography alone. Relevant interaction terms were included. Only the 2008 data were used for these models to avoid the confounding effects of drought. All models were checked for normality of residuals and heteroscedasticity. Dependent variables of models whose residuals did not follow a normal distribution were rank-transformed (cover of agricultural grassland species, mF, grasses-to-forbs ratio, evenness). R^2 values were calculated with the standardized generalized variance approach (function r2beta in Jaeger (2017)).

Differences (Δ) between 2008 and 2019 of the vegetation indices listed above were calculated as follows:

$$\Delta \text{Var} = \text{Var2019} - \text{Var2008}.$$

To test for differences in the means of these indices between 2008 and 2019, a Wilcoxon signed rank test was performed. The significance of overall vegetation change between 2008 and 2019 was tested by a permutational multivariate analysis of variance (PERMANOVA) based on cover-weighted Sørensen dissimilarities (function "adonis" in Oksanen et al., 2019). Differences in multivariate dispersion of the years 2008 and 2019 were tested with the function "betadisper".

To examine whether changes in species composition between 2008 and 2019 differ between sites with different microclimatic conditions, another set of linear mixed models was constructed. Changes (ΔVar) in the above-mentioned vegetation indices were used as dependent variables here. A categorical variable with the two levels "steep and south-facing slopes" and "flat or north-facing slopes" as adapted from Bennie et al. (2006) was used as predictor. Study site again served as a random factor. For each dependent ΔVar, their respective baseline values (Var2008) were also entered into the model to correct for the artefact of the so-called "regression to the mean" (European Medicines Agency, 2015; Mazalla & Diekmann, 2022). This phenomenon describes the tendency of change scores to be negatively related to their baseline values. Because the baseline values of most variables are already correlated with the predictor variable (e.g. there were lower species numbers on SSF slopes in 2008), regression to the mean might interfere with the effect of independent variables on the observed change. It is therefore crucial to correct for this artefact (Mazalla & Diekmann, 2022). We are aware that the model coefficients for the respective baseline variables are ecologically uninterpretable, as they are correlated with the error terms, and we will therefore not discuss them. The outcomes of these models are graphically displayed as boxplots, showing the predicted model values for the two categories "SSF slopes" and "FNF slopes", while fixing the effect of the baseline value at its mean value and averaging over all sites (function ggeffect; Lüdecke, 2018).

To visualise vegetation change, a non-metric multidimensional scaling (NMDS) ordination (Borcard et al., 2018) was performed based on Sørensen distances of square root transformed cover data of all species in both survey years, using the metaMDS function

Oksanen et al. (2019). For the reduction to two dimensions, stress was 0.25.

3 | RESULTS

3.1 | Influence of microclimate on species composition in the initial survey

Both heat index and soil phosphorus (P) had significant effects on the species composition in 2008 (Table 1). As expected, P had a positive influence on more nutrient-demanding species (species of agricultural grasslands), and also on mN and mF. At the same time, the proportion of dry grassland character species and other species of nutrient-poor grasslands was lower at higher P levels. Heat index and inclination affected the species composition in the opposite direction: the steeper and more sun-exposed the plot, the more dry grassland character species and fewer agricultural grassland species were present. Similarly, mF and mN were lower at higher heat indices, whereas mL increased at greater inclinations. Soil depth, field capacity, C/N ratio and management rarely had significant effects. However, soil depth and C/N often appeared in interaction terms, with inclination or heat index being less relevant when soil depth or C/N ratio were high. The form of land use was only important for the share of poor grassland species, with this being highest for grazing only, intermediate for mowing and lowest for a mixture of both methods. Soil pH did not have any significant influence on the vegetation. The models for total species richness, percentage of ruderal species and the grasses-to-forbs ratio showed no significant drivers among any of the available predictor variables. In the case of total species richness, 56% of variance was explained by the identity of the site as a random factor. The latter generally explained a high amount of variance in all models, with values ranging from 13% to 67% (mean 44%).

As an example, the model for the proportion of dry grassland character species is presented in more detail in Figure 2. The proportion of specialist species is positively influenced by the heat index (slope of the fitted model) and negatively by P (parallel lines of the fitted model). However, the heat index becomes less important as soil depth increases (Figure 2 from left to right). Therefore, the slope of the model estimates becomes increasingly flat and eventually nearly zero at a soil depth of 15 cm.

