

Floristic changes of xerothermic grasslands in Central Germany: A resurvey study based on quasi-permanent plots

Floristische Veränderungen der Xerothermrassen in Mitteldeutschland: Eine Wiederholungsstudie basierend auf quasi-permanenten Dauerflächen

Tim Meier¹*, Isabell Hensen^{1,2} & Monika Partzsch¹

¹*Institute of Biology/Geobotany and Botanical Garden, Martin Luther University Halle-Wittenberg, Am Kirchtor 1, 06108 Halle (Saale), Germany;*

²*German Centre for Integrative Biodiversity Research (iDiv) Halle-Jena-Leipzig, Puschstraße 4, 04103 Leipzig, Germany*

**Corresponding author, e-mail: tim.meier@botanik.uni-halle.de*

Abstract

Biodiversity has declined in the dry and semi-dry grasslands of Central Germany over the past three decades, mainly as a result of ‘Global Change’, including changes to traditional land use practices. Such processes have promoted the spread of grass species such as *Bromus erectus*, which has become increasingly dominant within xerothermic grasslands. The aim of the study was to investigate changes in the vegetation of such grasslands over the last two decades by comparing previous and recent vegetation relevés (quasi-permanent plots) from two regions in Saxony-Anhalt and Thuringia (Saaletal north-west of Halle (Saale), Kyffhäuser). The floristic comparison was carried out between dry and semi-dry grasslands (by calculation of the Sørensen index) and within functional groups (annuals, graminoids, forbs). The following statistical analyses were performed: detrended correspondence analysis (DCA), paired t-tests, Wilcoxon signed-rank tests and Pearson correlations. Generally, there was no change in species number over time, but vegetation cover increased significantly. Dry grasslands showed a higher floristic similarity between the previous and recent relevés than semi-dry grasslands, indicating that plant communities in drier grasslands show relatively higher stability, which is likely due to local ecological conditions. Comparing the functional groups, annuals (e.g. *Hornungia petraea*) and graminoids (e.g. *B. erectus*) showed an increase and some new species were recorded over time (e.g. *Descurainia sophia*, *Convolvulus arvensis*). In contrast, endangered forbs declined (e.g. *Asperula cynanchica*, *Euphrasia stricta*, *Silene otites*). While the dominant grasses *B. erectus* (highest increase in dry and semi-dry grasslands), *Festuca rupicola* and *Helictotrichon pratense* showed significant increases in coverage, species richness in the investigated plant communities was hardly affected as a result. We consequently concluded that an expansion of traditional land use measures may be required to halt the increasing spread of graminoids and to protect the biodiversity of the xerothermic grasslands in Central Germany.

Keywords: *Bromus erectus*, dominant grass species, *Festuco-Brometea*, functional group, global change, land use, nature conservation, Sørensen index, vegetation relevés

Erweiterte deutsche Zusammenfassung am Ende des Artikels

1. Introduction

Dry and semi-dry grasslands in Europe are considered the most species-rich plant communities worldwide (WILSON et al. 2012, CHYTRÝ et al. 2015, DENGLER et al. 2020). Such xerothermic grasslands are characterized by their high biodiversity and large proportion of rare and (critically) endangered species (KORNECK et al. 1996, VAN SWAAY et al. 2006, VEEN et al. 2009, DENGLER et al. 2014), such that their protection is of the highest priority in nature conservation (JANSSEN et al. 2016, FRANK et al. 2020).

Natural and semi-natural xerothermic grasslands have experienced dramatic declines in species richness in recent decades (BRUELHEIDE et al. 2020), which is caused by increasing fragmentation and isolation of the landscape following agricultural intensification or abandonment (LINDBORG et al. 2014, DEÁK et al. 2016, JANSSEN et al. 2016). Such land use change has led to declining biodiversity, even among more common species, in many regions of Germany (DIEKMANN et al. 2014, PEPLER-LISBACH & KÖNITZ 2017, STRUBELT et al. 2017, JANSSEN et al. 2020, EICHENBERG et al. 2021). The trend is of particular concern where species-rich xerothermic grasslands have been replaced by species-poor plant communities (PARTZSCH 2000, RÖMERMAN et al. 2005, ENYEDI et al. 2008).

‘Global Change’ refers to diverse processes such as climate warming, soil acidification, increasing atmospheric nitrogen input and land use changes, which on grasslands leads to the dominance of grasses over dicotyledonous species and declining biodiversity (WILLEMS 1987, BOBBINK et al. 1998, 2010, DUPRÉ et al. 2010, WESCHE et al. 2012, DIEKMANN et al. 2014, ENRIGHT et al. 2014). In north-western Germany, increased atmospheric nitrogen input over 70 years led to the loss of typical xerothermic grassland species which was exacerbated by them being more limited by water and phosphorus availability in the soil (DIEKMANN et al. 2014). Not negligible is the nitrogen deposition, which on the one hand promotes the growth of grass species and on the other hand can lead to a change in nutrient cycles and thus to a change in species composition and soil conditions (GILLIAM 2006, PERRING et al. 2018). In addition, seasonal weather conditions can have different effects on grasslands (PETŘÍK et al. 2011), in that extreme temperatures lead to lethal effects in many species, whereas higher precipitation in the previous vegetation period may support the germination and establishment of species in the following growing season (FITTER & HAY 2001).

Particular changes in traditional land use, such as grazing and mowing, cause declines in biodiversity in xerothermic plant communities (POSCHLOD & WALLIS DE VRIES 2002, HÜLBER et al. 2017, VALKÓ et al. 2018). The lack of grazing promotes both the spread of dominant grass species and the immigration of ruderal and adventive species (PARTZSCH & MAHN 2001, ELIAS et al. 2018). In particular, grasses are considered to be stronger competitors than dicotyledonous species (DEL-VAL & CRAWLEY 2005, PARTZSCH et al. 2018), as they accumulate higher layers of litter, which can consequently reduce light availability at lower levels (HEGEDUŠOVÁ & SENKO 2011). Therefore, an increasing abundance of grasses is largely responsible for the conversion of formerly species-rich xerothermic grasslands into more species-poor plant communities (DONOHUE et al. 2000, ENYEDI et al. 2008, WESCHE et al. 2012). This is supported by several studies that found xerothermic grasslands to be increasingly dominated by various grass species such as *Bromus erectus*, *Brachypodium pinnatum*, *Festuca* sp., *Helictotrichon* sp. or *Stipa* sp. (BOBBINK et al. 1998, PARTZSCH 2000, 2001, PUSCH & BARTHEL 2003, BORNKAMM 2006, 2008, KLIMASCHIEWSKI et al. 2006, DOSTÁLEK & FRANTÍK 2008, SILANTYEVA et al. 2012, MEIER & PARTZSCH 2018).

In Central Germany, the indigenous dominant grass species *Bromus erectus*, which is a characteristic species of the order *Brometalia erecti* (SCHUBERT et al. 2001), has become increasingly widespread across xerothermic grasslands (ZÜNDORF et al. 2006, BORNKAMM 2006, 2008, HELMECKE 2017) and therefore has an associated invasive character (VALÉRY et al. 2009). The species is classified as a neophyte in Germany in the federal states of Thuringia and Saxony-Anhalt (HEINRICH 2010, FRANK & SCHNITTER 2016). The increasing dominance of *B. erectus* is likely linked to a sharp decline in sheep and goat grazing and the consequent reduction in grazing pressure (BRIEMLE 1999, BORNKAMM 2008, DIEKMANN et al. 2014). In fact, *B. erectus* is now migrating into neighboring xerothermic plant communities, including *Stipa* grasslands (BIERINGER & SAUBERER 2001, MEIER & PARTZSCH 2018). As such, the question of the increasing dominance of grass species including *B. erectus* across the xerothermic grasslands of Central Germany and the underlying mechanisms of change in species composition is unresolved. From a nature conservation point of view, it is of crucial importance to understand how the increasing spread of dominant grass species occurs, especially for *B. erectus*, and how it can be prevented in order to counteract the decline of species of xerothermic grasslands.

In order to detect temporal and spatial changes in plant communities over time, many studies have compared previous and current vegetation relevés to determine any basis for ‘Global Change’ (e.g. JANTSCH et al. 2013, KUDERNATSCH et al. 2016). However, when recording quasi-permanent plots, there is a risk of pseudo-turnover, since changes over time (including fluctuations) are more difficult to record than spatial ones (FISCHER & STÖCKLIN 1997, VYMAZALOVÁ et al. 2012). Nevertheless, a renewed resumption of the vegetation by means of quasi-permanent plots should represent a more robust method for deriving and interpreting decadal changes in plant communities, although inaccurate plot sizes and observer errors cannot be neglected (ARCHAUX et al. 2006, VERHEYEN et al. 2018). Therefore, permanent marking of these plots with coordinates and magnets is a prerequisite for future accurate biodiversity monitoring (CHYTRÝ et al. 2014).

The aim of this study was to document temporal and spatial changes in the vegetation of sampled xerothermic grasslands in Central Germany over a more or less twenty-year period. An increase in grass species (especially *B. erectus*) was anticipated, and we set-out to assess the effects this would have on species composition among different plant communities of the dry and semi-dry grasslands. The approach involved a floristic comparison being undertaken between previous (1995–2002) and recent (2018/19) plots on vegetation relevés from two grassland locations in the dry region of Central Germany. A further aim of the study was to identify potential measures for applied nature conservation.

The study therefore set out to answer the following two questions: (1) Does the comparison of previous and recent relevés reveal changes in the floristic composition of plant communities of dry and semi-dry grasslands? (2) Does the comparison of previous and recent relevés reveal a change in the functional groups of species and is there an increasing dominance of grass species?

