

Are recent climate change and airborne nitrogen deposition responsible for vegetation changes in a central German dry grassland between 1995 and 2019?

Sind der aktuelle Klimawandel und Stickstoffeinträge aus der Luft für die Vegetationsveränderungen in einem mitteldeutschen Trockenrasen zwischen 1995 und 2019 verantwortlich?

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This article is dedicated to the botanical conservationist Albert Keding, Naumburg (Saale), who protected the Schaffberg from being converted into a vineyard in the 1980s by assessing the site as unsuitable for viticulture in order to preserve the dry grasslands.

Abstract

Temperate dry grasslands are adapted to heat and drought and may therefore be resilient to global warming. We investigated vegetation changes in a dry grassland comprising three xeric associations (*Carici-Seslerietum*, *Festuco-Stipetum*, *Trinio-Caricetum*) and one meso-xeric association (*Gentiano-Koelerietum*) in the dry region of Central Germany (lower Unstrut valley) between 1995 and 2019 by one-time repetition of 46 permanent 1 m² plots distributed along a 244 m line. During this period, the mean summer temperature in the region has increased by 3.1 °C, and the frequency and intensity of heat waves and drought events have increased strongly. Because there was also persistent airborne N deposition, we hypothesized both environmental factors as major causes of potential vegetation changes. We found a significant change in vegetation composition indicated by a 50% species turnover based on the presence/absence of species. However, the mean indicator value for nutrients did not increase and the mean indicator value for moisture did not decrease. This result contradicts to our prediction, but can be explained by the fact that both indicator values were strongly intercorrelated, i.e. eutrophication and drought compensated for each other in their indicator values. In addition, a sharp decline in the proportion of meso-xerophilic plant species (as opposed to that of xerophilic species) clearly indicated increasing drought. Another indication of the now drier conditions was the strong increase in winter annuals, which was presumably due to the drought-induced lower competition from perennial plants. In addition, many graminoids and all of the few summer annuals declined sharply, probably due to drought, while sub-ruderal biennials increased, probably due to the combination of eutrophication and drought. Among graminoids, only the xerophilic *Stipa capillata* and the xero-tolerant *Bromus erectus* increased, probably due to the drier summers (*S. capillata*) and due to milder

winters (*B. erectus*). These increased Mediterranean climate conditions were also indicated by a decreased continentality indicator value. The positive correlation of the NMDS axis of vegetation change and the mean Ellenberg indicator value for nutrients indicated eutrophication (airborne N deposition) as a reason of vegetation change. However, N deposition without increasing drought would have resulted in denser and more mesophilic grasslands, i.e. the opposite pattern than we observed. Therefore, we assume that climate change (mainly summer drought, but also mild winters) was the main cause for the observed changes. This assessment is also supported by the fact that the grasslands became floristic more heterogeneous (because prevailing eutrophication would have led to homogenisation). With 29 loser species and 9 winner species, and 18.2% decline in species richness and 30% decline in the number of threatened species, we conclude that the conservation value of our grassland has decreased significantly. Overall, we conclude that dry grasslands in the dry area of Central Germany, are already affected by climate change (especially increased drought) in addition to N deposition, and that climate change is very likely the greatest threat to these grasslands.

Keywords: Atmospheric nitrogen deposition, *Bromus erectus*, drought, eutrophication, *Festuco-Brometea*, global warming, monitoring, permanent plot, plant functional types, xeric grassland

Erweiterte deutsche Zusammenfassung am Ende des Artikels

1. Introduction

Central European dry grasslands are particularly species-rich, but their occurrences have declined sharply in size and number. Therefore, they are considered to be particularly valuable and highly endangered (VEEN et al. 2009, WILSON et al. 2012, JANSSEN et al. 2016, DENGLER et al. 2020). Their significant reduction (POSCHLOD & WALLIS DE VRIES 2002, ENYEDI et al. 2008) and fragmentation (LINDBORG et al. 2014, DEÁK et al. 2016) was caused by intensification or abandonment of land use, starting with the use of artificial fertilizers since the beginning of the 20th century and especially after World War II. A current threat to dry grassland is airborne or atmospheric nitrogen deposition and an assumed future threat is climate change. Dry grasslands are adapted to heat and drought and may therefore be resilient to climate change which is generally considered to be the greatest future threat to biodiversity (MOSBRUGGER et al. 2012, PÖRTNER et al. 2021). Both positive and negative effects of climate change on dry grasslands are possible. A positive effect would be if climate change compensates for nitrogen inputs due to drought and thus also slows down the rate of succession of dry grasslands. Irreversible heat and drought damage would be negative. Because of their generally precarious situation and their low regeneration potential, PETERMANN et al. (2007) attested dry grasslands a high sensitivity to climate change. A feature of climate change is that extreme weather events such as heat waves and droughts have increased in frequency and intensity, currently particularly in Western and Central Europe (ROUSI et al. 2022). In Central Germany, the heat waves and drought events of 2003, 2015, 2018 and 2019 (as well as 2020 and 2022 following our study), were particularly extreme (BOERGENS et al. 2020, EDO 2021) and are considered the most severe in 2000 years (BÜNTGEN et al. 2021). Especially the 2018 drought (the year before our resurvey) was severe, while the 2019 drought was less so, but soils had a higher water deficit because the deep-water storage was greatly reduced in 2018 and not refilled in winter 2018–2019 (BOERGENS et al. 2020). Drought events are mainly caused by less precipitation, but also by higher temperature leading to increased evapotranspiration. In the town Artern, close to our study area and with comparable climate, annual precipitation in 2018 was only 273 mm, 58% of the average of 1961–1990 (WETTERKONTOR 2022). The mean spring temperature in Artern in 2018 was 10.8 °C and the mean summer temperature 20.8 °C, i.e. 2.7 °C and

3.8 °C above the average, respectively, and the sunshine duration in 2018 was 34% above the average. Altogether, in Artern, over the period 2015–2019 (which is expected to be most relevant here), annual temperature and sunshine duration increased by 2.0 °C (from 8.5 °C to 10.5 °C) and 20% (from 1457 h to 1749 h), respectively, and annual precipitation decreased by 9% (from 475 mm to 430 mm), compared with 1961–1990 (WETTERKONTOR 2022). However, mean values over several years must not adequately reflect weather extremes such as drought events (BENISTON et al. 2007). Another feature of climate change in Central Europe has been mild winters since decades (KREYLING & HENRY 2011). Mild winters and dry summers are expected to increase and increasingly influence ecosystems (SCHÄDLER et al. 2019).

Airborne nitrogen deposition (hereafter referred simply as N deposition), in contrast, have been effective for longer time. Eutrophication effects due to N deposition are known from many regions in Central Europe, especially from nutrient-poor habitats such as heathlands (BOBBINK et al. 1992), acid grasslands (DUPRÉ et al. 2010, MAZALLA et al. 2021) and meso-xeric calcareous grasslands (DIEKMANN et al. 2014). Studies of N deposition in true xeric grasslands are largely missing, but in xeric grasslands, eutrophication is certainly suppressed by water-limitation hindering nutrient uptake by the plants (ELLENBERG & LEUSCHNER 2010). Deposition of nitrogen has the potential to change nutrient-poor grasslands fundamentally (BOBBINK et al. 1998, PAYNE et al. 2017). It favours nitrophilic plants but also mesophilic plants, as nitrogen compensates for dryness (ELLENBERG & LEUSCHNER 2010: 929). In addition, N deposition may increase successional speed of abandoned dry grasslands (BOHNER et al. 2020). Current N deposition rates of 10–16 kg ha⁻¹ y⁻¹ in the study area (SCHAAP et al. 2018) are at the level of the critical loads for dry grasslands (8–15 kg ha⁻¹ y⁻¹) (BOBBINK & HETTELINGH 2011). N deposition is also often leading to floristic homogenisation of the community, mainly by replacement of many less-competitive loser species by few competitive winner species (MCKINNEY & LOCKWOOD 1999). Floristic heterogenisation, in contrast, is often driven by disturbance (MORI et al. 2018). Homogenisation was often found in forests (KEITH et al. 2009, NAAF & WULF 2010, REINECKE et al. 2014) and rarely in grasslands (DIEKMANN et al. 2019; for positive examples see ROSS et al. 2012 and HANSEN et al. 2021).

Dry grasslands in a broader sense can be divided into dry (xeric) types in a narrow sense and semi-dry (meso-xeric) types being considered near-natural/natural and semi-natural, respectively (ELLENBERG & LEUSCHNER 2010, DENGLER et al. 2020). Meso-xeric grasslands grow under moderately dry conditions and can only be maintained by cyclic disturbance, i.e. biomass must regularly be removed by moderate grazing or mowing for maintaining high species richness (PETRAITIS et al. 1989, KELEMEN et al. 2014). Xeric grasslands, in contrast, grow under drier conditions thus having lower successional potential and therefore need to be managed at most irregularly for maintenance (ELLENBERG & LEUSCHNER 2010). Within xeric and meso-xeric grasslands, various further dry grassland types can be distinguished representing ecological entities. This makes them particularly suitable for studying the effects of habitat differences on vegetation change. A key species group within dry grasslands are graminoids mainly from the *Poaceae* family but also *Cyperaceae* species. Because these matrix species often produce the main biomass, they affect the community in different ways, including above- and below-ground competition, nutrient cycling due to differences in litter decomposition rates, and influence vegetation structure and thus microclimatic conditions for e.g. insects (STEVENS & GOWING 2014, PONIATOWSKI et al. 2018). Many graminoids have clear ecological preferences regarding nutrient and water

supply and can therefore be used as ecological indicators (ELLENBERG 1986). Short-lived plants, on the other hand, need open soil patches with low competition for germination and recruitment thus being ruderal strategists and therefore indicators for disturbance e.g. by trampling of livestock or even drought events (FISCHER et al. 2020, MEIER et al. 2021). In addition, graminoids and short-lived plants have high reproduction rates and high dispersal potential and therefore can establish rapidly (GRIME 2001), allowing them to respond quickly to environmental changes.