In summary, indices reflecting typical calcareous grasslands were consistently higher at sites with SSF slopes (Figure 3). The proportion of dry grassland character species was on average high at all sites, but significantly higher on SSF slopes (mean 37%) than on FNF sites (mean 30%). The absolute number of character species was also higher on extremely dry and hot sites (mean 7.2) compared with FNF sites (mean 6.7) (not shown). The proportion of agricultural grassland species was lower on SSF (mean 10%) than on FNF sites (mean 13%). Accordingly, the consistently low mN value (between 3 and 3.5 in the majority of sites) was even lower on south-facing slopes. Overall species richness was significantly lower at the driest sites (mean 22.6 vs. 20.1).

3.2 | General vegetation change between 2008 and 2019

The impacts of recent droughts are reflected in changes in the species composition between 2008 and 2019 (Table 2). The average number of species per plot increased only slightly, but the species composition changed significantly (PERMANOVA: $R^2 = 0.04$, $p < 0.001$). However, dispersion was also significantly greater in 2019 than in 2008 ($p = 0.02$). The vegetation became sparser, as total cover decreased. Species groups that profited over the 11 resurvey years were specialist species of dry grasslands, ruderal species and fallow indicators. Grassland species adapted to nutrient-poor conditions but not to drought decreased in number and proportion of cover, whereas agricultural grassland species decreased in cover only. Of the mean Ellenberg indicator values, only mF decreased, whereas mN and mL remained unchanged. The grasses-to-forbs ratio was significantly reduced, as was evenness. The latter was highly negatively correlated with the cover of *Bromus erectus* (Spearman's $\rho = -0.57$, $p < 0.001$). Where evenness decreased the most (lowest 25% quantile: decrease greater than −0.09%), *Bromus erectus* had also increased most, resulting in mean cover values of 41% in 2019. Whereas *Bromus erectus* was able to spread, *Brachypodium pinnatum* as the second potentially dominant grass suffered significant losses.

3.3 | Vegetation changes under different microclimatic conditions

Comparison of SSF slopes with FNF sites reveals some important site differences in vegetation change between 2008 and 2019. Total species number, which was already lower on SSF slopes in 2008, decreased further on these sites, whereas it increased on FNF sites (Figure 4). Turnover, expressed by the Sørensen index, was significantly lower on the driest sites. Differences in other indices between the two site types were not statistically significant, but contribute to the overall picture. Total cover generally decreased, but more so on SSF slopes. The number of dry grassland character species per plot tended to decrease on SSF slopes, but to increase on sites with less extreme conditions. The same was true for the number of agricultural grassland species. The number of other grassland species with low nutrient demands generally decreased, whereas the number of ruderal species increased. Changes in mean Ellenberg indicator values were influenced by the microclimatic conditions in the sites, with SSF slopes showing higher mL and decreasing mN values. By contrast, FNF slopes increased in mN. Changes in the grasses-to-forbs ratio differed only slightly between the categories. Evenness decreased throughout, but more on south-facing sites.

In summary, the effects of the recent droughts were stronger on the driest slopes, resulting in a reduction in total species richness, including dry grassland character species. Signs of ongoing nutrient accumulation (increase in agricultural grassland species and mN) were present only in the moderately dry, north-facing sites.

The NMDS ordination of all sites in both years shows a summary of the vegetation shifts between 2008 and 2019 (Figure 5). A

TABLE 1 Summary of mixed linear models for vegetation variables in 2008

	R^2	Heat index	Inclination	p	Soil depth	Field capacity	C/N	Land use	Heat index: soil depth	Inclination: soil depth	Soil depth: Field capacity	Heat index: C/N	Site variation (%)
Dry grasslands character species													
% species	0.26	+		−					−				48
% cover	0.31	+		−			+						66
Agricultural grassland species													
% species	0.37	−	−	+								+	13
% cover	0.39	−	−	+			−			+		+	32
Other poor grassland species													
% species	0.30		+	−	+	+		+/−			−		19
Other indices													
mL	0.14		+							−			56
mF	0.30	−		+								+	67
mN	0.50	−	−	+	−	−				+	+	+	44
Evenness	0.10	−											35