2. Material and Methods

2.1 Study areas

Seven study areas were selected from two regions in Central Germany that have pronounced occurrences of xerothermic grasslands: (1) Saaletal northwest of Halle (Saale) and (2) Kyffhäuser (Fig. 1, Supplement E1). The climate across the regions is characterized by low annual precipitation of around

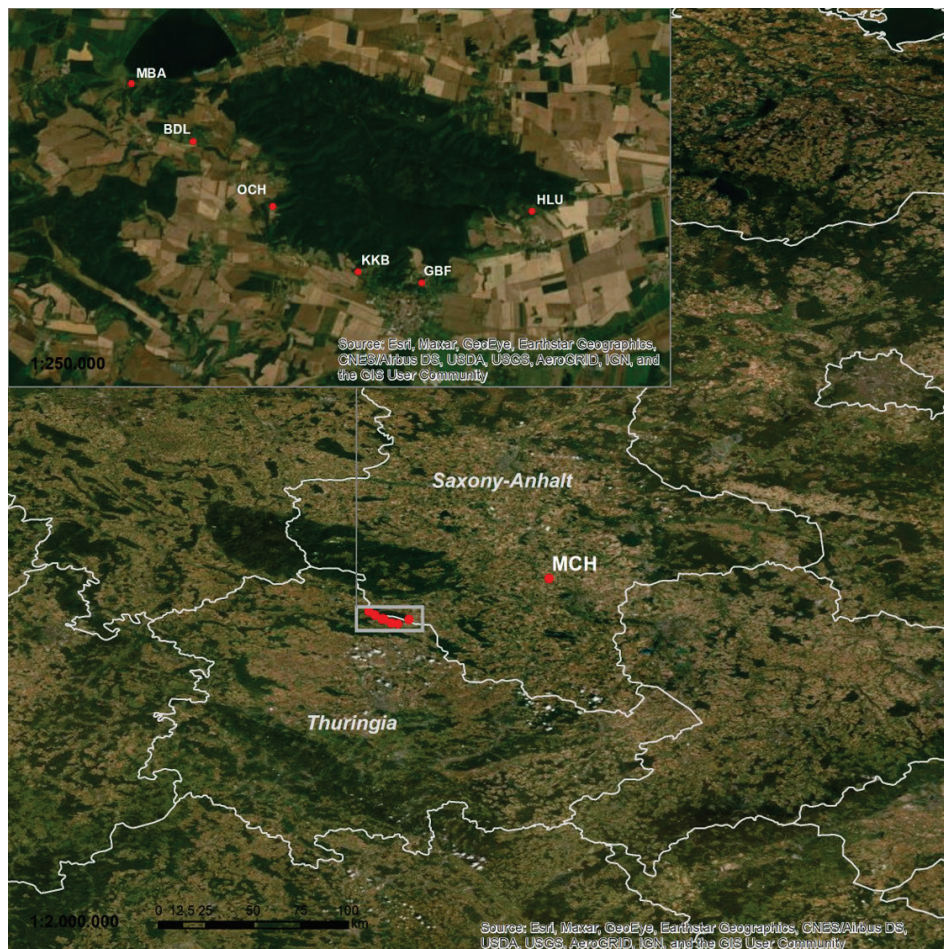


Fig. 1. Overview map (created in ArcGIS 9) of the studied xerothermic grasslands in the Central German dry region (for abbreviations see Supplement E1). Detailed maps of the quasi-permanent plots and their respective coordinates are given in Supplement E2 and E5).

Abb. 1. Übersichtskarte (Erstellung in ArcGIS 9) der untersuchten Xerothermrassen im Mitteldeutschen Trockengebiet (Abkürzungen siehe Anhang E1). Detaillierte Karten der quasi-permanenten Flächen und deren jeweiligen Koordinaten sind in den Anhängen E2 und E5 angegeben.

450–550 mm and annual mean temperatures of 8.5–9.2 °C (DÖRING 2004). Typical soils belong mostly to the types protorendzina or rendzina and to partially degraded chernozem with different parent rocks (e.g. porphyry, limestone, gypsum) (MAHN 1965). The regions have been intensively studied and documented by various authors (see MEUSEL 1939, MAHN 1965, ANDRES 1994, HENSEN 1995, SCHNEIDER 1996, JANDT 1999, PARTZSCH 2000, 2001, RICHTER 2002, RICHTER et al. 2003, PUSCH & BARTHEL 2003, BECKER et al. 2011, HAHN et al. 2013, MEIER & PARTZSCH 2018 for detailed descriptions).

2.2 Plant communities

The xerothermic grasslands of Central Germany are characterized by their often quite rare plant communities, which are generally divided into the two classes *Koelerio-Corynephoretea* (acid or siliceous and sandy grasslands) and *Festuco-Brometea* (basiphytic calcareous grasslands). The investigated plant communities are included in the following system (according to SCHUBERT et al. 1995):

- Class: *Koelerio-Corynephoretea* Klika ap. Klika et Nowak 1941
 - Order: *Sedo-Scleranthetalia* Br.Bl. 1955
 - Suborder: *Alysso-Sedion* Oberd. et Th. Müll. ap. Th. Müll. 1961
 - Association: *Teucro-Festucetum cinereae* Mahn 1959
 - Order: *Festuco-Sedetalia* R.Tx. 1951
 - Suborder: *Armerion elongatae* Krausch 1961
 - Association: *Filipendulo-Helictotrichetum pratensis* Mahn 1965
- Class: *Festuco-Brometea* Br.Bl. et R. Tx. 1943
 - Order: *Festucetalia valesiacae* Br.Bl. et R. Tx. 1943
 - Suborder: *Festucion valesiacae* Klika 1931
 - Association: *Festuco valesiacae-Stipetum capillatae* (Libb. 1931) Mahn 1959 emend.
 - Suborder: *Cirsio-Brachypodion* Hadač et Klika 1944
 - Association: *Stipetum stenophyllae* (Podp. 1930) Meusel 1938
 - Association: *Festuco rupicolae-Brachypodietum pinnati* Mahn 1959 emend.
 - Order: *Brometalia erecti* Br.Bl. 1936
 - Suborder: *Xerobromion* (Br.Bl. et Moor 1938) Moravec in Holub et al. 1967
 - Association: *Fumano-Seslerietum variae* W. Schub. 1963
 - Suborder: *Mesobromion erecti* (Br.Bl. et Moor 1938) R. Knapp 1942 ex Oberd. 1957
 - Association: *Onobrychido-Brometum erecti* Th. Müll. 1968
 - Association: *Gentiano-Koelerietum pyramidatae* Knapp 1942 ex Bornk. 1960

2.3 Vegetation relevés

A total of 57 previously sampled vegetation relevés were revisited in 2018 and 2019 including:

- 21 relevés of RICHTER (2002) from the porphyry landscape near Mücheln (Wettin);
- 30 relevés of SCHNEIDER (1996) from the Ochsenburg within the Kyffhäuser; and
- 6 relevés of PUSCH & BARTHEL (2003) from the Kyffhäuser area.

The vegetation relevés were assigned to the 8 associations listed above in Section 2.2.

The previous plots were identified using location sketches or vegetation maps prepared by the authors of the studies (SCHNEIDER 1996, RICHTER 2002). Using GoogleEarth (image overlay), the position for each plot could be relocated and its GPS coordinate specified, while GPS coordinates were already available in PUSCH & BARTHEL (2003). The new vegetation relevés were carried out using the same methodology as that adopted in the original study (including area size, recording time, cover-abundance values). Since the previous plots were not marked with magnets, a deviation of approx. 3 m from the newly created plots was assumed. These quasi-permanent plots allowed for an approximate resumption of the same position (CHYTRÝ et al. 2014).

The recent relevés were then marked out with magnets and the GPS coordinates were noted to facilitate monitoring in the future (CHYTRÝ et al. 2014). The field studies were then carried out during the same months as on the previous relevés, i.e. from the end of April to August in the years 2018 and 2019, and on two occasions, to ensure both early and late flowering species were recorded. Plot size varied from 9 to 25 m², due to paid attention to homogeneity. Geographical data such as height, exposition and inclination were documented. Coverage of the herb and cryptogamy layer (in %) as well as coverage of the plant species were determined using the 9-part Braun-Blanquet scale (REICHELT & WILMANN 1973) (Supplement E3). The nomenclature of vascular plants was based on JÄGER (2017), that of the plant communities on SCHUBERT et al. (1995); cryptogams were not considered.

2.4 Data analysis

In the previous vegetation relevés by PUSCH & BARTHEL (2003), species coverage values followed the original 7-part Braun-Blanquet scale (BRAUN-BLANQUET 1964), such that the coverage levels for all other relevés had to be adjusted accordingly (including recent vegetation relevés). Correspondingly, the estimate values 2a (> 5–15% cover) and 2b (> 15–25% cover) of the 9-part Braun-Blanquet scale (REICHELTELT & WILMANN 1973) were summarized as estimate value 2 (> 5–25% cover) of the 7-part Braun-Blanquet scale. In contrast, the estimated value 2m (many individuals, < 5% cover) given on the 9-part scale was converted into the estimate value 1 (> 1–5% cover) of the 7-part scale. The previous and recent vegetation relevés are presented in Supplement E3 and E4, including both the originally recorded and the adjusted coverage levels of the respective species. For all the other analyses, the adjusted coverage levels of the 7-part Braun-Blanquet scale were transformed as follows (according to DIERSCHKE 1994): $r = 0.1\%$, $+$ = 0.5% , $1 = 2.5\%$, $2 = 15\%$, $3 = 37.5\%$, $4 = 62.5\%$, $5 = 87.5\%$. The unweighted mean indicator values (ELLENBERG et al. 2001) for light, temperature, moisture, reaction and nutrients per plot (previous and recent relevés) were also calculated. Moreover, the plant communities were pooled into dry (*Teucrio-Festucetum*, *Festuco-Stipetum*, *Fumano-Seslerietum*) and semi-dry (*Filipendulo-Helictotrichetum*, *Stipetum stenophyllae*, *Festuco-Brachypodietum*, *Onobrychido-Brometum*, *Gentiano-Koelerietum*) grasslands.

Floristic-ecological gradients in the vegetation between previous and recent relevés were examined using detrended correspondence analysis (DCA). The data were logarithmically transformed (i.e. coverage levels $(x+1)$ -logarithmized) in order to give less weighting to rarer species (DIERSCHKE & BECKER 2020). We applied DCA (function: `decorana`, gradient length of the first axis > 4) to investigate relationships between the mean indicator values and the dry and semi-dry grasslands. Explanatory variables (mean indicator values for light, temperature, moisture, reaction and nutrients) that significantly correlated ($p < 0.05$) with the axes of the ordination were post hoc fitted to the ordination diagram as vectors (function: `envfit`). The significance of these variables was checked using the Monte-Carlo test (9999 permutations). Additionally, a species ordination diagram was generated. DCA was carried out with the program R 3.6.0 (R CORE TEAM 2019), using the package `vegan` (OKSANEN et al. 2020).

To represent changes in the floristic composition of the dry and semi-dry grasslands, the similarity of the previous and recent vegetation relevés was calculated using the Sørensen index (SØRENSEN 1948), wherein more common species were more strongly weighted. The dimensionless index varied between 0 and 100, with values of over 75 indicating a high floristic similarity (MEIER & PARTZSCH 2018).