In order to detect changes in dry grassland vegetation over time, several studies have compared previous and current vegetation on semi-permanent plots (e.g. PARTZSCH 2000, BENNIE et al. 2006, TOROK & SZITAR 2010, NEWTON et al. 2012, HAHN et al. 2013, DIEKMANN et al. 2014, 2019, BAUER & ALBRECHT 2020, RIDDING et al. 2020, CHARMILLOT et al. 2021, MEIER et al. 2021, MAZALLA et al. 2022, SCHÜLE et al. 2022), while resurvey studies based on permanent plots are still largely missing. Of these studies, to our knowledge, only MAZALLA et al. (2022) found evidence of climate change effects on meso-xeric calcareous grasslands so far. Furthermore, climate change impacts on acidic sand grassland (SCHÜLE et al. 2022) and alpine calcareous grasslands (KUDERNATSCH et al. 2016) have been identified.

We studied vegetation changes in dry grasslands in Central Germany (which are often referred to as xerothermic grasslands). After 24 years, we repeated 46 permanent 1 m² plots along a 244 m long transect line that passed through four associations. We selected a set of species traits and vegetation characteristics that have been widely used to measure vegetation change in dry grasslands but focused on variables likely to indicate nutrient input and climate change, such as drought, which we expect to be the main drivers of potential change. In detail, we focus on ecological indicator values, life forms especially of short-lived plants, CSR strategies, graminoids and species richness. We applied ordination analysis for detecting directional vegetation change and tested for taxonomic homogenisation. In particular, we expected an increased mean indicator value for temperature and nutrients and a decreased mean indicator value for moisture. We further expected a decrease of meso-xerophytic plants and an increase of short-lived plants and SR strategists because both species groups normally do profit from drought, especially in combination with nutrient input (GRIME 2001). We also expected a decrease in species richness. Regarding homogenisation, we were ambiguous: we either expected an increase due to possibly increased competition due to N deposition or a decrease (i.e. heterogenisation) due to disturbance by drought events. In order to draw sound conclusions, we were particularly interested in the possible mechanisms of the assumed changes. Our hypotheses are summarized in Table 1.

2. Study site and system

The study was conducted at the Schafberg in the lower Unstrut valley nearby the village Zscheiplitz (Saxony-Anhalt, Central Germany) (Fig. 1). The Schafberg is located at the southern edge of the tectonic limestone plate Querfurter Platte which steeply drops down to the Unstrut river around Freyburg. The Schafberg, on the other hand, has gentler slopes (about 20° inclination) especially in south-western (210°) exposure. At the top of the hill (206 m a.s.l.), the Lower Muschelkalk outcrops, while below frost debris layers form the substrate (for soil profiles see BECKER 1998a). At the foot of the hill (135 m a.s.l.), these gravel and loam layers can be 1 m thick.

The macroclimate at the Schafberg site is distinctly dry and warm in summer, but the microclimate is significantly drier due to the southwest-exposed slope and, according to data logger measurements from June to August 2019, about 3 °C warmer than the macroclimate (T. Meier, unpublished data; for temperature, evaporation and humidity patterns over the day at the Schafberg, see BECKER 1998a). Between 1991 and 2020, the mean annual precipitation in Laucha, about 3 km away, was 542 mm and the mean annual temperature in Querfurt, about 20 km away, was 9.3 °C (July mean 18.6 °C) (DWD 2022).

The weather of the first year of recording (1995) was average overall. Spring (March to May, the most important season for development of our xeric grassland) and summer (June to August) were 0.5 °C and 1.4 °C warmer and slightly wetter (106% precipitation) and slightly drier (92% precipitation), respectively, than the 1960–1990 means of the Artern climate station about 30 km west of the study area with comparable climate (WETTER-KONTOR 2022). The weather in the resurvey year 2019 was also $\pm$ average in spring (+0.3 °C, 100% precipitation), but warmer and drier than average in summer (+2.2 °C, 56% precipitation) compared to the more recent comparison period 1991–2020 (which was already 1.2 °C warmer and 1% wetter in the area than the period 1961–1990) (WETTER-KONTOR 2022).

During the first survey, the dry grasslands on the Schafberg were assigned to four associations within the class *Festuco-Brometea* Br.-Bl. & Tx. ex Klíka & Hadač 1944 (BECKER 1998a, b). The association names used at that time are still current with the exception of *Teucris-Seslerietum* Volk 1937, which was renamed *Carici humilis-Seslerietum* Zlatník 1928 in the EuroVegChecklist for priority reasons (cf. BERGMIEIER 2020). Only the higher syntaxonomic levels of our associations have partially changed (cf. BERGMIEIER 2020). The meso-xeric grassland on the north-east exposed back of the hill was assigned to the *Gentiano-Koelerietum pyramidatae* Knapp 1942 ex Bornk. 1960 as xeric-calcareous subassociation *teucrisetosum* Mösseler 1989 (hereafter abbreviated as *Koeleria* grassland). The xeric grassland on the south-western slope was divided into three associations: The dry grassland on the uppermost south-western slope on raw, flat soil was assigned to *Carici humilis-Seslerietum albicantis* Zlatník 1928 (*Sesleria* grassland). The dry grassland on the middle and lower south-western slope on more or less flat ground was assigned to the *Trinio-Caricetum humilis* Volk ex Br.-Bl. et Moor 1938 as meso-xeric subassociation *cirsietosum* Becker 1998 (*Carex humilis* grassland). The dry grassland on the lower central south-western slope on shallow clay soil was assigned to *Festuco valesiacae-Stipetum capillatae* (Libbert 1931) Mahn 1959 as calcareous subassociation *teucrisetosum* Becker 1998 (*Stipa* grassland). The order of associations along the transect from the back of the hilltop across the hilltop along the large SW slope to the base of the hill was *Gentiano-Koelerietum* → *Carici-Seslerietum* → *Trinio-Caricetum* → *Festuco-Stipetum* → *Trinio-Caricetum* (BECKER 1998a, b).

The Schafberg with its approximately 25 ha of dry grassland is a hotspot of rare and endangered plant species and thus has eminent nature conservation value. It is part of the Natura 2000 site “Schafberg und Nüssenberg bei Zscheiplitz” (EU FFH code: DE 4736-305, federal code: FFH0148, 211 ha) (JENTZSCH & REICHHOFF 2013). During the study period from 1995 to 2019, the Schafberg dry grassland was continuously grazed by sheep, with interruptions in individual years. However, due to the nutrient-poor soils and the xeric conditions, the Schafberg dry grassland is very less productive and therefore less susceptible to succession.



Fig. 1. Aerial view of the 244 m long transect (yellow line) on the Schafberg. The transect ranged from the north slope (upper right) across the crest of the hill (small white gap) to the foot of the large south-west slope (lower left). The upper photo **a)** dates from 2000 and the lower one **b)** from 2020. The light shimmering areas in the lower photo show the less productive (sparser) vegetation due to drought. The degree of shrub cover has hardly changed. The old-growth *Pinus nigra* forest (above centre left cut) on the plateau largely died during the 2018 drought. The complex of shrubland and limestone heaps on the right indicates a former quarry (Images from Google Earth, a) 01.06.2000, b) 11.09.2020).

Abb. 1. Luftbild des 244 m langen Transekte (gelbe Linie) am Schafberg. Der Transekt reicht vom Nordhang (oben rechts) über die Kuppe (kleine weiße Blänke) zum Fuß des großen Südwesthangs (unten links). Das obere Luftbild **a)** stammt aus dem Jahr 2000 und das untere **b)** aus dem Jahr 2020. Die hell schimmernden Flächen auf dem unteren Foto zeigen die dürrebedingt weniger produktive (schütterere) Vegetation. Der geringe Verbuschungsgrad ist dagegen fast unverändert. Der in der Bildmitte oben links angeschnittene ältere Schwarzkiefernforst ist während der Dürre 2018 weitgehend abgestorben. Der Komplex aus Gebüsch und Schutthalde rechts auf dem Plateau zeigt einen ehemaligen Steinbruch (Luftbilder aus Google Earth, Aufnahmedatum a) 01.06.2000, b) 11.09.2020).