Note: +, significantly positive; −, significantly negative effect of the predictor (columns) on the dependent variable (rows); mL, mF and mN, mean Ellenberg indicator values for light, soil moisture and nutrients; P, soil phosphorus content; C/N, soil carbon to nitrogen ratio; Site variation (%), share of variance explained by the site as the random factor. For full table with estimates see Appendix S2.

general shift in the positive direction along the first axis is visible. This is associated with increasing cover of ruderal species and lower cover of poor grassland species not specially adapted to drought conditions. Total species richness and mF also decrease in this direction. The shift in species composition differed between FNF slopes and SSF ones. The latter moved slightly into the negative direction along the second axis. This is mainly correlated with an increase in the cover of character species of dry grasslands and in mL, a reduction in total cover and fallow indicators. By contrast, communities on FNF slopes shifted slightly in the positive direction along the second axis, where mN and species of agricultural grasslands increased.

4 | DISCUSSION

4.1 | H1: Particularly warm and dry microclimates generally have a positive effect on the characteristic species composition of dry grasslands

In the initial survey in 2008, the typical species of calcareous grasslands were more abundant where topography created a particularly hot and dry microclimate, i.e. on SSF slopes, confirming our first hypothesis. In the models, a positive relationship between the heat index and the number of dry grassland specialists was found, as well as a negative relationship between heat index and more mesic, nutrient-demanding and competitive agricultural grassland species. This is also reflected in a negative correlation between the heat index and mF and mN. Proportional cover and the absolute number of dry grassland specialists were significantly higher on SSF slopes than on FNF slopes. This supports the idea that dry conditions can

have a stabilising effect on the species composition in dry grasslands because they push back more competitive species that are less well adapted to drought stress (Bennie et al., 2006; Fischer et al., 2020).

Soil nutrient conditions, especially P availability, played an equally important role. These findings coincide with observations from Adriaens et al. (2006), who also identified productivity and insolation as the two main factors determining species composition in Belgian calcareous grasslands. We found a significantly positive relationship of P concentrations with indicators of eutrophication (share of agricultural grassland species, mF and mN). There was, however, no effect of P levels on evenness or the grasses-to-forbs ratio in the models. Calcareous grasslands are commonly considered to be P-limited (Carroll et al., 2003) and the atmospheric input of P is generally low. This explains why the influence of P was significantly greater than the influence of the C/N ratio in the models. Nutrient-demanding and competitive species are restricted to sites with sufficient P supply, whereas those with efficient P economies can avoid competition on less well-supplied sites.

In the context of eutrophication via atmospheric nitrogen deposition, the two factors of water availability and P supply can be interpreted as limiting factors in the sense of Liebig's law of the minimum (von Liebig, 1840). When water and/or P act as limiting resources, more productive species that are generally promoted by higher nutrient levels cannot fully exploit the deposited additional nitrogen. Therefore, the effects of eutrophication are weak on particularly dry and phosphorus-poor sites (Bennie et al., 2006; Dengler et al., 2014; Diekmann et al., 2014), which favours the specialised species of calcareous grasslands that are the target species for nature conservation in our sites.

Among the site-specific variables in the models, reflecting water availability, nutrient supply and management type, no significant
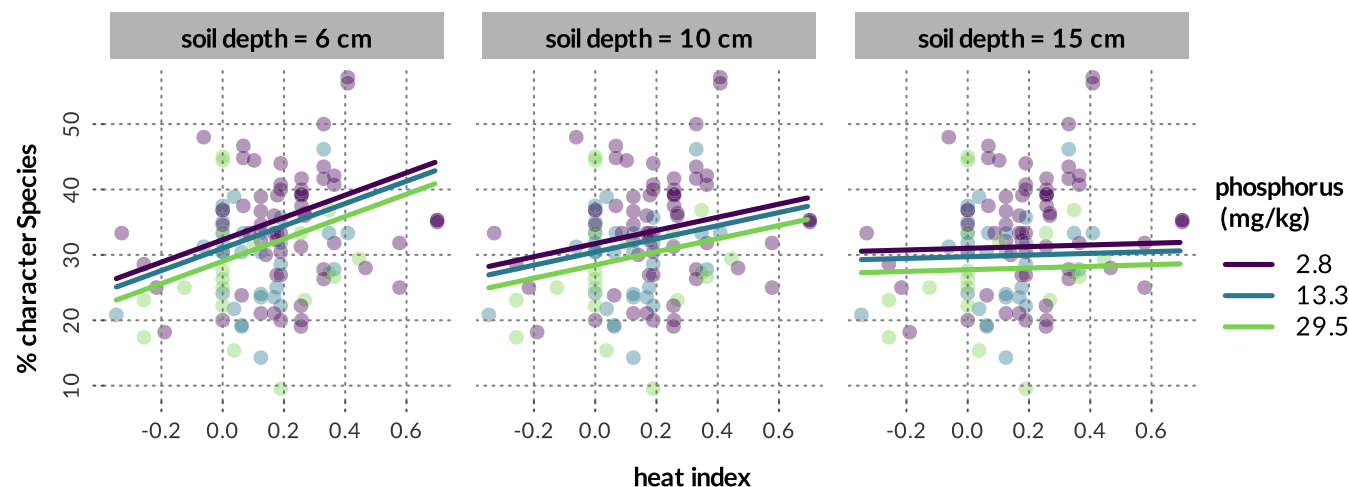
FIGURE 2 Proportion of dry grassland character species per plot in 2008 as a function of heat index, soil phosphorus and soil depth.