In addition, species number and vegetation cover (1) between the previous and recent relevés within the dry and semi-dry grasslands, and (2) between the previous and recent relevés within functional groups were studied. For the functional species group comparison, the species were previously divided into annuals, graminoids and forbs, and the cover of the five most common grasses was compared. Particular focus was placed on comparing the cover of *Bromus erectus* within the dry and semi-dry grasslands. The transformed data on the species number (log-transformed) and vegetation cover (arcsin-root-transformed) were checked for normal distribution using the Kolmogorov-Smirnov test. Using paired t-tests, it was possible to check for significant differences between the previous and recent relevés. The Pearson correlation coefficient was then used to calculate whether the increasing dominance of grass species had an effect on the species richness of the plant communities.

In order to investigate changes in the abundance of each species, species constancy (i.e. species occurrence in relation to the total number of vegetation relevés) between the previous and recent relevés was compared. The difference in constancy could then be used to show increases or decreases, with significant changes in constancy being determined using a Wilcoxon signed-rank test. Only species that appeared more than five times in the relevés were considered. To improve visualization, the different species were then listed according to their functional group. Finally, the percentage of changing species per functional group was calculated.

All statistical analyses were considered significant where $p < 0.05$. The statistical analyses (exception: DCA) were carried out using WinSTAT 2007.

3. Results

3.1 Floristic comparison of the dry and semi-dry grasslands

DCA did not reveal any changes between the previous and recent vegetation relevés (Fig. 2a). The indicator values for nutrients and moisture as well as vegetation cover were positively correlated with the first and second DCA-axes. The indicator values for light and temperature were also positively correlated, but they correlated negatively with those for nutrients and moisture. Thus, a clear differentiation between the nutrient-poorer, drier and more gappy dry grasslands and the more nutrient-rich and moist semi-dry grasslands was detected (Fig. 2a). The ordination species diagram supported the fact that there were differences in species composition between dry and semi-dry grasslands, as there tended to be a differentiation between dry grassland specialists and nutrient-depending species (Fig. 2b).

However, a comparison of the previous and recent relevés of the xerothermic grasslands based on the Sørensen index revealed significant differences ($F = 3.167$; $p = 0.003$) (Fig. 3). The dry grasslands were relatively stable (Sørensen index: 57), which indicates a higher floristic similarity between the previous and recent vegetation relevés compared to the semi-dry grasslands (Sørensen index: 49).

The comparison of the species numbers (previous relevés: in total 198 species; recent relevés: in total 210 species) of the dry and semi-dry grasslands did not show significant changes between the previous and recent relevés, but it revealed a significant increase in the vegetation cover (Fig. 4). The dry grasslands showed the highest increase of partly 50% in vegetation cover between the previous and recent relevés.

3.2 Floristic comparison of the functional groups of species

In the recent relevés, perennial forbs were the functional group with the highest number of species (mean: 20 species per relevé; total: 166 species), while the graminoids represented only a third of the total (mean: 7 species per relevé; total: 35 species), similar to the annuals (mean: 4 species per relevé; total: 38 species) (Fig. 5, Table 1). Annuals and graminoids were shown to have significantly increased in species number between the previous and recent relevés, while the number of forbs remained constant (Fig. 5). In the recent relevés, graminoids had a cover of approx. 75% and the forbs around 79%, while the small-grown and low-competitive annuals had a cover of approx. 7% (Fig. 5). The cover for graminoids and forbs therefore showed a significant increase between relevés while the annuals did not.

The comparison of constancy between the functional groups showed that 29% of the annuals and 49% of the graminoid species increased over time, while 23% of the forb species decreased (Table 1). In particular, annuals such as *Holosteum umbellatum*, *Draba verna* and *Hornungia petraea* increased significantly (Table 2). The dominant grass *Bromus erectus* increased significantly in presence, as did forbs such as *Euphorbia cyparissias*, *Falcaria vulgaris* and *Eryngium campestre*. The species *Descurainia sophia*, *Festuca csikhegyensis*, *Convolvulus arvensis* and *Polygala comosa* were all new to the recent relevés, while typical grasses and forbs of xerothermic grasslands including *Briza media*, *Euphrasia stricta*, *Asperula cynanchica*, *Silene otites* and *Allium lusitanicum* decreased significantly. *Linum catharticum* was the only annual species that showed a significant decrease. The species for which no significant increase or decrease could be detected are listed in the supplementary table (Supplement E6).

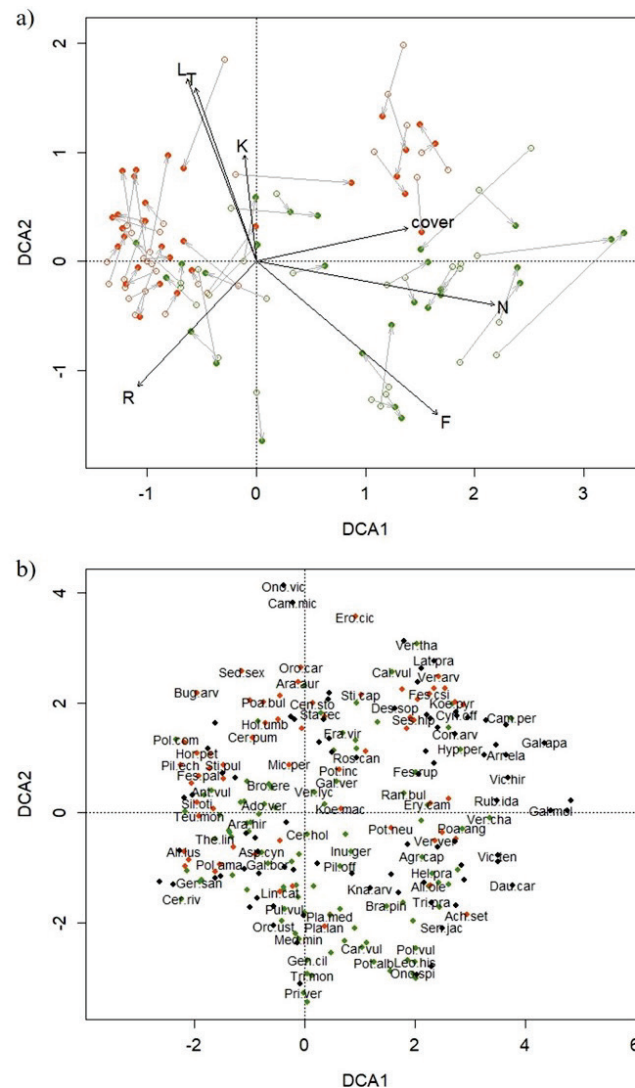


Fig. 2. Detrended Correspondence Analysis (DCA) of 57 quasi-permanent plots of the xerothermic grasslands in Central Germany. **a)** Diagram of the previous (1995–2002, empty symbols) and recent (2018/19, filled symbols) relevés for the dry grasslands (red) and semi-dry grasslands (green); relevé pairs are indicated by arrows. Ellenberg mean indicator values and vegetation cover, which are significantly correlated ($p < 0.05$) with the axes of the ordination, are shown as vector arrows. Eigenvalues: axis 1 = 0.588, axis 2 = 0.313; gradient length: axis 1 = 4.738, axis 2 = 3.627. **b)** Species diagram. Red: dry grassland species, green: semi-dry grassland species, black: other species).

Abb. 2. Detrended Korrespondenzanalyse (DCA) von 57 quasi-permanenten Dauerflächen der Xerothermrasen in Mitteldeutschland. **a)** Diagramm der früheren (1995–2002, leere Symbole) und aktuellen (2018/19, gefüllte Symbole) Vegetationsaufnahmen (insgesamt 114 Aufnahme­flächen) für die Trockenrasen (rot) und Halbtrockenrasen (grün); Aufnahmepaare sind durch Pfeile gekennzeichnet. Die mittleren Ellenberg'schen Zeigerwerte und die Vegetationsbedeckung, die signifikant mit den Achsen der Ordination korrelieren ($p < 0,05$), sind als Vektorpfeile dargestellt. Eigenvalues: Achse 1 = 0,588; Achse 2 = 0,313; Gradientenlängen: Achse 1 = 4,738; Achse 2 = 3,627. **b)** Diagramm der Arten. Rot: Trockenrasenarten, grüne: Halbtrockenrasenarten, schwarz: Sonstige).

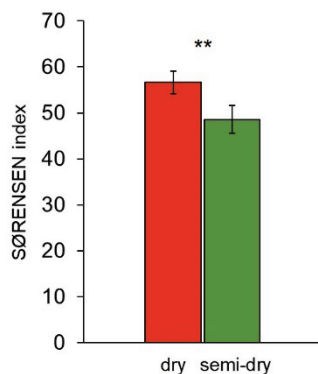


Fig. 3. Comparison of the Sørensen index (SØRENSEN 1948) between previous and recent vegetation relevés of the dry grasslands ($n = 60$) and semi-dry grasslands ($n = 54$) (mean + SE). Result of the t-test: ** $p < 0.01$.

Abb. 3. Vergleich des Sørensen-Index (SØRENSEN 1948) zwischen früheren und aktuellen Vegetationsaufnahmen der Trockenrasen ($n = 60$) und Halbtrockenrasen ($n = 54$) (Mittelwert + SE). Ergebnis des t-Tests: ** $p < 0,01$.

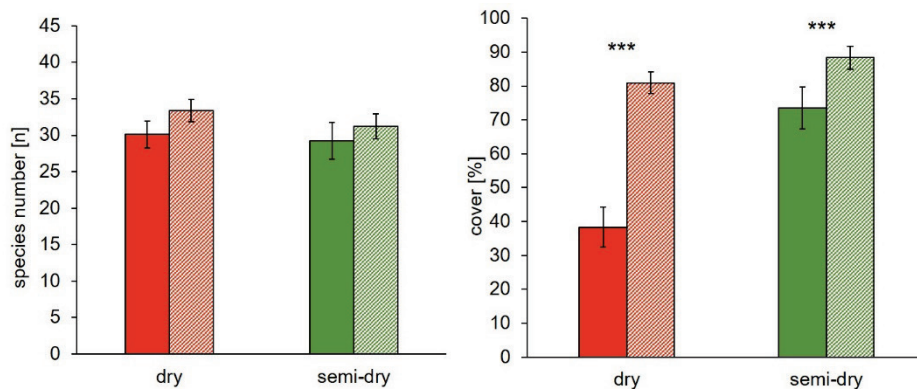


Fig. 4. Comparison of the species number (left) and vegetation cover (right) between the dry grasslands ($n = 60$) and semi-dry grasslands ($n = 54$). The filled bars represent the previous relevés; the hatched bars show the recent relevés (mean + SE). Significant differences between the previous and recent relevés show results from the paired t-tests: *** $p < 0.001$.