According to the German Red List, the communities are classified as endangered (*Gentiano-Koelerietum* and *Carici-Seslerietum*) or critically endangered (*Festuco-Stipetum* and *Trinio-Caricetum*) (RENNWALD & MITARB. 2000). In Saxony-Anhalt, all communities are classified as endangered (SCHUBERT & MITARB. 2020). The *Gentiano-Koelerietum* corresponds to the EU priority habitat type 6210 (Near-natural dry grasslands and shrubs on calcareous substrates (*Festuco-Brometalia*), important orchid sites), the *Festuco-Stipetum* to the priority habitat type 6240 (Sub-Pannonian steppe dry grasslands) and the *Trinio-Caricetum* shows a mixture of the priority habitat types 6210 and 6240 (SSYMANK et al. 2021). The *Carici-Seslerietum* corresponds to the non-priority habitat type 6210 (Semi-natural dry grasslands and scrubland facies on calcareous substrates (*Festuco-Brometalia*)).

The lower Unstrut valley is a main area of dry grasslands in Central Germany with high supra-regional nature conservation value (BECKER 2000). Here, the combination of dry climate and calcareous substrate leads to a distinctive mixture of plants with continental and sub-Mediterranean distribution, which is the main characteristic of the dry grasslands of the lower Unstrut valley (BECKER 1998b). The dry grasslands of the lower Unstrut valley as a whole (an approx. 20 km long valley section) were studied by BECKER (1998b). A detailed study was carried out on the Schafberg, focusing on microclimatic and edaphic factors for community differentiation (BECKER 1998a). In addition, several studies on life strategies in individual communities have been carried out in this area (BÖTTNER et al. 1997, HENSEN 1997, MEIER & PARTZSCH 2018, MEIER et al. 2019). All this knowledge, gained mainly by us authors, was used here as background for the interpretation of the results and for conclusions. Figures 2–3 show the grassland areas in 1995.

3. Methods

3.1 Vegetation survey and resurvey

The first survey was carried out on 25–27 June and 3 July 1995. 46 plots of 1 m² were distributed along a 244 m long linearly line running from the north-exposed back of the hill (running metres 1–21) to the foot of the southwest-exposed front of the hill (running metres 22–243) (BECKER 1998a). Along this line the plots were distributed more or less regularly, with the aim to cover all important grassland types with a larger number of samples. The beginning and the end of this transect were permanently marked with a buried magnet, while the position of the plots was measured in running metres from the starting point with a tape measure. Plots were delineated with a 1 × 1 m wooden frame, and vascular plant species were recorded per plot with their cover according to the standard Braun-Blanquet scale, with cover class 2 divided into 2a (5–15% cover) and 2b (> 15–25% cover).

The resurvey was carried out on 5 and 21 June 2019 in the same way as the first survey, i.e. the buried magnets at the beginning and end were found again with a detector, and the plots were found again with a tape measure and based on their distances from the beginning. Both data sets were merged and species names were harmonised according to the Checklist of Vascular Plants of Germany (HAND et al. 2022). The micro species *Achillea pannonica* and *A. millefolium* s. str. were aggregated to *A. millefolium* agg.; no further aggregation was necessary. During the re-survey, all plots were permanently marked with a buried magnet in their centre (plot no. 1: N 51° 12' 58.62" E 11° 43' 17.10", no. 46: N 51° 12' 58.14" E 11° 43' 16.44"). We consider the plots to be permanent, but the newly surveyed plots can be moved slightly (up to about 1 m).



Fig. 2. First record of the *Carex humilis* grassland (*Trinio-Caricetum*) on the middle SW slope of the Schafberg. In late June 1995, a climatically average summer at the time, the vegetation was still without severe water deficit. The 244 m long red transect line along which the plots were distributed is visible. *Brachypodium pinnatum* in flower (Photo: T. Becker, 26.06.1995).

Abb. 2. Erstaufnahme des Erdseggen-Trockenrasens (*Trinio-Caricetum*) am mittleren Südwesthang des Schafbergs. Ende Juni 1995, einem damals klimatisch durchschnittlichen Sommer, zeigte die Vegetation noch keinen stärkeren Wassermangel. Sichtbar ist die rote Transektschnur entlang der die 46 Aufnahmeflächen lagen. *Brachypodium pinnatum* in Blüte (Foto: T. Becker, 26.06.1995).

3.2 Vegetation variables

The following variables were calculated from the vegetation data per plot in each year (cf. Supplement E1): 1) Mean unweighted ecological indicator values for light, temperature, continentality, moisture, soil reaction and nutrients according to ELLENBERG et al. (2001). 2) Proportion and number of xerophilic or meso-xerophilic plants (summarised as moisture types or moisture behaviour, respectively) as an additional measure for dryness. Xerophilic plants were defined as those that were diagnostic for xeric grassland types (assoc. *Festuco-Stipetum* and *Carici-Seslerietum*, and subassocs. *Trinio-Caricetum stipetosum* and *festucetosum pallentis*, and rock-ledge communities of the class *Sedo-Scleranthetea*) according to the survey by BECKER (1998b). Meso-xerophilic plants were defined as those that were diagnostic of meso-xeric grassland types (assoc. *Gentiano-Koelerietum* and subassoc. *Trinio-Caricetum cirsietosum*). The meso-xerophilic species showed a significantly higher mean indicator value for moisture than the xerophilic species (3.5 ± 0.14 vs. 2.4 ± 0.15 , $p < 0.001$). 3) Proportions of the general Raunkiaer life forms chamaephytes, hemicryptophytes and therophytes (annuals) according to ELLENBERG et al. (2001) and numbers of special life forms of short-lived plants, i.e. summer and winter annuals as well as biennials (monocarpic perennials) according to standard books and own observations. 4) Proportions of the CSR strategy types CS, CSR and SR according to KLOTZ et al. (2002) (other strategy types and life forms proved negligible and were therefore not taken into account). 5) Occurrence of graminoids and short-lived plants as product of presence $\times$ ordinal-transformed cover ($r = 1, + = 2, 1 = 3$, etc.). 6) Richness of vascular plant species (α -diversity). 7) Number of threatened vascular plant species (including critically endangered, endangered and near threatened (Vorwarnliste) species according to the German Red List; METZING et al. 2018). 8) Temporal species turnover

(Bray-Curtis dissimilarity, β -diversity) was calculated pairwise for old and new plots based on species presence/absence and species cover. 9) Total β -diversity of associations was calculated for plot collectives and compared between years based on species presence/absence and species cover. Total β -diversity was used as a measure of homogenisation (decreasing β -diversity over time) or heterogenisation (increasing β -diversity). β -diversity (species turnover/dissimilarity) was bounded between 0 and 1, where 0 means that the two samples have the same composition (that they have all species in common) and 1 means that the two sites have no species in common.

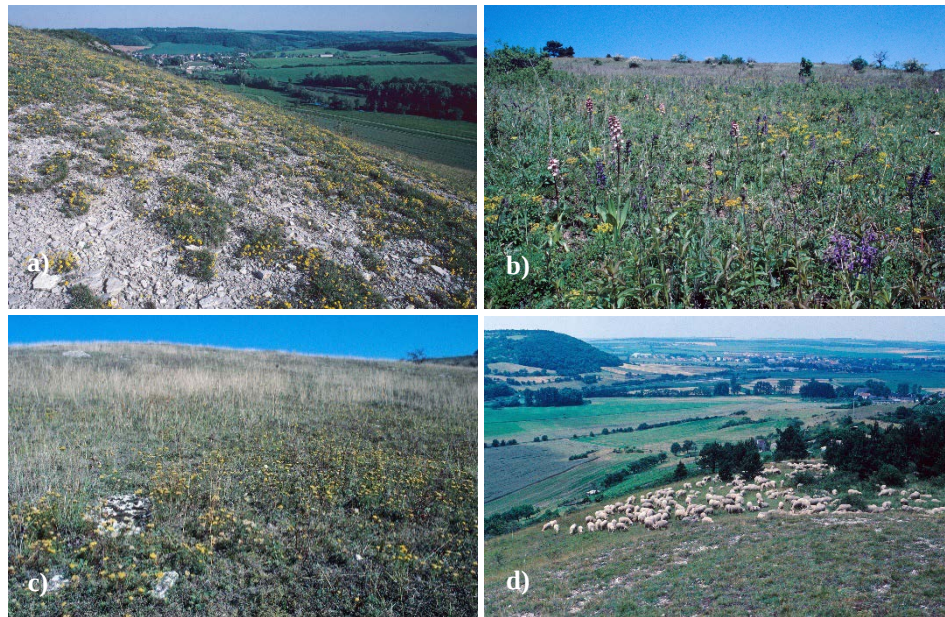


Fig. 3. **a)** *Sesleria* grassland (*Carici-Seslerietum*) in the transect area on the Schafberg hilltop during the flower of *Helianthemum canum* in May 1995. Of the four associations, the *Carici-Seslerietum* had changed the least. **b)** Fresh green *Carex humilis* grassland (*Trinio-Caricetum*) in the transect area of the middle SW slope of the Schafberg. In mid-June 1995, *Euphorbia cyparissias*, *Orchis purpurea* and *Salvia pratensis* were in flower. In front: *Inula hirta* vegetatively. **c)** *Carex humilis* grassland (*Trinio-Caricetum*) at the middle SW slope of the Schafberg in the transect area in 1995. Back then, the vegetation was still green in September. *Galatella linosyris* in flower. The dried grass flower shoots belong to *Brachypodium pinnatum*. **d)** Grazing sheep in the *Sesleria* grassland (*Carici-Seslerietum*) on the Schafberg hilltop in July 1995. Even in midsummer, the vegetation was green during that time. On the right the village of Weischütz and in the background the small town of Laucha (Photos: T. Becker).