FIGURE 3 Comparison of vegetation parameters between steep, south-facing slopes and flat or north-facing slopes in 2008. For the grasses-to-forbs ratio, three extreme outliers were removed from the graph for better readability. p-values were computed with a Wilcoxon signed rank test for unpaired data.
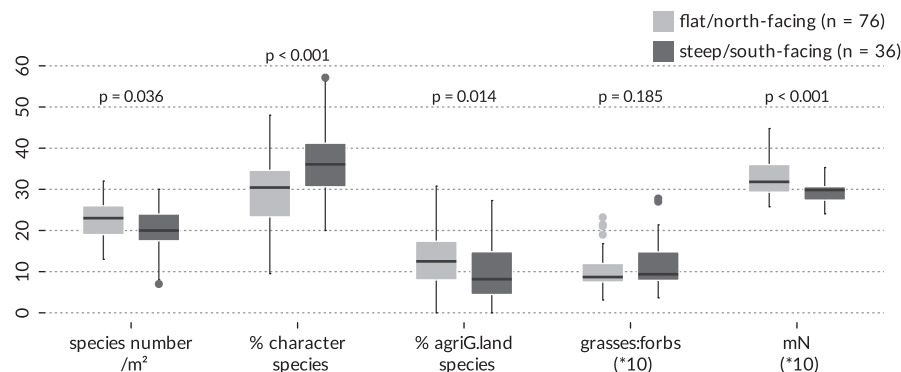
predictors of total species richness were found. Yet, we did not account for variables characterising the surrounding landscape, such as management history, isolation, habitat area and diversity. Fragmentation and landscape context are known to be important factors for species richness in semi-natural grasslands (Adriaens et al., 2006; Zulka et al., 2014). Because site identity explained a big part of the variation in species richness (56%), it is plausible that factors such as these strongly influenced total species richness. However, although total species number is often considered a measure of "quality" in ecology (Bobbink & Willems, 1987), the number of specialised species is more important from the perspective of conservation.

4.2 | H2: The species composition of semi-arid calcareous grasslands is generally robust to the exceptional droughts of the past decade

Contrary to results from experimental studies (Grime et al., 2008; Maalouf et al., 2012), the changes in vegetation between 2008 and 2019 show clear signs of the intense droughts of the past decade. Total cover and mF decreased significantly, an effect previously reported by, for example, Sternberg et al. (1999) and Morecroft et al. (2004).

Species adapted to dry conditions, i.e. character species of dry grasslands, profited most over this period, as anticipated by Behrens et al. (2009) and Pompe et al. (2011). By contrast, grassland species adapted to low-nutrient conditions but not to drought declined most in number and cover. Agricultural grassland species, which are likewise not adapted to drought but are more nutrient-demanding, were not as severely affected and only decreased in cover, but not in species number. Ruderal species were able to benefit from the dry conditions, a process that was reported as "grassland ruderalisation after a drought event" by Fischer et al. (2020). The drought most likely acted as a disturbance and the resulting bare soil patches opened up opportunities for the short-lived and fast-colonising ruderal species. The spread of shrub and tree species points to a tendency towards less intensive land use of our study sites, even though they were all actively managed within conservation programs. These results represent conservative estimates of change, especially for fallow indicators, because overgrown areas in the sites were avoided while resampling to match the original methodology.