Abb. 4. Vergleich der Artenzahl und Vegetationsbedeckung zwischen den Trockenrasen ($n = 60$) und Halbtrockenrasen ($n = 54$). Die ausgefüllten Balken repräsentieren die früheren Aufnahmen, die schraffierten Balken die aktuellen Aufnahmen (Mittelwert + SE). Signifikante Unterschiede zwischen den früheren und aktuellen Aufnahmen sind als Ergebnisse der gepaarten t-Tests angegeben: *** $p < 0,001$.

The cover of the five most common dominant grasses varied between approx. 5% and 13% in the previous relevés and increased between approx. 8% and 33% in the recent relevés (Fig. 6). With the exception of *B. pinnatum* and *S. capillata*, the cover of grasses such as *B. erectus*, *F. rupicola* and *H. pratense* increased significantly by about 50% to 60%. *Bromus erectus* showed the highest cover and the greatest increase. While *B. erectus* did occur only with low percentages of presence in the dry and semi-dry grasslands, its cover increased significantly in the recent relevés (Fig. 7). *Bromus erectus* showed the strongest increase in semi-dry grasslands, especially in the *Onobrychido-Brometum* (from approx. 13% to approx. 52% cover).

The increasing dominance of grass species had an impact on the species richness of the plant communities in the case of *B. pinnatum* ($r = -0.437$, $p = 0.033$) and *S. capillata* ($r = -0.442$, $p = 0.031$) but not in the other grasses (*B. erectus*: $r = 0.073$, $p = 0.344$; *F. rupicola*: $r = -0.210$, $p = 0.250$; *H. pratense*: $r = -0.085$, $p = 0.357$).

Table 1. Total species number and percentage increase or decrease of the functional groups (annuals, graminoids, forbs) in their constancy between the previous (1995–2002) and recent relevés (2018/19).

Tabelle 1. Gesamtartenzahl und prozentualer Anteil zugenommener und abgenommener Arten der funktionellen Gruppen (Annuelle, Gräser, Kräuter) in der Stetigkeit zwischen den früheren (1995–2002) und aktuellen Aufnahmen (2018/19).

Functional group	Species number [<i>n</i>]	Increase [%]	Decrease [%]	No change [%]
annuals	38	29	8	63
graminoids	35	49	14	37
forbs	166	22	23	54

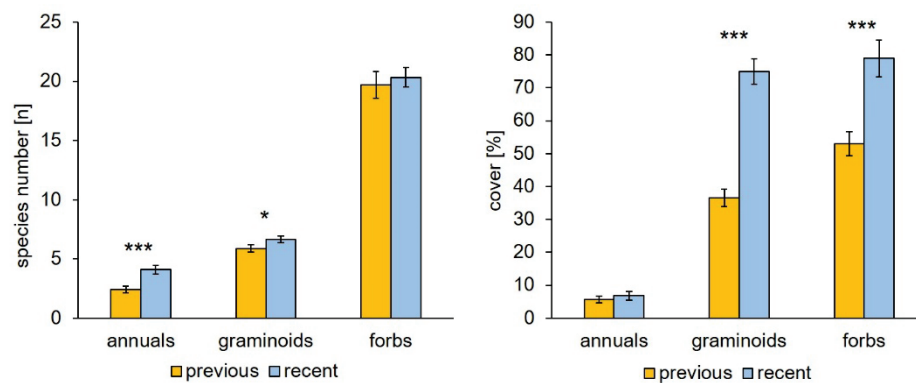


Fig. 5. Comparison of the species number (left) and vegetation cover (right) of the functional groups (annuals, graminoids, forbs) between previous ($n = 57$) and recent ($n = 57$) relevés (mean + SE). Significant differences between the previous and recent relevés show results from the paired t-tests: * $p < 0.05$, *** $p < 0.001$.

Abb. 5. Vergleich der Artenzahl (links) und Vegetationsbedeckung (rechts) der funktionellen Gruppen (Annuelle, Gräser, Kräuter) zwischen den früheren ($n = 57$) und aktuellen ($n = 57$) Aufnahmen (Mittelwert + SE). Signifikante Unterschiede zwischen den früheren und aktuellen Aufnahmen sind als Ergebnisse der gepaarten t-Tests angegeben: * $p < 0,05$; *** $p < 0,001$.

4. Discussion

Generally, a dramatic loss of species comparing the number of species between previous and recent vegetation relevés has not taken place over the last two decades for the xerothermic grasslands in Central Germany. The dry grasslands had a higher level of stability in terms of ecological site conditions than the semi-dry grasslands. Comparing functional groups, annuals and graminoids increased over time, while several endangered forbs showed a decline. The five most common dominant grasses increased in cover, which however did not affect species richness of forbs in the xerothermic grasslands in Central Germany.

4.1 Changes in dry and semi-dry grasslands

Based on the DCA, there were nearly no changes between the previous and recent floristic composition, which was also demonstrated in a resurvey study for the xerothermic grasslands of the 'Badraer Lehde-Großer Eller' in the area 'Kyffhäuser' (HAHN et al. 2013) and

Table 2. Species with increased or decreased constancy (presence/ absence) between previous (1995–2002) and recent (2018/19) vegetation relevés. The species are divided into functional groups (FG): annuals (A), graminoids (G), forbs (F). Within the functional groups, the species are sorted in descending order of difference. Only species with a significant change in constancy are shown. *P*-value: result of the Wilcoxon signed-rank test. Species without a significant change in constancy are shown in the Supplement E6. In addition, the status (0 – extinct or lost, 1 – threatened with extinction, 2 – critically endangered, 3 – endangered, D – insufficient data, V – warning list) according to the Red Lists (RL) of Saxony-Anhalt (SA; FRANK et al. 2020) and Thuringia (TH; KORSCH et al. 2011) as well as the legal protection status under the Federal Species Protection Regulation (S) are given.

Tabelle 2. Arten mit zunehmender und abnehmender Stetigkeit (Präsenz/ Absenz) zwischen den früheren (1995–2002) und aktuellen (2018/19) Vegetationsaufnahmen. Die Arten sind in funktionelle Artengruppen eingeteilt (FG): Annuelle (A), Gräser (G), Kräuter (F). Innerhalb der funktionellen Gruppen sind die Arten nach absteigender Differenz sortiert. Es sind nur Arten dargestellt, die eine signifikante Veränderung in der Stetigkeit aufweisen. *P*-Wert: Ergebnis des Wilcoxon-Signed-Rank-Tests. Arten ohne signifikante Veränderung in der Stetigkeit sind im Anhang E6. Außerdem sind der Gefährdungsstatus (0 – ausgestorben oder verschollen, 1 – vom Aussterben bedroht, 2 – stark gefährdet, 3 – gefährdet, D – Daten defizitär, V – Vorwarnliste) nach den Roten Listen (RL) von Sachsen-Anhalt (SA; FRANK et al. 2020) und Thüringen (TH; KORSCH et al. 2011) sowie der gesetzliche Schutz nach Bundesartenschutzverordnung (S) angegeben.

FG	RL		S	species	constancy		difference	p
	SA	TH			1995–2002	2018/19		
increase of species								
A				<i>Holosteum umbellatum</i>	5	23	18	< 0.001
A				<i>Draba verna</i>	10	23	13	0.003
A	3	2		<i>Hornungia petraea</i>	2	12	10	0.011
A				<i>Microthlaspi perfoliatum</i>	2	12	10	0.011
A	D	2		<i>Buglossoides arvensis</i>	3	11	8	0.025
A	3	3		<i>Veronica praecox</i>	6	13	7	0.018
A				<i>Descurainia sophia</i>	0	6	6	0.028
G				<i>Bromus erectus</i>	23	33	10	0.039
G				<i>Festuca csikhegyensis</i>	0	5	5	0.043
F				<i>Euphorbia cyparissias</i>	44	56	12	0.002
F				<i>Falcaria vulgaris</i>	3	13	10	0.005
F				<i>Eryngium campestre</i>	13	22	9	0.028
F				<i>Convolvulus arvensis</i>	0	9	9	0.008
F	2			<i>Erysimum marschallianum</i>	5	12	7	0.038
F				<i>Vicia hirsuta</i>	1	7	6	0.028
F	3			<i>Polygala comosa</i>	0	5	5	0.043
F				<i>Daucus carota</i>	2	7	5	0.043
decrease of species								
A	V			<i>Linum catharticum</i>	13	3	-10	0.028
G				<i>Agrostis gigantea</i>	6	0	-6	0.028
G	3			<i>Briza media</i>	18	6	-12	0.005
F				<i>Carlina vulgaris</i>	7	2	-5	0.043
F				<i>Knautia arvensis</i>	6	0	-6	0.028
F				<i>Teucrium montanum</i>	26	19	-7	0.038
F	3	3	§	<i>Allium lusitanicum</i>	12	5	-7	0.041
F	2	3		<i>Silene otites</i>	24	16	-8	0.041
F	3			<i>Asperula cynanchica</i>	25	15	-10	0.028
F				<i>Campanula rotundifolia</i>	14	4	-10	0.019
F	2			<i>Polygala amarella</i>	20	8	-12	0.005
F	V	3		<i>Euphrasia stricta</i>	17	1	-16	< 0.001

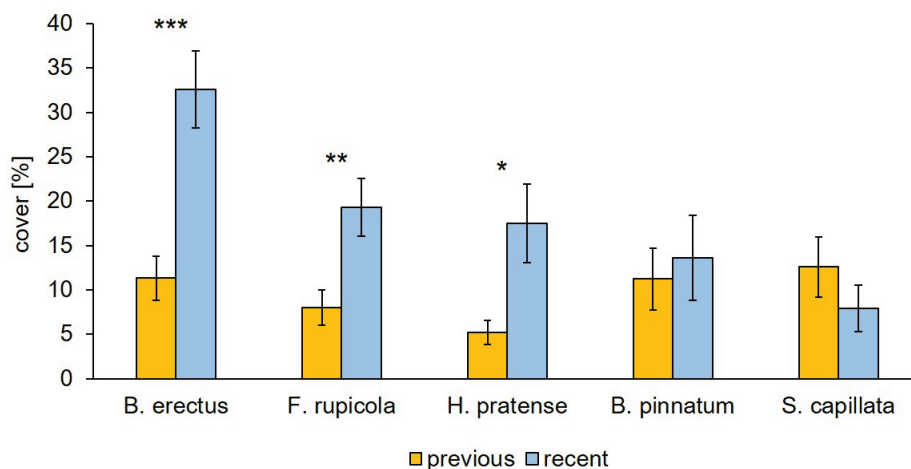


Fig. 6. Comparison of the cover of the dominant grasses between previous and recent relevés (mean + SE). Significant differences between the previous and recent relevés show results from the paired t-tests: * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$.