Abb. 3. **a)** Blaugras-Trockenrasen (*Carici-Seslerietum*) im Bereich des Transekts an der Schafberg-Kuppe im Mai 1995 zur Blüte von *Helianthemum canum*. Von den vier Assoziationen hatte sich das *Carici-Seslerietum* am wenigsten verändert. **b)** Frisch grüner Erdseggen-Trockenrasen (*Trinio-Caricetum*) im Bereich des Transekts am mittleren Südwesthang des Schafbergs. Mitte Juni 1995 blühten hier *Euphorbia cyparissias*, *Orchis purpurea* und *Salvia pratensis*. Im Vordergrund: *Inula hirta* vegetativ. **c)** Erdseggen-Trockenrasen (*Trinio-Caricetum*) im Bereich des Transekts am mittleren Südwesthang des Schafbergs im September 1995. Die Vegetation war damals noch im September grün. *Galatella linosyris* in Blüte. Die vertrockneten Grasblütentriebe gehören zu *Brachypodium pinnatum*. **d)** Schafbeweidung im Blaugras-Trockenrasen (*Carici-Seslerietum*) auf der Schafberg-Kuppe im Juli 1995. Auch im Hochsommer war die Vegetation damals noch grün. Rechts angeschnitten das Dorf Weischütz und hinten die Kleinstadt Laucha (Fotos: T. Becker).

3.3 Statistical analyses

Prior to statistical analyses, Braun-Blanquet coverage values were converted to the mean percentage of the corresponding class as follows: $r = 0.1\%$, $+ = 0.5\%$, $1 = 2.5\%$, $2a = 10\%$, $2b = 20\%$, $3 = 37.5\%$, $4 = 62.5\%$, $5 = 87.5\%$. For indicator species analysis (ISA) and non-metric multi-dimensional scaling (NMDS), the cover values were then $\log(x + 1)$ transformed to avoid the processes being dominated by a few very abundant species. For the cover turnover analysis (Bray-Curtis), the cover values were left untransformed (to test for maximum cover effects). ISA (DUFRÈNE & LEGENDRE 1997) was used to identify species characteristic of the associations in either 1995 (loser species) or 2019 (winner species). The ecological indicator values obtained were tested for significance by Monte Carlo permutation tests with 9999 runs. NMDS (MCCUNE & GRACE 2002) with Bray-Curtis as distance metric was used to extract floristic dimensions (gradients). A Monte Carlo permutation test revealed highly significant ($p < 0.01$) low stress. The final stress for the two-dimensional NMDS solution was 11.8. The relationships between NMDS axis 2 and the variables of environmental conditions, including the climate variables of the two years (see introduction), and the proportions of xerophilic and meso-xerophilic plants were analysed using Pearson correlation. The same was done for the analysis of the relationship between the Ellenberg indicator values for moisture and nutrients. Pair-wise temporal turnover between old and new plots (BRAY & CURTIS 1957) was used to assess changes in species composition, and overall turnover of plots within associations and years was used to assess homogenisation or heterogenisation of vegetation. Both tests were applied with solely presence/absence data and untransformed cover data each. To obtain sound diagnostic species within the previous data and current data a Fisher's exact test was defined with JUICE 7.0 (TICHÝ 2002). Mean values of Ellenberg indicator values, life forms, CSR strategies, and moisture types were compared between previous and recent plots with pairwise t test or one-way ANOVA with subsequent Tukey post-hoc tests. The normal distribution of the residuals of all variables was visually checked and confirmed using histograms. ISA, NMDS and β -diversity calculation were performed with PC-ORD 6.0 (MCCUNE & MEFFORD 2011), and Pearson correlation, t test and ANOVA with SPSS 22 (IBM CORP. RELEASED 2013).

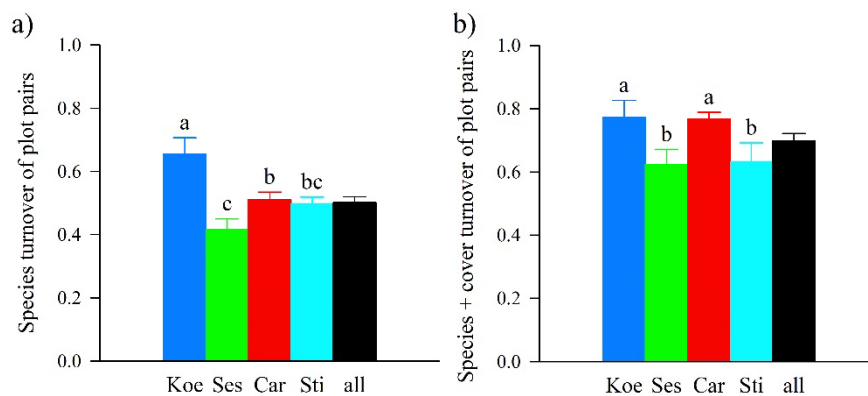


Fig. 4. Species turnover (Bray-Curtis β -diversity) of plot pairs 1995/2019 based on **a)** presence/absence and **b)** cover. A value of 1 indicates 100% species turnover. Four dry grassland associations separately and together: *Car* – *Carex humilis* grassland, *Koe* – *Koeleria* grassland, *Ses* – *Sesleria* grassland, *Sti* – *Stipa* grassland. Mean values and 1 SE. Mean values with different letters differ significantly at $p < 0.05$.

Abb. 4. Artumsatz (Bray-Curtis β -Diversität) der Aufnahmepaare 1995/2019 nach **a)** Präsenz/Absenz und **b)** Deckung der Arten. Ein Wert von 1 bedeutet einen Artumsatz von 100 %. Vier Trockenrasen-assoziationen einzeln und zusammen (die Bedeutung der Kürzel geht aus der englischen Abbildungs-unterschrift her). Mittelwerte und einfache Standardfehler. Mittelwerte mit unterschiedlichen Buchstaben unterscheiden sich signifikant bei $p < 0,05$.

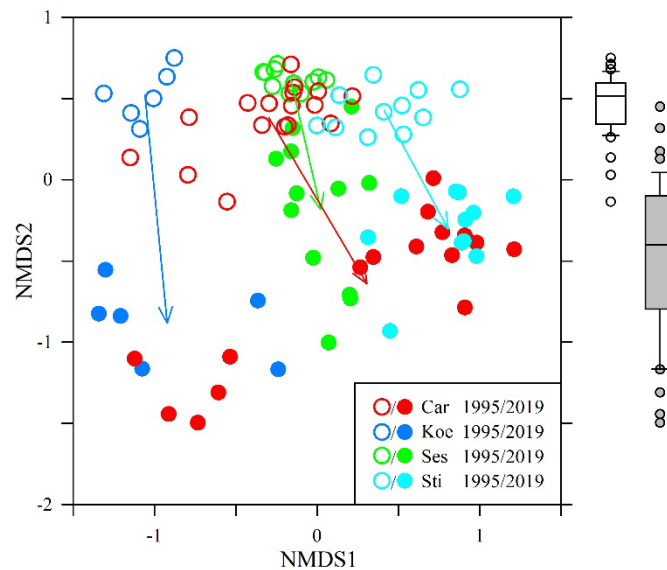


Fig. 5. NMDS of four dry grassland associations in 1995 (empty circles) and 2019 (filled circles). Car – *Carex humilis* grassland, Koe – *Koeleria* grassland, Ses – *Sesleria* grassland, Sti – *Stipa* grassland. Minimal stress of axis 2 is 11.8. Vectors between 1995/2019 centroids indicate direction and change extent of each association along the first two NMDS axes. Box whisker plots show score variance 1995 (empty boxes and circles) and 2019 (grey boxes and circles) along axis 2.

Abb. 5. NMDS von vier Trockenrasenassoziationen in den Jahren 1995 (leere Kreise) und 2019 (gefüllte Kreise). Die Bedeutung der Kürzel der Assoziationen geht aus der englischen Abbildungsunterschrift hervor. Der minimale Stresswert von Achse 2 beträgt 11,8. Vektoren zwischen den Zentroiden 1995/2019 zeigen die Richtung und den Umfang der Veränderung der einzelnen Assoziationen entlang der ersten beiden NMDS-Achsen an. Die Kastengraphiken zeigen die Varianz der Werte aus 1995 (leere Kästen und Kreise) und 2019 (graue Kästen und Kreise) entlang Achse 2.

4. Results

Most of the associations were still present after 24 years. Only the *Gentiano-Koelerietum* on the back of the hill had become a ruderalised *Onobrychido-Brometum* (Scherrer 1925) Th. Müller 1966, and the *Trinio-Caricetum* could no longer be assigned to the slightly meso-xeric subassociation *cirsietosum*, but developed into the more xeric subassociation *typicum*. However, the former diagnostic species groups of the associations have thinned out considerably and to a lesser extent new diagnostic species groups have formed (Supplement E2).