Evenness as a measure of diversity decreased over the course of the 11 years, indicating a more pronounced dominance structure. However, mean evenness in 2019 was still at a very high level (0.81), compared with other calcareous grassland sites (Haeupler, 1982). As pointed out by Bornkamm (2006), the dominance structure

TABLE 2 Mean values of vegetation parameters in 2008 and 2019, with standard deviations in parentheses

		2008	2019	*p*-value
	Total richness	21.8 (4.9)	22.5 (6.2)	0.226
⇓	Total cover	77.3 (10.6)	73.9 (16.7)	0.023
Dry grassland character species				
	Number	6.9 (2.4)	7.3 (2.4)	0.054
⇑	Percentage cover	40.1 (8.8)	49.2 (17.7)	<0.001
Other poor grassland species				
⇓	Number	4.2 (1.9)	3.6 (2.0)	0.003
⇓	Percentage cover	16.4 (8.6)	12.4 (9.6)	<0.001
Agricultural grassland species				
	Number	2.6 (1.7)	2.6 (2.0)	0.969
⇓	Percentage cover	9.3 (7.9)	7.4 (6.7)	0.008
Fallow indicators				
	Number	3.1 (1.8)	3.5 (2.3)	0.079
⇑	Percentage cover	8.3 (6.1)	13.4 (13.7)	<0.001
Ruderal species				
⇑	Number	0.7 (0.7)	0.9 (0.9)	0.035
	Percentage cover	1.7 (1.9)	1.8 (2.2)	0.678
	mL	7.24 (0.15)	7.26 (0.22)	0.103
⇓	mF	3.94 (0.24)	3.87 (0.30)	<0.001
	mN	3.16 (0.42)	3.18 (0.48)	0.896
⇓	Evenness	0.85 (0.06)	0.81 (0.11)	<0.001
⇓	Grasses: forbs	1.19 (0.96)	1.16 (1.5)	0.031
⇑	*Bromus erectus* cover	12.6 (15.3)	16.6 (20.0)	0.008
⇓	*Brachypodium pinnatum* cover	9.6 (11.3)	5.5 (7.0)	0.001

Note: mL, mF and mN, mean Ellenberg indicator values for light, soil moisture and nutrients. Differences in average values were examined with a Wilcoxon signed rank test. Arrows denote a significant increase or decrease over time, respectively.

appeared to be determined mainly by one species: *Bromus erectus*. In general, there was a significant spread of *Bromus erectus*, whereas *Brachypodium pinnatum* declined simultaneously. The shift in the competitive relationship between these two grasses can be approached from several angles. First, *Bromus erectus* is a relatively late invader to the study area and was still very rare just 100 years ago (Bornkamm, 2006). It may simply not yet have reached its final range. Second, *Bromus* is reportedly more drought tolerant than *Brachypodium* and has a higher colonisation ability after disturbance (Corcket et al., 2003). This might have given *Bromus* an advantage over *Brachypodium* during the drought spells. Third, management as a complex factor composed of management type (mowing or grazing) and intensity (time of year, but also kind of animal, stocking density and grazing duration) may play an important, but difficult to disentangle role. It is known that *Bromus* is preferably eaten by

grazers and *Brachypodium* is sensitive to early mowing or grazing (Leuschner & Ellenberg, 2017b). The fact that all four sites where *Bromus* increased the most are under the management regime of one single municipality supports the theory that management had a strong influence on the species' dynamics.

4.3 | H3: Changes in species composition and diversity induced by drought depend on the microclimatic conditions of the site