Abb. 6. Vergleich der Deckung der dominanten Grasarten zwischen den früheren und aktuellen Aufnahmen (Mittelwert + SE). Signifikante Unterschiede zwischen den früheren und aktuellen Aufnahmen sind als Ergebnisse der gepaarten t-Tests angegeben: * $p < 0,05$; ** $p < 0,01$; *** $p < 0,001$.

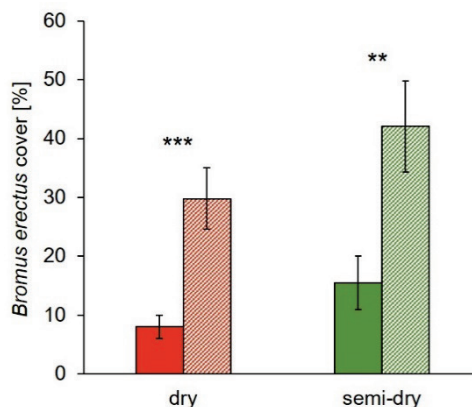


Fig. 7. Comparison of the *Bromus erectus* cover within the dry grasslands and semi-dry grasslands between previous (filled bars) and recent (hatched bars) relevés (mean + SE). Significant differences between the previous and recent relevés show results from the paired t-tests: ** $p < 0.01$, *** $p < 0.001$.

Abb. 7. Vergleich der Deckung von *Bromus erectus* innerhalb der Trockenrasen und Halbtrockenrasen zwischen den früheren (ausgefüllte Balken) und aktuellen (schraffierte Balken) Aufnahmen (Mittelwert + SE). Signifikante Unterschiede zwischen den früheren und aktuellen Aufnahmen sind als Ergebnisse der gepaarten t-Tests angegeben: ** $p < 0,01$; *** $p < 0,001$.

‘Gabower Hänge’ in Brandenburg (HÜLLBUSCH et al. 2016). Our DCA revealed positive correlations between the indicator values for nutrients and moisture, and negative correlations between the indicator values for light and temperature that have been proven by many studies of xerothermic grasslands (LÖBEL & DENGLER 2008, DÚBRAVKOVÁ et al. 2010,

BECKER et al. 2011, HAHN et al. 2013, DIEKMANN et al. 2019), which indicates that water availability is the strongest driver for differentiation of the vegetation units (BECKER et al. 2011).

In general, the average number of species of the dry and semi-dry grasslands did not change significantly between the previous and recent relevés. This supports the assumption that phytodiversity did not decline at the local scale over time (VELLEND et al. 2013, GONZALEZ et al. 2016, CARDINALE et al. 2018). The results of a meta-analysis of xerothermic grasslands in Western and Central Europe demonstrated that particularly the number of xerothermic grassland specialists declined (DIEKMANN et al. 2019).

We found a higher floristic similarity of dry grasslands (Sørensen index: 57) compared to semi-dry grasslands (Sørensen index: 49) between both time windows. Due to their natural conditions (shallow soil depth, steep inclination, extreme drought and light, low land use), dry grasslands have a high level of stability in terms of site conditions (KRUMBIEGEL et al. 1998, PARTZSCH 2000, MEIER & PARTZSCH 2018). In contrast, semi-dry grasslands have higher water availability, which allows for higher nutrient uptake. As such, these grasslands are subject to succession by e.g. shrub encroachment, which can lead to a series of plant communities by changing the floristic composition over time (ELLENBERG & LEUSCHNER 2010). Also, higher water and nutrient availability are generally responsible for the higher vegetation cover of semi-dry grasslands in comparison to the more extreme dry grasslands. Furthermore, vegetation cover in general and cover values of different life forms could depend on weather conditions (PETŘÍK et al. 2011).

4.2 Changes in functional groups

In the last 20 years, the species number of annuals and graminoids significantly increased while that of forbs remained constant. When comparing the constancy of the species of the functional groups, a partially different pattern was found. While around 29% of the annuals and about 49% of the graminoids increased, 23% of the forbs decreased.

The change in biodiversity takes place differently in the species of the various functional groups due to the respective biological-ecological plant traits, caused by land use changes and possibly nutrient inputs or weather extremes. Many species can vary in density of individuals, which can generally be traced back to vegetation-dynamic processes such as fluctuation or succession (DIERSCHKE 1994, ELLENBERG & LEUSCHNER 2010). Annuals in particular can fluctuate strongly, as they are influenced by seasonal weather events or the availability of resources. Such non-competitive species occur more frequently in years with good germination or establishment conditions in the preceding autumn or winter (sufficient moisture, short periods of frost) (HAHN et al. 2013). Furthermore, these species are associated with open soil sections caused by disturbance such as grazing (BECKER et al. 2011). Livestock create small gaps by trampling, which can serve as regeneration niches for seedlings for low-competitive and light-demanding species, and the diaspore bank can be activated (BULLOCK et al. 1994, RUPRECHT et al. 2010, SCHWABE et al. 2013, FREUND et al. 2015, KÖHLER et al. 2016, ELIAS et al. 2018). We detected a significant increase in seven annuals, including *Hornungia petraea*, a critically endangered species (KORSCH et al. 2011). In contrast, rare *Linum catharticum* was the only annual species that decreased significantly, which was also reported by HAHN et al. (2013).

The grass *B. erectus* increased significantly in presence, which is in line with the analysis of DIEKMANN et al. (2019). Forbs that increased or newly appeared are mainly ruderal species (e.g. *Convolvulus arvensis*, *Falcaria vulgaris*). Due to nutrient inputs, these species can

immigrate from adjacent arable fields and fallows into xerothermic grasslands (KRUMBIEGEL et al. 1998, BRANDES & PFÜTZENREUTER 2013), but their sporadic occurrence does not currently threaten the xerothermic grassland communities (MEIER & PARTZSCH 2018).

We found that within the last two decades, typical xerothermic species (e.g. *Asperula cynanchica*, *Euphrasia stricta*) significantly decreased. This agrees with the results of DIEKMANN et al. (2019), who observed that only grass specialists of dry grassland declined. These are usually small, light-demanding and evergreen species with smaller seeds and scleromorphic leaves (DIEKMANN et al. 2014). In a resurvey study on the xerothermic grasslands in southern England, the increase in *B. erectus* and the decrease in *A. cynanchica* and *L. catharticum* could also be recorded after 30 years (RIDDING et al. 2020).

A significant increase in cover was proven over time for the functional groups of graminoids, likely due to the increasing atmospheric nitrogen input and changes in land use. The aboveground phytomass of graminoids can be strongly promoted and their dominance over dicotyledons can be favoured under such conditions (DIEKMANN et al. 2014, BAI et al. 2015, DEMALACH et al. 2017).

As such, the importance of the five most common dominant grass species in the relevés was highlighted. *Bromus erectus*, *F. rupicola* and *H. pratense* had significantly increased their cover; but we found no changes for *B. pinnatum* (see DIEKMANN et al. 2014) and *S. capillata*. After 35 years, an increase in both presence and cover of dominant grass species (e.g. *B. erectus*, *B. pinnatum*, *F. rupicola*, *H. pratense*) could be detected for the xerothermic grasslands of ‘Garching Heide’ in Bavaria (BAUER & ALBRECHT 2020, BAUER et al. 2020). All five grasses have a highly competitive and stress-tolerant strategy type (CS) (GRIME 2001), which affords them greater adaptation (i.e. long life), even under changing abiotic conditions.

There was a special focus on the increasing dominance of *B. erectus* in the dry and semi-dry grasslands. Currently, the grass is found in almost all studied plant communities of the classes *Koeleria-Corynephoretea* and *Festuco-Brometea*. This is most likely a successive process, as it is also reported that this grass immigrated into the communities of the class *Sedo-Scleranthetea* Br.-Bl. 1955 em. Th. Müller 1961 (LÖHR-BÖGER & FÖRSTER 2013). It also occurs more frequently in disturbed and ruderalized communities, such as the *Convolvulo-Agropyron* Görs 1966 (BORNKAMM 2008). The morphology of large tussocks with well-developed root systems (MARTI 1994, JÄGER 2017) is advantageous for the species to emigrate to new sites quickly (ZSCHOKKE et al. 2000), and as a non-deciduous species, it can continuously produce phytomass for a large part of the year (BORNKAMM 2006).

Cover of *B. erectus* in dry and semi-dry grasslands has tripled in the past two decades. This was already found for the *Festuco-Stipetum* (MEIER & PARTZSCH 2018), where the species currently reached higher coverage values above 30%. *Bromus erectus* showed a higher cover in the semi-dry grasslands than in the dry grasslands due to higher water and nutrient availability (ELLENBERG & LEUSCHNER 2010) and compared to other xerothermic grassland species (BIERINGER & SAUBERER 2001, RIDDING et al. 2020). Particularly in *Onobrychido-Brometum*, the grass achieved mean coverage values of over 50%, but other typical character species (e.g. *Onobrychis viciifolia*, *Orchis militaris*) were missed (HOPP & DENGLER 2015).

Nowadays, it seems that *B. erectus* is increasingly spreading in the xerothermic grasslands in Central Germany, although it has not yet fully achieved the potential of its competitive ability, as we have not yet been able to demonstrate any significant influence of the cover of this grass species on the biodiversity of the plant communities (the same applies to

the dominant grass species *F. rupicola* and *H. pratense*). In contrast, in the grasslands of Tuscany in Italy, species richness decreased with increasing cover of *B. erectus* (MACCHERINI et al. 2000). The grass accumulates higher layers of litter, which significantly negatively affects the growth of surrounding smaller species (e.g. *Campanula glomerata*, *Pulsatilla vulgaris*) due to the reduced availability of light on the ground (WALKER & PINCHES 2011, RIDDING et al. 2020), which sooner or later could lead to a local loss of species (PARTZSCH 2000, WALKER et al. 2009). From our results, we did not find any typical xerothermic grassland species that were exclusively displaced by the increasing dominance of *B. erectus*.