The species turnover (Bray-Curtis dissimilarity) of the 1995/2019 plot pairs based on presence/absence in all associations was 0.502, which means that on average 50.2% of the species were replaced at plot level during the study period. Replacement was highest in the *Koeleria* grassland (65.4%) and lowest in the *Sesleria* grassland (41.6%) (Fig. 4a). This order corresponded to the ratio of winner/loser species, reflecting the ranking of associations by decreasing change: *Gentiano-Koelerietum* → *Trinio-Caricetum* → *Festuco-Stipetum* → *Carici-Seslerietum* (Table 2). Species turnover of plot pairs based on species cover was higher than based on presence/absence of species (69.8% replaced species in all associations), indicating that cover has also changed (Fig. 4b).

Table 1. Expected and observed changes in 12 individual characteristics due to climate change (winter mildness and summer drought) and N deposition. Up-pointing arrows “↑” indicate positive and down-pointing arrows “↓” negative relationships. Symbols and arrow numbers indicate the relative strength of the expected relationships: Hyphens “–” no change was expected, arrows in brackets “(↑/↓)” weak change, simple arrows “↑/↓” strong change, double arrows “↑↑/↓↓” even stronger change. Question marks “?” indicate ambiguous expectations (positive or negative relationship). CC = climate change [differentiated according to winter mildness (w) and summer drought (s) or both together (ws)] and ND = N deposition indicate the assumed causes for the observed vegetation change. CC→ND indicates that both factors presumably play a role but that N deposition only can let to the pattern under given climate change. $p = ***$, $p < 0.001$, $** p < 0.01$, $* p < 0.05$ ($n = 46$).

Tabelle 1. Erwartete und festgestellte Veränderung von 12 Einzelmerkmalen bei Klimawandel (Wintermilde und Sommerdürre) und Stickstoffeinträgen. Pfeile nach oben “↑” oder unten “↓” zeigen positive oder negative (erwartete oder beobachtete) Effekte des Klimawandels bzw. der N-Depositionen auf die untersuchten Einzelmerkmale an. Die Symbole bzw. Anzahl der Pfeile zeigen die relative erwartete Stärke der erwarteten Zusammenhänge: – = keine Veränderung, (↑/↓) = schwache Veränderung, ↑/↓ = starke Veränderung, ↑↑/↓↓ = noch stärkere Veränderung. Unentschiedene Erwartungen (positiver oder negativer Zusammenhang) sind mit Fragezeichen „?“ gekennzeichnet. CC = Klimawandel [unterschieden nach Wintermilde (w) und Sommerdürre (s) oder Beides zusammen (ws)] und ND = N-Depositionen geben die mutmaßlichen Gründe der beobachteten Vegetationsänderung an. CC→ND bedeutet, dass beide Faktoren eine Rolle spielen aber der zweite nur unter dem ersten das beobachtete Ergebnis erklären kann. Die Stärke der festgestellten Veränderungen ist nicht angegeben. $*** p < 0,001$, $** p < 0,01$, $* p < 0,05$ ($n = 46$).

	Expected change due to:			Detected change	Detected change explained by:
	Solely climate change	Solely N deposition	Both climate change and N deposition		
Indicator values and moisture types					
Light (L)	↑	↓	—	↑ *	CC _s
Temperature (T)	↑	—	↑	↑ **	CC _w
Continentality (K)	↓	—	↓	↓ ***	CC _w
Moisture (F)	↓	(↑)	?	—	CC _s ¹⁾
Nutrients (N)	(↓)	↑	?	—	ND ¹⁾
% xerophilic species	↑	(↓)	(↑)	↑ ***	CC _s
% meso-xerophilic species	↓	—	(↓)	↓ ***	CC _s
Life forms and strategy types					
Winter annuals	↑	↓	↑↑	↑ ***	CC _{ws} →ND
Summer annuals	↓	—	↓	↓ *	CC _s
Biennials	(↑)	(↑)	↑↑	↑ *	CC _{ws} →ND
SR strategy	↑	—	↑↑	↑ **	CC _{ws} →ND
Increased graminoids					
<i>Bromus erectus</i>	↑	↑	↑↑	↑ ***	CC _w →ND
<i>Stipa capillata</i>	↑	—	↑	↑ ***	CC _s →ND
Species richness	↓	↓	↓	↓ ***	CC _s
Homogenisation	↓	↑	?	↓ ***	CC _s

¹⁾ Considering that F and N were intercorrelated, the non-significant change in the two indicator values can be interpreted as an indication of actually drier and more nutrient-rich conditions.

The NMDS revealed directional floristic changes in all associations along axis 2 (Fig. 5). This axis was positively correlated with time (and all time-related binary climate variables mentioned in the introduction for climate change evidence) and the mean Ellenberg indicator value for nutrients, and negatively correlated with the mean indicator values for continentality and soil reaction (Table 3). In a direct comparison between 1995 and 2019, the mean Ellenberg indicator values of all plots together changed as follows: The indicator values for light and temperature increased and the indicator value for continentality decreased, while the indicator values for moisture, soil reaction and nutrients did not change significantly (Fig. 6a). However, the indicator values for moisture and nutrients were strongly positively intercorrelated (Fig. 6b). The proportion of meso-xerophilic species decreased, while the proportion of xerophilic species increased (Fig. 6c). These changes were due to a decrease in meso-xerophilic species rather than an increase in xerophilic species (Fig. 6d).

In terms of life forms, chamaephytes and hemicryptophytes decreased, while therophytes (annual plants) increased (Fig. 7a). These changes were more pronounced in the *Sesleria* and *Carex humilis* grasslands than in the *Koeleria* and *Stipa* grasslands. Among short-lived plants, winter annuals increased and summer annuals decreased (Fig. 7b). Biennial plants were generally rare but increased. Within plant strategy types, competitive stress (CS) and competitive ruderal strategists (CSR) decreased, but stress ruderals (SR) increased (Fig. 8). This pattern was very clear in the *Sesleria* and *Carex humilis* grasslands, while there was only a weak trend in the *Koeleria* and *Stipa* grasslands.

A total of 38 species (36% of all species) increased or decreased significantly in at least one association (Table 2). Within these species, nine winners (species that increased) faced 29 losers (species that decreased). Winners included five xerophilic winter annuals (e.g. *Cerastium pumilum* s. str., *Draba verna*, *Hornungia petraea*), one xerophilic biennial (*Centaurea stoebe*), two graminoids (*Bromus erectus*, *Stipa capillata*, the first with indifferent moisture behaviour within dry grasslands, the other xerophilic) and one shrub (*Prunus spinosa*) with indifferent moisture behaviour.

Among loser species were nine graminoids of which six were meso-xerophilic, one xerophilic, and two moisture indifferent (Fig. 9a, and see below), eight meso-xerophilic hemicryptophytes (e.g. *Asperula cynanchica*, *Pimpinella saxifraga*) and three xerophilic hemicryptophytes (e.g. *Potentilla incana*, *Seseli hippomarathrum*) and three moisture indifferent hemicryptophytes (e.g. *Euphorbia cyparissias*, *Hippocrepis comosa*), three xerophilic chamaephytes (e.g. *Helianthemum canum*, *Teucrium montanum*) and one moisture indifferent chamaephyte (*Thymus praecox*), and two summer annuals (the meso-xerophilic *Linum catharticum* and the moisture indifferent *Cuscuta epithymum*). The increase and decrease of short-lived plants such as annual and biennial winter and summer flowers is summarised in Figure 9b.

Sixty-three species (64%) did not change significantly in all associations together or in any single association, many of which were too rare to detect any possible change (Supplement E3). Most graminoids decreased in frequency/abundance (Fig. 9b). *Carex humilis*, *Sesleria caerulea* and *Brachypodium pinnatum* (in that order) decreased the most. *Helictochloa pratensis* disappeared from the plots, while *Bromus erectus* and *Stipa capillata* increased. Especially in the *Koeleria* and *Carex humilis* plots, *B. erectus* increased significantly (Table 2).

Table 2. Vascular plant species in four dry grassland associations separately and together after winner and loser. *Car* – *Carex humilis* grassland (*Trinio-Caricetum*), *Koe* – *Koeleria* grassland (*Gentiano-Koelerietum*), *Ses* – *Sesleria* grassland (*Carici-Seslerietum*), *Sti* – *Stipa* grassland (*Festuco-Stipetum*). Frequencies (constancies) in percent and mean percent cover values in uppercase. Bold type indicates at least marginal significant changes: ↑ – increase, ↓ – decrease. *** $p < 0.001$, ** $p < 0.01$, * $p < 0.05$, + $p < 0.1$. Normal type indicates no significant changes at $p < 0.1$. p values derive from ISA. Line symbols indicate that a species did not occur in the association neither in 1995 nor in 2019. For constant species or species that are too rare for assessing change see Supplement E3.