A different perspective emerges when differentiating between sites with varying levels of drought exposure. On SSF slopes, total species richness decreased, affecting all species groups except ruderal species. Remarkably, this also applied to character species of dry grasslands whose adaptations to dry conditions may be insufficient to endure the severity of the recent droughts on sites with the most extreme microclimate. This is a first warning signal that some semi-arid grassland species may not be able to persist under the unfolding climate change scenarios that predict more intense and frequent droughts (IPCC, 2014; DWD, 2018). The increase in bare soil on steep slopes, together with the predicted increase in heavy rainfall events, may additionally lead to higher erosion. By contrast, conditions on FNF sites promoted an increase in total species number and the share of specialised species, but also an increase in nutrient-demanding common species and higher mN values. These eutrophication processes, which are frequently observed in this type of grassland and pose a threat to species diversity (Bennie et al., 2006; Jandt et al., 2011; Bauer & Albrecht, 2020), were apparently not halted even during a drought period. Consequently, if management and nutrient deposition continue as at present, the FNF sites cannot be seen as long-term refugia for mesic dry grassland character species because the ongoing process of eutrophication by nitrogen deposition may hinder their establishment. The role of conservation strategies affecting biotic and abiotic framework conditions was highlighted by Petermann et al. (2007). The current impairment of calcareous grasslands through, for example, nutrient enrichment, area loss, fragmentation and thus degradation of genetic diversity and loss of functional interrelations makes them more sensitive to additional stressors such as climate change (Petermann et al., 2007). For a conservation strategy adapted to climate change, it would be crucial to consider these aspects to ensure that sites with less extreme microclimates can serve as refugia in the future.

Species turnover was higher on the more mesic sites, a result also reported by Bennie et al. (2006). This is caused by greater changes in species cover values and more newly appearing species (gains) in north-facing plots, whereas the number of disappearing species (losses) did not differ between SSF and FNF sites. Lower turnover promises more stability and a better conservation of species and habitats. However, the direction of change is of great importance. In the current case, the more "stable" south-facing sites
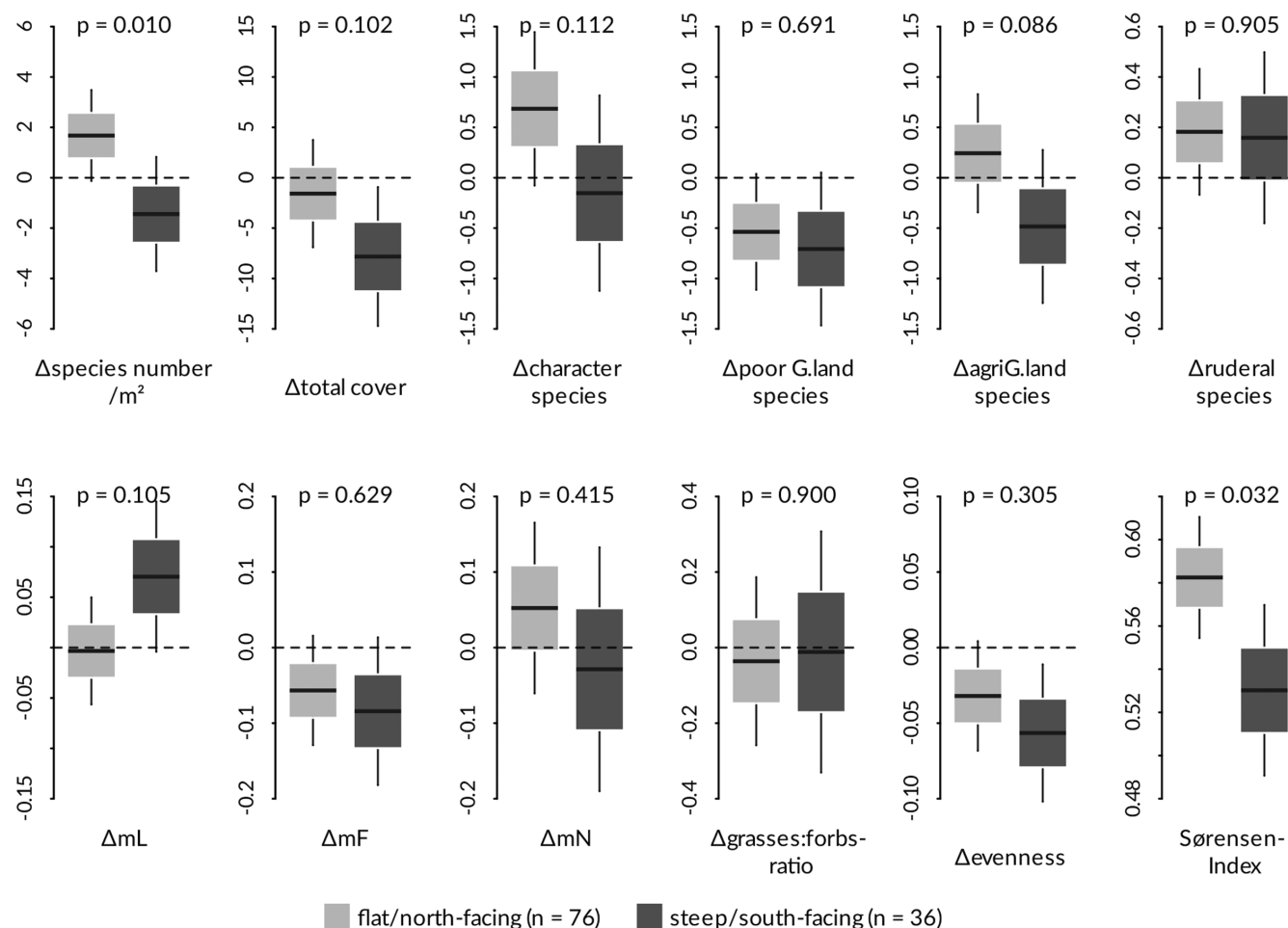
FIGURE 4 Results of linear mixed models showing the differences in vegetation change from 2008 to 2019 between the two categories steep/south-facing vs. flat/north-facing slopes. Shown are the predicted model values of the respective variable for both categories and their 95% quantiles, with the effect fixed at the mean of the variable in 2008 and averaged over all 25 study sites. *p*-values give the significance of difference between the two sites type categories Δcharacter species, Δpoor G.land species, ΔagriG.Land species, Δruderal species: differences in numbers of dry grassland character species, other species of nutrient-poor grasslands, species of agricultural grasslands and ruderal species per plot, respectively, between 2008 and 2019. ΔmL, ΔmF, ΔmN: differences of community-weighted Ellenberg indicator values for light, soil moisture and nutrients between 2008 and 2019.