However, the cover of *B. pinnatum* and *S. capillata* showed a significantly negative effect on the species richness of the plant communities. Cover of *B. pinnatum* may also be favored by shading from surrounding shrubs that could suppress the growth of light-demanding species (BAIER & TISCHEW 2004). Although *S. capillata* has its main occurrence in the *Festuco-Stipetum* (SCHUBERT et al. 1995), the species is also able to grow in ruderalized communities (MAHN 1965, BRANDES & PFÜTZENREUTER 2013).

4.3 Nature conservation assessment

All investigated dry and semi-dry grassland communities are classified as endangered or critically endangered according to the Red List of Thuringia (HEINRICH et al. 2011) and Saxony-Anhalt (SCHUBERT et al. 2020). Moreover, many of the xerothermic grassland species we have recorded are also listed in the Red List of Thuringia (KORSCH et al. 2011) and Saxony-Anhalt (FRANK et al. 2020) as well as for Germany (METZING et al. 2018) as endangered or critically endangered. Hence, these rare and species-rich plant communities are subject to permanent biomonitoring (SSYMANK 1998), which, due to their high nature conservation value, are designated as priority habitats according to the Fauna-Flora-Habitat Directive, and they are subject to FFH-LRT 6210 ‘Semi-natural calcareous dry grasslands and their stages of shrub encroachment (*Festuco-Brometalia*) (* special stands with remarkable orchids)’ as well as FFH-LRT 6240* ‘Sub-Pannonian steppe dry grasslands’ (FRANK 2007, LANDESAMT FÜR UMWELTSCHUTZ SACHSEN-ANHALT 2014).

Indeed, endangered and critically endangered species such as *Allium lusitanicum*, *Polygala amarella* and *Silene otites*, decreased in abundance. Therefore, appropriate management measures, such as more traditional land use practices, are necessary to counteract the loss of xerothermic grassland specialists. However, there are also doubts that traditional land use in many sites is not sufficient (low grazing and mowing intensity, unfavorable timing of management) to stop the loss of typical xerothermic grassland species (DIEKMANN et al. 2019). Mowing alone, instead of grazing, does not seem to be a suitable solution, as this promotes the growth of *B. erectus* (DIEKMANN et al. 2019). According to our own studies, we saw that in summer the leaves of larger tussocks of *B. erectus* were partially grazed, which consequently allowed the leaves to quickly resprout again in autumn. This supports the assumption that *B. erectus* probably has a higher competitive ability than expected. For this reason, intensive spring grazing is an opportunity to suppress competitive grasses, as the freshly sprouting shoots provide higher amounts of nutrients for livestock and are not spurned (DOSTÁLEK & FRANTÍK 2012, ELIAS & TISCHEW 2016, ELIAS et al. 2018). In addition to sheep, goats should also be used in order to prevent increasing shrub cover (ELIAS et al. 2013, 2018). In the case of more gappy and steeper dry grasslands with valuable species inventory, it is recommended to pay attention to a lower stocking rate and grazing intensity (MANN & NECKER 2019). A one-year or two-year mowing, primarily in semi-dry grasslands and depending on the location, as well as mechanical cutting of shrubs, should be included

as supplementary management measures (PUSCH verbal information). In order to preserve and protect the biodiversity of the species-rich xerothermic grasslands, traditional land use must be continued or reintroduced and can create a good balance between the competitive grasses and the often-endangered dicots.

Erweiterte deutsche Zusammenfassung

Einleitung – Trocken- und Halbtrockenrasen besitzen eine hohe Biodiversität und sind gekennzeichnet durch einen hohen Anteil an seltenen oder gefährdeten sowie stark gefährdeten Arten (DENGELER et al. 2014, FRANK et al. 2020). Jedoch zeichnet sich seit den letzten drei Jahrzehnten ein dramatischer Artenverlust ab (BRUELHEIDE et al. 2020, EICHENBERG et al. 2021), der vor allem durch die Prozesse des „Global Change“ und dem damit verbundenen Rückgang der traditionellen Landnutzung verursacht wird (DUPRÉ et al. 2010, DIEKMANN et al. 2014, HÜLBER et al. 2017, VALKÓ et al. 2018). Die ehemals artenreichen Xerothermrasen werden zunehmend von verschiedenen Grasarten dominiert, wie *Bromus erectus*, *Brachypodium pinnatum*, *Festuca* sp., *Helictotrichon* sp. oder *Stipa* sp. (BOBBINK et al. 1988, PARTZSCH 2000, 2001, PUSCH & BARTHEL 2003, BORNKAMM 2006, DOSTÁLEK & FRANTÍK 2008, SILANTYEVA et al. 2012, MEIER & PARTZSCH 2018). Besonders in Mitteldeutschland hat sich *B. erectus* zunehmend in den Xerothermrasen ausgebreitet (ZÜNDORF et al. 2006, BORNKAMM 2006, 2008, HELMECKE 2017). In dieser Studie sollte analysiert werden, ob es zu einer zeitlichen und räumlichen Veränderung in den mitteldeutschen Trocken- und Halbtrockenrasen innerhalb der letzten zwei Jahrzehnte gekommen ist und diese mit Veränderungen innerhalb der funktionellen Gruppen (Annuelle, Gräser, Kräuter) sowie mit einer eventuellen Zunahme der Grasarten einhergegangen ist. Die Ergebnisse sollten auch ermöglichen, eine naturschutzfachliche Bewertung hinsichtlich eines zukünftigen Pflegemanagements zur Erhaltung von artenreichen Xerothermrasen abzuleiten.

Material und Methoden – Für diese Studie wurde ein floristischer Vergleich zwischen früheren und aktuellen Vegetationsaufnahmen von Trocken- und Halbtrockenrasen herangezogen. Als Grundlage dienten 57 vorangegangene Vegetationsaufnahmen aus zwei Regionen des Mitteldeutschen Trockengebietes (Saaletal nordwestlich von Halle (Saale), Kyffhäuser), die nach ca. 20 Jahren noch annähernd genau lokalisiert werden konnten und erneut aufgenommen wurden. Um ein zukünftiges flächenbezogenes Biodiversitätsmonitoring zu gewährleisten, wurden die aktuellen Aufnahmeflächen mit Magneten dauerhaft markiert und GPS-Koordinaten erhoben. Die floristisch-ökologischen Gradienten in den Xerothermrasen zwischen den früheren und aktuellen Vegetationsaufnahmen wurden mit einer Detrended Korrespondenzanalyse (DCA) anhand der ungewichteten Zeigerwerte (ELLENBERG et al. 2001) und Vegetationsbedeckung nachgewiesen. Um Veränderungen in der floristischen Zusammensetzung der Trocken- und Halbtrockenrasen darzustellen, wurde die Ähnlichkeit der früheren und aktuellen Vegetationsaufnahmen mittels Sørensen-Index (SØRENSEN 1948) berechnet. Außerdem wurden die Artenzahl und Vegetationsbedeckung der Aufnahmen beider Zeitpunkte (1) innerhalb der Trocken- und Halbtrockenrasen und (2) innerhalb von funktionellen Artengruppen (Annuelle, Gräser, Kräuter) untersucht. Zur Überprüfung von zunehmenden und abnehmenden Arten wurde ein Stetigkeitsvergleich zwischen den funktionellen Artengruppen ausgeführt. Die Deckung der fünf dominierenden Gräser wurde zwischen den früheren und aktuellen Aufnahmen verglichen, wobei ein besonderer Fokus auf dem Vergleich der Deckung von *B. erectus* zwischen den Trocken- und Halbtrockenrasen lag. Es wurde geprüft, ob die zunehmende Dominanz der Grasarten einen Einfluss auf die Artenvielfalt der Pflanzengesellschaften hatte.

Ergebnisse – Anhand der DCA ergaben sich keine Unterschiede zwischen den früheren und aktuellen Vegetationsaufnahmen, jedoch eine klare Differenzierung zwischen Trocken- und Halbtrockenrasen. Der Sørensen-Index zeigte, dass die Trockenrasen eine signifikant höhere floristische Ähnlichkeit gegenüber den Halbtrockenrasen aufwiesen. Im Allgemeinen waren innerhalb der letzten 20 Jahre keine Veränderungen in der Gesamtartenzahl erkennbar, jedoch eine signifikante Zunahme in der Vegetationsbedeckung. Deshalb wurde ein Vergleich der funktionellen Artengruppen durchgeführt, der zeigte,

dass die Zahl der Kräuter konstant blieb, die der Annuellen und Gräser signifikant zunahm. Hinsichtlich der Deckung nahm die der Gräser und Kräuter signifikant zu, jedoch nicht die der Annuellen. Dabei hatten die kurzlebigen Annuellen (z. B. *Holosteum umbellatum*, *Draba verna*, *Hornungia petraea*) innerhalb der letzten zwei Jahrzehnte eine hohe Zunahme in der Stetigkeit. Das dominante Gras *Bromus erectus* sowie krautige Arten mit ruderalem Charakter (z. B. *Convolvulus arvensis*, *Falcaria vulgaris*) nahmen ebenfalls in ihrer Stetigkeit signifikant zu bzw. traten neu auf. Im Gegensatz dazu wurde eine signifikante Abnahme typischer Xerothermrasenarten wie *Linum catharticum*, *Briza media*, *Asperula cynanchica*, *Euphrasia stricta* und *Silene otites* verzeichnet. Die dominanten Gräser *B. erectus* (höchste Zunahme), *Festuca rupicola* und *Helictotrichon pratense* nahmen innerhalb der letzten 20 Jahre in der Deckung signifikant zu, während sich bei *Brachypodium pinnatum* und *Stipa capillata* keine Änderung zeigte. Die Deckung von *B. erectus* hat mittlerweile in den Trocken- und Halbtrockenrasen sehr stark zugenommen. Trotzdem hatte die Deckung der dominanten Grasarten (außer *B. pinnatum* und *S. capillata*) keinen signifikanten Einfluss auf die Artenvielfalt der Pflanzengesellschaften.