Table 2. Gefäßpflanzenarten in vier Trockenrasenassoziationen einzeln und zusammen nach Gewinnern und Verlierern. *Car* – *Carex humilis*-Trockenrasen (*Trinio-Caricetum*), *Koe* – *Koeleria*-Halbtrockenrasen (*Gentiano-Koelerietum*), *Ses* – *Sesleria*-Trockenrasen (*Carici-Seslerietum*), *Sti* – *Stipa*-Trockenrasen (*Festuco-Stipetum*). Prozentsteigkeiten und mittlere Prozentdeckungen (hochgestellt). Fettgedruckte Werte zeigen zumindest marginal-signifikante Veränderungen an: ↑ – Zunahme, ↓ – Abnahme. *** $p < 0.001$, ** $p < 0.01$, * $p < 0.05$, + $p < 0.1$. Werte ohne Signifikanzsymbol unterscheiden sich nicht-signifikant bei $p < 0.1$. Die p -Werte stammen aus ISA. Striche (–) kennzeichnen nicht vorkommende Arten. Konstante Arten sowie Arten, welche zu selten sind, um ihre Veränderung zu bemessen, s. Beilage E3.

	Koe ($n = 6$)			Ses ($n = 12$)			Car ($n = 17$)			Sti ($n = 11$)			all ($n = 46$)		
	1995	2019	p	1995	2019	p	1995	2019	p	1995	2019	p	1995	2019	p
Winner species															
Graminoids															
<i>Bromus erectus</i>	17 ³	100 ⁴⁶	↑ **	0 [–]	92 ¹⁴	↑ ***	12 ³	47 ³²	↑ *	0 [–]	55 ¹⁶	↑ *	7 ³	67 ²⁵	↑ ***
<i>Stipa capillata</i>	–	–	–	–	–	–	35 ²	65 ³⁶	↑ *	91 ¹⁹	100 ⁴²	↑ *	35 ¹³	48 ³⁹	↑ *
Herbs															
<i>Centaurea stoebe</i>	–	–	–	–	–	–	0 [–]	35 ^{0.8}	↑ *	0 [–]	27 ^{0.5}	–	0 [–]	20 ^{0.7}	↑ ***
<i>Cerastium pumilum</i> s. str.	–	–	–	0 [–]	42 ¹	↑ *	6 ^{0.5}	47 ¹	↑ *	36 ³	64 ^{0.8}	–	11 ²	43 ¹	↑ ***
<i>Cerastium semidecandrum</i>	0 [–]	67 ^{0.4}	↑ +	0 [–]	50 ^{0.8}	↑ *	0 [–]	59 ¹	↑ ***	0 [–]	64 ²	↑ **	0 [–]	59 ¹	↑ ***
<i>Draba verna</i>	0 [–]	67 ¹	↑ +	0 [–]	83 ¹	↑ ***	0 [–]	65 ^{0.9}	↑ ***	55 ³	64 ^{0.5}	–	13 ³	70 ^{0.9}	↑ ***
<i>Hornungia petraea</i>	–	–	–	0 [–]	92 ²	↑ ***	0 [–]	82 ¹	↑ ***	55 ³	91 ²	–	13 ³	76 ¹	↑ ***
<i>Microthlaspi perfoliatum</i>	–	–	–	0 [–]	33 ^{0.4}	↑ +	0 [–]	24 ²	–	–	–	–	0 [–]	17 ¹	↑ **
Woody species	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
<i>Prunus spinosa</i> juv.	–	–	–	–	–	–	6 ³	41 ⁴	↑ *	–	–	–	2 ³	15 ⁴	↑ *
Loser species															
Graminoids															
<i>Brachypodium pinnatum</i>	0 [–]	50 ^{0.4}	–	50 ¹⁰	67 ¹³	–	94 ¹⁷	47 ¹¹	↑ ***	36 ¹⁸	18 ¹	–	57 ¹⁵	46 ⁹	↓ *
<i>Carex caryophyllaea</i>	83 ³	0 [–]	↓ *	–	–	–	–	–	–	–	–	–	11 ³	0 [–]	↓ +
<i>Carex humilis</i>	100 ¹⁵	100 ¹¹	–	100 ¹⁷	100 ¹⁴	↑ +	76 ³⁸	71 ⁸	↑ +	100 ¹⁷	100 ¹²	–	91 ²³	89 ¹¹	↑ ***
<i>Festuca csikhegyensis</i>	17 ^{0.5}	0 [–]	–	100 ⁶	92 ⁵	–	71 ²	35 ^{0.7}	↑ ***	100 ²	18 ^{0.1}	–	78 ⁴	41 ³	↑ ***
<i>Festuca rupicola</i>	100 ¹¹	17 ^{0.5}	↓ **	–	–	–	65 ⁵	18 ⁸	↑ ***	9 ³	0 [–]	–	39 ⁷	9 ⁶	↑ ***
<i>Helictotricha pratensis</i>	83 ³	0 [–]	↓ *	67 ³	0 [–]	↓ ***	88 ³	0 [–]	↑ ***	36 ²	0 [–]	–	70 ²	0 [–]	↑ ***
<i>Koeleria macrantha</i>	33 ³	0 [–]	–	25 ²	0 [–]	–	59 ²	18 ^{0.2}	↑ ***	73 ³	9 ^{0.1}	–	50 ²	9 ^{0.2}	↑ ***
<i>Koeleria pyramidata</i>	67 ³	0 [–]	↓ +	33 ²	0 [–]	↓ +	6 ^{0.5}	0 [–]	–	–	–	–	20 ²	0 [–]	↓ **
<i>Sesleria caerulea</i>	100 ³⁹	0 [–]	↓ **	100 ²²	58 ²⁰	↓ **	–	–	–	–	–	–	39 ²⁷	15 ²⁰	↓ **

	Koe (n = 6)			Ses (n = 12)			Car (n = 17)			Sti (n = 11)			all (n = 46)		
	1995	2019	p	1995	2019	p	1995	2019	p	1995	2019	p	1995	2019	p
Herbs															
<i>Adonis vernalis</i>	—	—		25 ²	8 ^{0.5}		47 ²	35 ^{0.6}		36 ³	18 ^{0.3}		33 ²	20 ^{0.5}	↓ *
<i>Anthyllis vulneraria</i>	100 ¹³	67 ³	↓ *	8 ³	0 ⁻		—	—		—	—		15 ¹²	9 ³	↓ ***
<i>Asperula cynanchica</i>	100 ⁴	0 ⁻	↓ **	67 ³	0 ⁻	↓ **	53 ³	0 ⁻	↓ **	55 ²	0 ⁻	↓ *	63 ³	0 ⁻	↓ ***
<i>Cuscuta epithymum</i>	—	—		25 ³	0 ⁻		71 ²	29 ^{0.5}	↓ **	36 ²	0 ⁻	↓ +	41 ²	11 ^{0.5}	↓ ***
<i>Euphorbia cyparissias</i>	50 ³	17 ³		58 ⁴	92 ^{0.8}		100 ⁴	82 ²	↓ **	36 ³	64 ^{0.7}		67 ⁴	72 ¹	↓ +
<i>Helianthemum canum</i>	100 ²³	33 ¹⁰	↓ **	100 ¹⁶	75 ⁹	↓ **	88 ¹³	71 ³	↓ **	100 ¹¹	100 ⁴	↓ +	96 ¹⁵	74 ⁵	↓ ***
<i>Hippocrepis comosa</i>	33 ³	0 ⁻		58 ²	17 ^{0.5}	↓ *	59 ⁴	24 ⁴	↓ *	0 ⁻	9 ^{0.1}		41 ³	15 ²	↓ **
<i>Linum catharticum</i>	100 ³	0 ⁻	↓ **	8 ³	0 ⁻		12 ³	0 ⁻		—	—		20 ³	0 ⁻	↓ **
<i>Lotus corniculatus</i>	50 ³	33 ^{0.5}		17 ³	0 ⁻		12 ³	0 ⁻		—	—		15 ³	4 ^{0.5}	↓ *
<i>Pimpinella saxifraga</i>	83 ⁶	0 ⁻	↓ *	8 ^{0.5}	0 ⁻		59 ²	0 ⁻	↓ ****	—	—		35 ³	0 ⁻	↓ ***
<i>Potentilla heptaphylla</i>	67 ³	0 ⁻	↓ +	8 ^{0.5}	8 ^{0.5}		35 ²	0 ⁻	↓ *	9 ³	0 ⁻		26 ²	2 ^{0.5}	↓ ***
<i>Potentilla incana</i>	—	—		83 ³	58 ¹	↓ *	59 ³	29 ^{0.9}	↓ *	55 ⁴	36 ^{0.9}		57 ³	35 ¹	↓ **
<i>Potentilla verna</i>	100 ³	50 ²	↓ +	25 ³	0 ⁻		24 ²	0 ⁻		—	—		28 ²	7 ²	↓ **
<i>Salvia pratensis</i>	—	—		0 ⁻	33 ^{0.4}	↑ +	94 ⁶	71 ¹	↓ ****	36 ³	73 ¹		43 ⁶	52 ¹	↓ +
<i>Sanguisorba minor</i>	83 ³	67 ¹¹		75 ³	67 ²		53 ²	29 ^{0.9}	↓ *	27 ²	0 ⁻		57 ²	37 ⁴	↓ +
<i>Seseli hippomarathrum</i>	17 ³	17 ^{0.1}		100 ²	92 ³		71 ⁵	41 ²	↓ **	73 ³	73 ⁴		72 ³	59 ³	↓ +
<i>Taraxacum</i> sect. <i>Erythrosperma</i>	33 ³	0 ⁻		8 ³	0 ⁻		24 ²	0 ⁻		45 ³	0 ⁻	↓ *	26 ²	0 ⁻	↓ ***
<i>Teucrium montanum</i>	67 ³	17 ¹⁰		100 ⁴	75 ¹²		71 ⁶	41 ¹	↓ **	73 ¹⁷	36 ⁶	↓ +	78 ⁷	46 ⁷	↓ ***
<i>Teucrium chamaedrys</i>	100 ⁸	17 ^{0.5}	↓ **	100 ¹⁷	75 ¹⁵	↓ +	88 ⁹	94 ⁸		64 ⁸	100 ⁶	↑ +	87 ¹¹	80 ⁹	↓ ***
<i>Thymus praecox</i>	33 ¹¹	67 ¹		92 ⁸	75 ⁴		100 ²⁸	24 ¹	↓ ****	91 ²²	18 ^{0.5}	↓ ****	87 ²⁰	41 ²	↓ ***
Winner/loser ratio	3/13 = 0.23			7/9 = 0.78			8/19 = 0.42			4/9 = 0.44			9/26 = 0.35		