lost specialist species whereas these increased on the more "unstable" north-facing sites. Bennie et al. (2006) expressed the hope that more frequent and intense summer droughts might be profitable for the maintenance of stress-tolerant vegetation in the future. Our results confirmed the underlying assumption that higher drought intensities may inhibit eutrophication effects (see H1). The authors did, however, not anticipate any negative effects that we now see after a decade in which increased summer drought events have become a reality.

Our results show that it can be important to differentiate even within a data set of relatively homogeneous vegetation: not only between species groups with varying requirements, but also between sites with different microclimatic conditions. This allows us to identify more subtle changes or even opposing trends that may cancel each other out in the overall trend.

5 | CONCLUSION

The characteristic vegetation of semi-arid grasslands is commonly thought to profit from global warming, either by an increase in potential habitat area or by the positive, competition-reducing effects of droughts on the specialised species of these habitats. However, a substantial expansion of habitat area is unlikely in Europe's intensely used landscape because the vegetation relies on traditional land-use practises mostly only applied for nature conservation reasons. Our results confirmed that a warmer and drier microclimate promoted the specialised vegetation in the past, but this may no longer be the case with ongoing climate change. SSF sites lost species from all groups except ruderal species after a decade of intense drought, whereas species numbers increased on FNF sites. On these, eutrophication processes seemed to continue despite the intense drought period.

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FIGURE 5 Non-metric Multidimensional (Distance) Scaling of square root transformed vegetation data of both survey years. Ellipses mark the standard deviation of the points in the four groups. Flat/N, flat and north-facing slopes in 2008 and 2019; Steep/S, steep and south-facing slopes in 2008 and 2019. Arrows point from the centroid of the respective group in 2008 to the centroid of the same group in 2019. mL, mF and mN, community-weighted Ellenberg indicator values for light, soil moisture and nutrients; Spec.Num, total species number per plot; Char.Specs, share of cover of dry grasslands character species; poorG.Land, share of cover of species of other nutrient-poor grasslands; agriG. Land, share of cover of agricultural grassland species; fallow, share of cover of fallow species; ruderal, share of cover of ruderal species.

AUTHOR CONTRIBUTIONS

Leonie Mazalla and Martin Diekmann designed the study. Cecilia Duprè, Martin Diekmann and Leonie Mazalla collected the data. Leonie Mazalla conducted the analyses and wrote the first draft of the paper. Martin Diekmann and Leonie Mazalla discussed the interpretation of results, Martin Diekmann and Cecilia Duprè contributed substantially to the revisions. All authors gave their final approval for publication.

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

Appendix S1. Map of the 25 study sites in northwest Germany.
Appendix S2. Summary of mixed linear models for vegetation variables in 2008.

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