Diskussion – Die Trocken- und Halbtrockenrasen zeigten ein unterschiedliches ökologisches Verhalten, was auf die Wasserverfügbarkeit der Standorte als stärksten Treiber für die Differenzierung dieser Vegetationseinheiten hindeutet (BECKER et al. 2011, HAHN et al. 2013, DIEKMANN et al. 2019). Außerdem zeigten die untersuchten Trockenrasen eine höhere Stabilität hinsichtlich ihrer klimatischen und edaphischen Standortverhältnisse gegenüber den Halbtrockenrasen (KRUMBIEGEL et al. 1998, MEIER & PARTZSCH 2018). Die Gesamtartenzahl der mitteldeutschen Xerothermrasen hat sich innerhalb der letzten 20 Jahre nicht grundlegend geändert, sodass sich ein dramatischer Artenverlust (noch) nicht eingestellt hat (HÜLLBUSCH et al. 2016). Analysiert man die Arten nach ihren biologisch-ökologischen Merkmalen (funktionelle Artengruppen), zeigte sich, dass Annuelle und Gräser über die Zeit zunahmen, während typische Kräuter abnahmen (DIEKMANN et al. 2019), letztere gelten teilweise als gefährdet oder stark gefährdet (KORSCH et al. 2011, FRANK et al. 2020). Viele Arten können in ihrer Individuendichte schwanken, die sich allgemein auf vegetationsdynamische Prozesse, wie Fluktuation zurückführen lassen (DIERSCHKE 1994, ELLENBERG & LEUSCHNER 2010). Vor allem Annuelle können durch Beweidung gefördert werden, da die Trittbelastung der Weidetiere kleine Vegetationslücken schafft, die als Regenerationsnischen von Keimlingen für konkurrenzschwache und lichtliebende Arten sowie zur Aktivierung der Diasporenbank dienen können (SCHWABE et al. 2013, KÖHLER et al. 2016, ELIAS et al. 2018). Besonders die Deckung der dominierenden Gräser hatte zugenommen (vgl. BAUER et al. 2020); diese sind durch einen konkurrenzstarken und stresstoleranten Strategietypen (CS) (GRIME 2001) gekennzeichnet. Dies ermöglicht ihnen eine stärkere Anpassung (u.a. hohe Lebensdauer) auch unter verändernden abiotischen Bedingungen (z. B. erhöhte Stickstoffeinträge) (BOBBINK et al. 2010, BAI et al. 2015). Die Zunahme von *Bromus erectus* in fast allen untersuchten Pflanzengesellschaften ist offenbar ein sukzessiv verlaufender Prozess (BORNKAMM 2008). Trotzdem scheint das Potenzial der Konkurrenzkraft noch nicht vollständig erreicht zu sein, da die Deckung bisher kaum einen direkten Einfluss auf die Artenvielfalt der mitteldeutschen Xerothermrasen hatte. Durch die traditionelle Landnutzung kann eine gute Balance zwischen den konkurrenzkräftigen Gräsern und den häufig gefährdeten dikotylen Arten hergestellt werden, so dass ein entsprechendes Pflegemanagement auch in der Zukunft wichtig für die Erhaltung der artenreichen Xerothermrasen ist.

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Author contributions

TM conducted field work, performed statistical analyses and wrote the manuscript. MP supported the data analysis and helped writing the manuscript. IH helped with the final writing of the manuscript. IH and MP supervised the research work of TM.

Supplements

Additional supporting information may be found in the online version of this article.

Zusätzliche unterstützende Information ist in der Online-Version dieses Artikels zu finden.

Supplement E1. Regions and their study areas (see Fig. 1).

Anhang E1. Regionen und ihre Untersuchungsgebiete (vgl. Abb. 1).

Supplement E2. Detailed map of the quasi-permanent plots in the individual study areas. The relevé number refers to the recent vegetation relevés in Supplement E3. Coordinates are given in Supplement E5. **a)** near Mücheln (Wettin); **b)** Mittelberg (41) and Badraer Lehde (40) (Kyffhäuser); **c)** Ochsenburg (Kyffhäuser); **d)** Kosakenberg (24, 39), Grauer Berg (25) and Hämling (23) (Kyffhäuser).

Anhang E2. Detaillierte Karten der quasi-permanenten Aufnahme­flächen der einzelnen Untersuchungsgebiete. Die Aufnahme­nummer bezieht sich auf die aktuellen Vegetationsaufnahmen in Anhang E3. Koordinaten sind in Anhang E5 angegeben **a)** bei Mücheln (Wettin); **b)** Mittelberg (41) und Badraer Lehde (40) (Kyffhäuser); **c)** Ochsenburg (Kyffhäuser); **d)** Kosakenberg (24, 39), Grauer Berg (25) und Hämling (23) (Kyffhäuser).

Supplement E3. Comparison of the previous (1995–2002) and recent (2018/19; bold) vegetation relevés of the dry and semi-dry grasslands in Central Germany (original coverage of the species). The plant communities are classified according to SCHUBERT et al. (1995). In the recent relevés, the coverage of the species was estimated using the 9-part Braun-Blanquet scale (REICHELT & WILMANN 1973) (for adjusted coverage see Supplement E4).

Anhang E3. Vergleich der früheren (1995–2002) und aktuellen (2018/19; fett gedruckt) Vegetationsaufnahmen der Trockenrasen und Halbtrockenrasen in Mitteldeutschland (originale Deckungsgrade der Arten). Die Einteilung der Pflanzengesellschaften erfolgt nach SCHUBERT et al. (1995). Bei den aktuellen Aufnahmen wurden die Deckungsgrade der Arten nach der 9-teiligen Braun-Blanquet-Skala (REICHELT & WILMANN 1973) geschätzt (angepasste Deckungsgrade siehe Anhang E4).

Supplement E4. Comparison of the previous (1995–2002) and recent (2018/19; bold) vegetation relevés of the dry grasslands and semi-dry grasslands in Central Germany with adjusted coverages of the species. Explanations and abbreviations see Supplement E3.

Anhang E4. Vergleich der früheren (1995–2002) und aktuellen (2018/19; fett gedruckt) Vegetationsaufnahmen der Trockenrasen und Halbtrockenrasen in Mitteldeutschland mit angepassten Deckungsgraden der Arten. Erläuterungen und Abkürzungen siehe Supplement E3.

Supplement E5. Coordinates for the 57 quasi-permanent plots. The relevé number refers to the recent vegetation relevés in Supplement E3.

Anhang E5. Koordinaten für die 57 quasi-permanenten Aufnahme­flächen. Die Aufnahme­nummer bezieht sich auf die aktuellen Vegetationsaufnahmen in Anhang E3.

Supplement E6. Species with increased or decreased constancy (presence/ absence) between previous (1995–2002) and recent (2018/19) vegetation relevés. The species are divided into functional groups (FG): annuals (A), graminoids (G), forbs (F). Within the functional groups, the species are sorted in descending order of difference. Species without a significant change in constancy are shown. Only species that appeared more than five times in the relevés were considered.

Anhang E6. Arten mit zunehmender und abnehmender Stetigkeit (Präsenz/ Absenz) zwischen den früheren (1995–2002) und aktuellen (2018/19) Vegetationsaufnahmen. Die Arten sind in funktionelle Artengruppen eingeteilt (FG): Annuelle (A), Gräser (G), Kräuter (F). Innerhalb der funktionellen Gruppen sind die Arten nach absteigender Differenz sortiert. Es sind Arten dargestellt, die keine signifikante Veränderung in der Stetigkeit aufweisen. Dabei werden nur Arten berücksichtigt, die mehr als fünfmal in den Aufnahmen vorkamen.

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Supplement E1.Regions and their study areas (see Fig. 1).

Anhang E1. Regionen und ihre Untersuchungsgebiete (vgl. Abb. 1).

region	abbreviation	study area
Saaletal	MCH	Mücheln (Wettin)
Kyffhäuser	MBA	Mittelberg, Auleben
Kyffhäuser	BDL	Badraer Lehde, Badra
Kyffhäuser	OCH	Ochsenburg, Steinhaleben
Kyffhäuser	KKB	Kosakenberg, Bad Frankenhausen
Kyffhäuser	GBF	Grauer Berg, Bad Frankenhausen
Kyffhäuser	HLU	Hämling, Udersleben

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Supplement E2. Detailed map of the quasi-permanent plots in the individual study areas. The relevé number refers to the recent vegetation relevés in Supplement E3. Coordinates are given in Supplement E5. **a)** near Mücheln (Wettin); **b)** Mittelberg (41) and Badraer Lehde (40) (Kyffhäuser); **c)** Ochsenburg (Kyffhäuser); **d)** Kosakenberg (24, 39), Grauer Berg (25) and Hämling (23) (Kyffhäuser).

Anhang E2. Detaillierte Karten der quasi-permanenten Aufnahme­flächen der einzelnen Untersuchungsgebiete. Die Aufnahme­nummer bezieht sich auf die aktuellen Vegetationsaufnahmen in Anhang E3. Koordinaten sind in Anhang E5 angegeben **a)** bei Mücheln (Wettin); **b)** Mittelberg (41) und Badraer Lehde (40) (Kyffhäuser); **c)** Ochsenburg (Kyffhäuser); **d)** Kosakenberg (24, 39), Grauer Berg (25) und Hämling (23) (Kyffhäuser).



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Supplement E5. Coordinates for the 57 quasi-permanent plots. The relevé number refers to the recent vegetation relevés in Supplement E3.

Anhang E5. Koordinaten für die 57 quasi-permanenten Aufnahme­flächen. Die Aufnahme­nummer bezieht sich auf die aktuellen Vegetationsaufnahmen in Anhang E3.