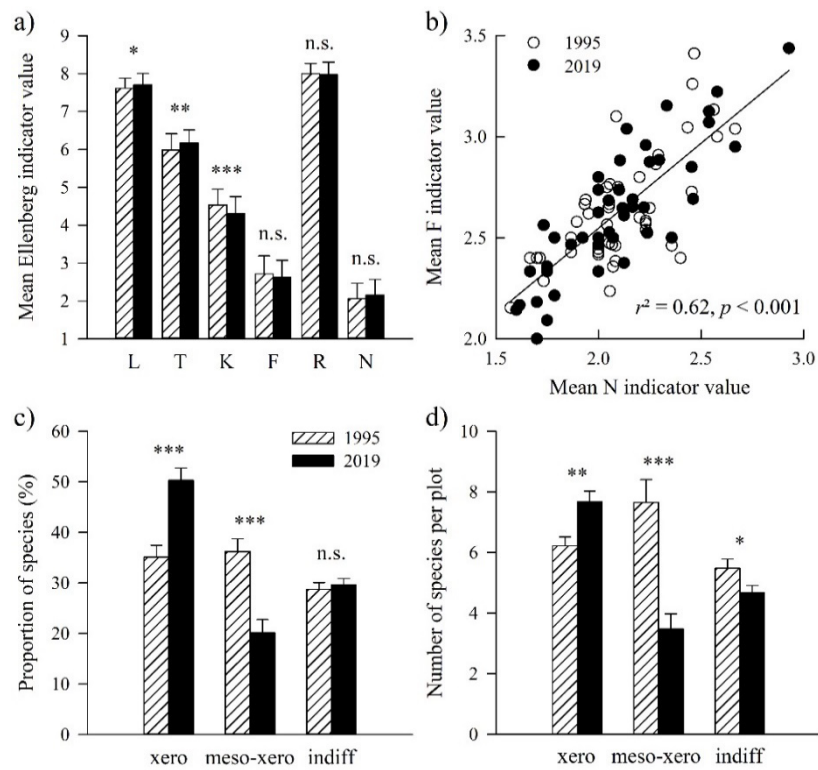


Fig. 6. **a)** Mean Ellenberg indicator values for L – light, T – temperature, K – continentality, F – moisture, R – soil reaction and N – nutrients, **b)** relationship between the mean N and F indicator value, **c)** proportions and **d)** numbers of xerophilic (*xero*), meso-xerophilic (*meso-xero*) and moisture indifferent (*indiff*) species in the dry grasslands. Mean values and 10 SE (in a) and 1 SE (in c, d). *** $p < 0.001$, ** $p < 0.01$, * $p < 0.05$, n.s. not significant.

Abb. 6. **a)** Mittlere Ellenberg-Zeigerwerte für L – Licht, T – Temperatur, K – Kontinentalität, F – Feuchte, R – Bodenreaktion und N – Nährstoff, **b)** Zusammenhang zwischen dem mittleren N- und F-Zeigerwert, **c)** Anteil und **d)** Anzahl der xerophilen (*xero*), meso-xerophilen (*meso-xero*) und Feuchte-indifferenten (*indiff*) Arten in den Trockenrasen. Mittelwerte und 10-fache (in a) bzw. 1-fache (in c, d) Standardfehler. *** $p < 0,001$, ** $p < 0,01$, * $p < 0,05$, n.s. nicht signifikant.

The species richness of the plots decreased significantly by 18.2% in all associations (from 19.3 to 15.8 species) (Fig. 10a). In the *Koeleria* grassland, species richness decreased by 41% (from 24.5 to 14.3 species) and in the *Carex humilis* grassland by 24% (from 22.9 to 17.5 species). In the *Sesleria* grassland and the *Stipa* grassland, species richness did not change significantly. Species richness of threatened plants decreased by 30% across all associations (from 12.0 to 8.4 species) (Fig. 10b). Again, *Koeleria* grassland and *Carex humilis* grassland showed higher losses (61.4% and 31.5%, respectively), but *Sesleria* grassland and *Stipa* grassland were also affected by losses of threatened plants (20.9% and 17.5%, respectively). The (cumulative) total number of species has developed as follows: 85 vascular plant species were found in all 1995 plots, compared to 75 species in all 2019 plots (Table 2). 26 species disappeared and 16 newly appeared in the plots. Among the species that disappeared were 11 threatened species and among the new species that appeared, five

Table 3. Pearson correlations between NMDS axis 2 and time (1995/2019), mean Ellenberg indicator values (EIV), and the proportions of xerophilic and meso-xerophilic plant species. Significant relationships in bold face.

Tabelle 3. Pearson-Korrelationen zwischen NMDS-Achse 2 und der Zeit (1995/2019) sowie mittleren Ellenberg-Zeigerwerten (EIV) und den Anteilen xerophiler und meso-xerophiler Pflanzenarten. Signifikante Zusammenhänge sind fettgedruckt.

	<i>r</i>	<i>p</i>
Year (and all binary climatic variables 1995 vs. 2019)	-0.81	< 0.001
EIV for light (L)	0.03	0.799
EIV for temperature (T)	0.18	0.093
EIV for continentality (K)	-0.26	0.012
EIV for moisture (F)	0.14	0.187
EIV for soil reaction (R)	-0.39	< 0.001
EIV for nutrients (N)	0.49	< 0.001
Proportion of xerophilic plants	-0.17	0.104
Proportion of meso-xerophilic plants	0.21	0.045

were threatened (Supplement E1). Most of the newly emerged species were annuals or biennials. In total, 45 threatened vascular plant species were found in the 1995 plots and 39 threatened species in the 2019 plots (Supplement E1).

Homogenisation of vegetation was only observed in the *Stipa* grassland, where the Bray-Curtis dissimilarity of species cover slightly decreased between 1995 and 2019 (Fig. 11b). Only the *Stipa* grassland showed no change in species turnover based on species presence/absence. In contrast, three out of four associations (*Koeleria*, *Sesleria*, and *Carex humilis* grassland) and all associations together showed heterogenisation in both species' presence/absence and species cover. When cover was considered in the analysis, species turnover was higher both within and between plots when only species presence was considered (Fig. 11a), indicating that not only species composition but also species cover changed. The NMDS also showed heterogeneity of associations through higher variance of 2019 values compared to 1995 values along axis 2 (Fig. 5). The condition of the grassland in 2018/2019 is shown in Figures 12–14.

5. Discussion

5.1 Changes in ecological indicator values and plant moisture types

Following our hypothesis that N deposition and climate change (especially summer drought but also mild winters) were the main drivers of vegetation change, we were surprised that only the mean indicator value for temperature increased but not that for nutrients (N), and that the indicator value for moisture (F) did not decrease. However, the nutrient value was still correlated with NMDS axis 2, the axis of vegetation change. The fact that the moisture value and nutrient value did not decrease or increase significantly (the F value decreased from 2.72 to 2.63, $p = 0.175$, and the N value increased from 2.06 to 2.16, $p = 0.096$) can be explained by their strong intercorrelation i.e., increasing nutrients (eutrophication) and decreasing moisture (drought) compensated each other in their indicator values which is in accordance to the farmer's theorem "nitrogen replaces water" (ELLENBERG 1986). Therefore, the fact that the moisture value did not decrease and the

nutrient value did not increase can be taken as an indication of increased dryness and nutrients. – Intercorrelated indicator values are not uncommon and cannot be easily mathematically disentangled within resurvey studies. The indicator values for nutrients and soil reaction (R) seem to be particularly often positively intercorrelated, which can then lead to increasing R values in the case of eutrophication, although the pH values remained constant (VAN CALSTER et al. 2007, SEIDLING & FISCHER 2008, REINECKE et al. 2014) or even decreased significantly (LITZA & DIEKMANN 2017). For N and F values, we are not (further) aware of such an intercorrelation in resurvey studies.

Independently from the indicator value for moisture, in our study, increased dryness was clearly indicated by the decreased proportion of meso-xerophilic plants, in contrast to the proportion of xerophilic plants that increased. However, there were some meso-xerophilic plants with storage taproots or rhizomes (e.g. *Anthericum ramosum*, *Cirsium acaulon*, *Peucedanum cervaria*) that declined only little, probably because these organs store water.