Relevé number	Coordinates	Relevé number	Coordinates
1	N51°23'10.08"; E11°2'12.66"	30	N51°23'13.31"; E11°2'36.14"
2	N51°23'8.59"; E11°2'12.58"	31	N51°34'46.26"; E11°49'31.38"
3	N51°23'10.44"; E11°2'16.62"	32	N51°34'44.28"; E11°49'42.24"
4	N51°34'44.76"; E11°49'32.28"	33	N51°34'44.1"; E11°49'41.88"
5	N51°34'44.76"; E11°49'32.82"	34	N51°34'46.08"; E11°49'31.32"
6	N51°34'45.18"; E11°49'31.92"	35	N51°34'45.9"; E11°49'31.26"
7	N51°34'45.84"; E11°49'29.4"	36	N51°34'49.92"; E11°49'28.62"
8	N51°34'46.08"; E11°49'28.56"	37	N51°34'49.8"; E11°49'28.5"
9	N51°34'46.44"; E11°49'27.66"	38	N51°34'44.22"; E11°49'42.06"
10	N51°23'11.7"; E11°2'14.64"	39	N51°22'5.16"; E11°4'37.2"
11	N51°23'10.71"; E11°2'14.94"	40	N51°24'22.54"; E10°59'59.46"
12	N51°23'8.52"; E11°2'9.78"	41	N51°25'23.95"; E10°58'13.87"
13	N51°23'10.57"; E11°2'11.04"	42	N51°34'43.08"; E11°49'48.42"
14	N51°23'10.68"; E11°2'9.72"	43	N51°34'43.14"; E11°49'49.8"
15	N51°23'9.90"; E11°2'22.50"	44	N51°34'43.26"; E11°49'49.44"
16	N51°23'12.24"; E11°2'27.9"	45	N51°34'44.26"; E11°49'39.09"
17	N51°23'12.30"; E11°2'8.59"	46	N51°34'44.54"; E11°49'39.25"
18	N51°23'10.98"; E11°2'12.84"	47	N51°34'44.91"; E11°49'39.74"
19	N51°23'13.15"; E11°2'7.73"	48	N51°34'44.76"; E11°49'39.40"
20	N51°23'10.56"; E11°2'7.56"	49	N51°23'13.38"; E11°2'5.64"
21	N51°23'12.97"; E11°2'6.17"	50	N51°23'10.25"; E11°2'15.76"
22	N51°23'15.49"; E11°2'6.12"	51	N51°23'8.16"; E11°2'14.1"
23	N51°23'7.22"; E11°9'38.34"	52	N51°23'7.98"; E11°2'13.09"
24	N51°22'2.4"; E11°4'44.46"	53	N51°23'8.4"; E11°2'9"
25	N51°21'51.12"; E11°6'30.24"	54	N51°23'19.36"; E11°2'14.35"
26	N51°23'9.60"; E11°2'8.99"	55	N51°23'11.58"; E11°2'12.78"
27	N51°23'9.24"; E11°2'9.72"	56	N51°23'17.52"; E11°2'9.54"
28	N51°23'7.44"; E11°2'13.2"	57	N51°23'20.70"; E11°2'15.99"
29	N51°23'9.35"; E11°2'14.86"		

Supplement E6. Species with increased or decreased constancy (presence/ absence) between previous (1995 - 2002) and recent (2018/19) vegetation relevés. The species are divided into functional groups (FG): annuals (A), graminoids (G), forbs (F). Within the functional groups, the species are sorted in descending order of difference. Species without a significant change in constancy are shown. Only species that appeared more than five times in the relevés were considered. P-value: result of the Wilcoxon signed-rank test. In addition, the status (0 - extinct or lost, 1 - threatened with extinction, 2 - critically endangered, 3 - endangered, D - insufficient data, V - warning list) according to the Red Lists (RL) of Saxony-Anhalt (SA; FRANK et al. 2020) and Thuringia (TH; KORSCH et al. 2011) as well as the legal protection status under the Federal Species Protection Regulation (S) are given.

Anhang E6. Arten mit zunehmender und abnehmender Stetigkeit (Präsenz/ Absenz) zwischen den früheren (1995 - 2002) und aktuellen (2018/19) Vegetationsaufnahmen. Die Arten sind in funktionelle Artengruppen eingeteilt (FG): Annuelle (A), Gräser (G), Kräuter (F). Innerhalb der funktionellen Gruppen sind die Arten nach absteigender Differenz sortiert. Es sind Arten dargestellt, die keine signifikante Veränderung in der Stetigkeit aufweisen. Dabei werden nur Arten berücksichtigt, die mehr als fünfmal in den Aufnahmen vorkamen. P-Wert: Ergebnis des Wilcoxon-Signed-Rank-Tests. Außerdem sind der Gefährdungsstatus (0 - ausgestorben oder verschollen, 1 - vom Aussterben bedroht, 2 - stark gefährdet, 3 - gefährdet, D - Daten defizitär, V - Vorwarnliste) nach den Roten Listen (RL) von Sachsen-Anhalt (SA; FRANK et al. 2020) und Thüringen (TH; KORSCH et al. 2011) sowie der gesetzliche Schutz nach Bundesartenschutzverordnung (S) angegeben.

FG	RL		S	species	constancy		difference	p
	SA	TH			1995-2002	2018/19		
				increase of species				
A	D			<i>Cerastium pumilum</i>	12	18	6	0.126
A	V			<i>Arabis hirsuta</i>	19	24	5	0.139
A				<i>Arenaria serpyllifolia</i>	10	15	5	0.221
A				<i>Cerastium semidecandrum</i>	6	7	1	0.735
G				<i>Brachypodium pinnatum</i>	16	23	7	0.112
G	V	3	§	<i>Stipa capillata</i>	16	23	7	0.062
G	V			<i>Carex humilis</i>	33	40	7	0.112
G				<i>Dactylis glomerata</i>	10	16	6	0.215
G				<i>Festuca rupicola</i>	26	31	5	0.287
G	V	2		<i>Poa bulbosa</i>	3	8	5	0.139
G	2	2		<i>Koeleria macrantha</i>	31	36	5	0.314
G	3	3	§	<i>Stipa pennata</i>	5	9	4	0.262
G	V	3		<i>Festuca valesiaca</i>	11	15	4	0.262
G				<i>Arrhenatherum elatius</i>	2	6	4	0.208
G				<i>Poa angustifolia</i>	13	16	3	0.424
G				<i>Agrostis capillaris</i>	7	9	2	0.529
G	2	3	§	<i>Stipa pulcherrima</i>	14	15	1	0.790
G	V	2		<i>Bothrichloa ischaemum</i>	7	8	1	0.317
G	V			<i>Helictotrichon pratense</i>	19	20	1	0.820
F				<i>Sanguisorba minor</i>	19	28	9	0.101
F	V	3		<i>Filipendula vulgaris</i>	15	23	8	0.060
F				<i>Centaurea stoebe</i>	9	17	8	0.060
F				<i>Dianthus carthusianorum</i>	22	29	7	0.087
F				<i>Lotus corniculatus</i>	7	13	6	0.126
F				<i>Hypericum perforatum</i>	9	15	6	0.187
F		3		<i>Taraxacum sect. Erythrosperma</i>	5	9	4	0.308
F		3		<i>Artemisia campestris</i>	9	13	4	0.308
F	1	2	§	<i>Scorzonera purpurea</i>	2	6	4	0.068
F				<i>Fragaria viridis</i>	5	9	4	0.142
F				<i>Viola arvensis</i>	1	5	4	0.142
F	3	2		<i>Viola rupestris</i>	9	12	3	0.374
F	V			<i>Hippocrepis comosa</i>	23	26	3	0.374
F	2	2		<i>Hypochoeris maculata</i>	6	9	3	0.225
F				<i>Pimpinella saxifraga</i>	5	8	3	0.310
F				<i>Viola hirta</i>	2	5	3	0.310
F				<i>Erysimum crepidifolium</i>	4	7	3	0.225
F				<i>Carduus nutans</i>	7	10	3	0.463
F	3	3	§	<i>Inula hirta</i>	3	5	2	0.361
F				<i>Scabiosa ochroleuca</i>	9	11	2	0.575
F	3	3		<i>Galatella linosyris</i>	15	17	2	0.529
F				<i>Plantago lanceolata</i>	6	8	2	0.463
F				<i>Agrimonia eupatoria</i>	14	16	2	0.529
F				<i>Verbascum densiflorum</i>	3	5	2	0.361
F				<i>Medicago falcata</i>	5	6	1	0.735
F				<i>Salvia pratensis</i>	28	29	1	0.735
F				<i>Galium verum</i>	36	37	1	0.767
F	V			<i>Centaurea scabiosa</i>	26	27	1	0.686
F				<i>Potentilla heptaphylla</i>	4	5	1	0.686
				decrease of species				
A				<i>Erodium cicutarium</i>	5	2	-3	0.225
A	V			<i>Acinos arvensis</i>	22	18	-4	0.346
G		3		<i>Festuca pallens</i>	23	20	-3	0.374
G				<i>Sesleria caerulea</i>	20	17	-3	0.310
G	3	3		<i>Phleum phleoides</i>	13	9	-4	0.262
F				<i>Achillea pannonica</i>	24	23	-1	0.721
F	3	3	§	<i>Adonis vernalis</i>	11	10	-1	0.767
F	3	3		<i>Astragalus danicus</i>	14	13	-1	0.735
F		3		<i>Potentilla incana</i>	30	29	-1	0.861
F	2	3	§	<i>Pulsatilla vulgaris</i>	5	4	-1	0.686
F				<i>Teucrium chamaedrys</i>	10	9	-1	0.686
F	V	2		<i>Helianthemum nummularium</i>	28	27	-1	0.735
F				<i>Myosotis stricta</i>	6	5	-1	0.767
F	V			<i>Thymus pulegioides</i>	5	4	-1	0.593
F	3	3		<i>Scabiosa canescens</i>	32	31	-1	0.767
F				<i>Vincetoxicum hirundinaria</i>	23	22	-1	0.735
F				<i>Verbascum lychnitis</i>	12	11	-1	0.767
F				<i>Bupleurum falcatum</i>	7	6	-1	0.767
F	V	3		<i>Galium glaucum</i>	7	6	-1	0.767
F	D			<i>Anthyllis vulneraria</i>	15	13	-2	0.660
F	3	3	§	<i>Gypsophila fastigiata</i>	23	21	-2	0.463
F	V			<i>Galium boreale</i>	7	5	-2	0.463
F	2	2		<i>Fumana procumbens</i>	9	7	-2	0.463
F	3	3		<i>Thalictrum minus</i>	15	13	-2	0.463
F	D			<i>Thymus praecox</i>	30	27	-3	0.496
F	V			<i>Cirsium acaule</i>	19	16	-3	0.424
F	3			<i>Prunella grandiflora</i>	8	5	-3	0.310
F				<i>Pilosella officinarum</i>	22	19	-3	0.600
F				<i>Vicia angustifolia</i>	6	2	-4	0.142
F	1	3		<i>Hypericum elegans</i>	8	4	-4	0.208
F	3	2		<i>Thesium linophyllum</i>	22	18	-4	0.208
F				<i>Epipactis atrorubens</i>	9	5	-4	0.208
F				<i>Echium vulgare</i>	9	5	-4	0.262
F	3	3	§	<i>Alyssum montanum</i>	26	21	-5	0.182
F				<i>Taraxacum sect. Ruderalia</i>	10	4	-6	0.126

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Zoologisch-Botanische Datenbank/Zoological-Botanical Database

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Autor(en)/Author(s): Meier Tim, Hensen Isabell, Partzsch Monika

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