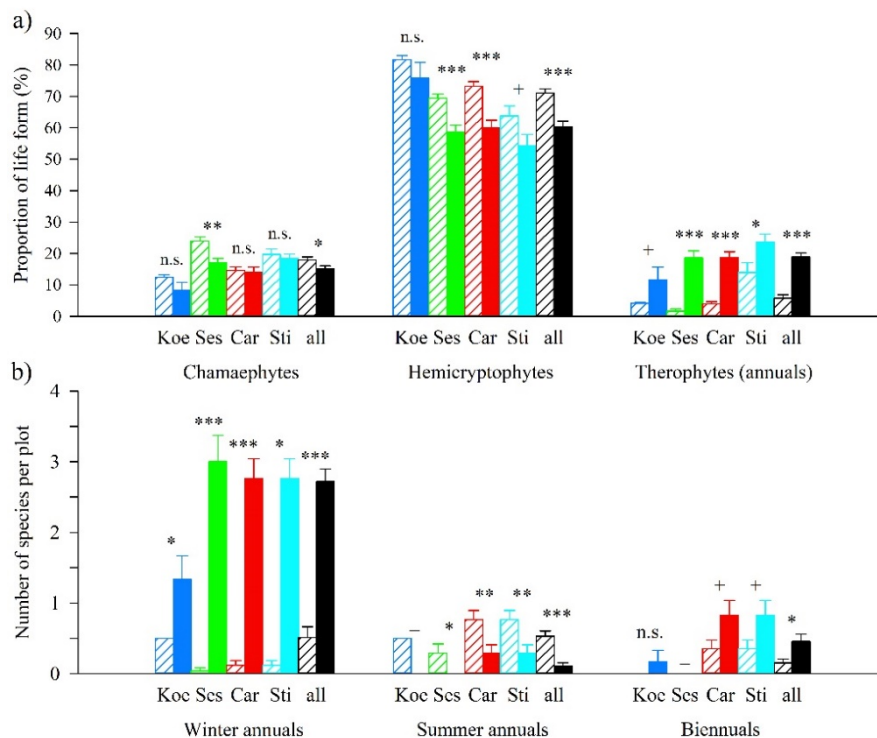


Fig. 7. a) Proportions of three general life forms and **b)** number of species of three special life forms of short-lived plant species in four dry grassland associations separately and together: Car – *Carex humilis* grassland, Koe – *Koeleria* grassland, Ses – *Sesleria* grassland, Sti – *Stipa* grassland. Hatched bars: 1995, filled bars: 2019. Mean values and 1 SE. *** $p < 0.001$, ** $p < 0.01$, * $p < 0.05$, + $p < 0.1$, n.s. not significant.

Abb. 7. a) Anteile von drei allgemeinen Lebensformen und **b)** Anzahl der Arten von drei speziellen Lebensformen kurzlebiger Pflanzenarten in vier Trockenrasenassoziationen getrennt und zusammen. Die Bedeutung der Kürzel geht aus der englischen Abbildungsunterschrift hervor. Schraffierte Balken: 1995, gefüllte Balken: 2019. Mittelwerte und einfache Standardfehler. *** $p < 0,001$, ** $p < 0,01$, * $p < 0,05$, + $p < 0,1$, n.s. nicht signifikant.

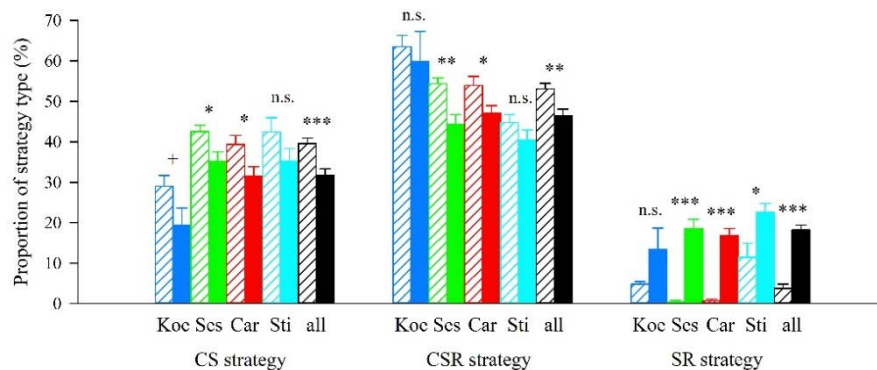


Fig. 8. Proportions of the plant strategy types CS – competition-stress-ruderal, and SR – stress-ruderal in four dry grassland associations separately and together: *Car* – *Carex humilis* grassland, *Koe* – *Koeleria* grassland, *Ses* – *Sesleria* grassland, *Sti* – *Stipa* grassland. Hatched bars: 1995, filled bars: 2019. Mean values and 1 SE. *** $p < 0.001$, ** $p < 0.01$, * $p < 0.05$, + $p < 0.1$, n.s. not significant.

Abb. 8. Anteile der Strategietypen CS – Konkurrenz-Stress-Strategie, CSR – Konkurrenz-Stress-Ruderal-Strategie und SR – Stress-Ruderal-Strategie in vier Trockenrasenassoziationen getrennt und zusammen. Die Bedeutung der Kürzel geht aus der englischen Abbildungsunterschrift hervor. Schraffierte Balken: 1995, gefüllte Balken: 2019. Mittelwerte und einfache Standardfehler. *** $p < 0,001$, ** $p < 0,01$, * $p < 0,05$, + $p < 0,1$, n.s. nicht signifikant.

The reaction value probably did not decrease because possible acidic compounds from deposition were buffered by the calcareous soil. The decreased continentality value indicates a shift in climate from more continental to more Mediterranean (not suboceanic, which is what low K values are supposed to indicate), i.e. winters became mild and humid but summers hot and arid. In fact, six winner species with sub-Mediterranean distribution (five winter annuals and *Bromus erectus*) faced one winner species with continental distribution (*Stipa capillata*) (*Centaurea stoebe* is sub-Mediterranean-continently distributed). The increased light value can be explained by the sparser vegetation due to drought influence.

5.2 Changes in life forms and plant strategy types

Perhaps the most striking change in vegetation in our study was the large increase in winter annuals, which are considered SR strategists (GRIME 2001), resulting in an increase in SR strategy. Of the four associations, in 1995, the winter annuals were restricted to the *Stipa* grassland, where they colonised open gaps between *S. capillata* tussocks (BECKER 1998a, b). These open gaps were the result of strong competition for water in summer. The absence of winter annuals in the dense *Koeleria* and *Carex humilis* grasslands in 1995 was probably due to strong light competition from perennial plants. The restriction of winter annuals to *Stipa* grassland has been highlighted (and documented) by many authors for different periods (for the lower Unstrut valley e.g. MEUSEL 1937, MAHN 1965, HENSEN 1997, BECKER 1998b) indicating a stable pattern over many decades. In 2019, however, winter annuals occurred in large numbers in all associations. In the *Koeleria* and *Carex humilis* grasslands, this change was most likely due to severe droughts in previous years, which led to a decline in perennial plant vegetation and thus to open gaps. An increase of winter annuals after drought events was also observed in other German regions, e.g. in Rhein Hesse and in the Rhenish Massif

(T. Becker, pers. observation). But an increase in winter annuals due to trampling by sheep, as found by MEIER et al. (2021) for the Kyffhäuser mountains, is unlikely in our study. This is because the Schafberg was regularly grazed over the entire period and the grazing intensity was not significantly increased, and because the dry grasslands in the lower Unstrut valley occur on cohesive shell limestone soils with a loamy texture, whereas in the Kyffhäuser mountains they occur on unstable gypsum soils with a sandy texture. This means that the soils on the steep slopes of the Kyffhäuser mountains are much more affected by trampling than in the Unstrut valley, especially not on the gentle slope of the Schafberg. Thus, we conclude that trampling was not the cause of the increased occurrence of winter annuals in our study.

Annual fluctuation effects due to merely favourable (wet and mild) or unfavourable (dry and cold) previous winters (PETŘÍK et al. 2011, FISCHER et al. 2020) are also unlikely to be causes of the increase in winter annuals, as the winter of 1994–95 was climatically average and the restriction of winter annuals to *Stipa* grassland has been a constant pattern at least since 1994. In fact, however, winters have become wetter and milder (i.e. more Mediterranean), which, in addition to open vegetation, probably permanently favours winter annuals. In the Czech dry grasslands, recent summer drought events also led to the death of perennial plants and favoured short-lived and fast-growing annual plants (FISCHER et al. 2020).

Only the colonisation of the *Sesleria* grassland by winter annuals cannot be plausibly necessarily explained by drought. The *Sesleria* grasslands both on the Schafberg and in the entire Unstrut valley already had open vegetation in 1995, but no winter annuals (cf. Table 8 in BECKER 1998b). In the decades before our study, winter annuals were still almost completely absent from xeric *Sesleria* grasslands on Muschelkalk in the entire Unstrut valley (SCHUBERT 1963) and adjacent regions (SCHMIDT 2000). We therefore assume that the colonisation of the *Sesleria* grasslands by winter annuals was mainly caused by a nutrient input due to airborne N deposition. This means that the probable reason for the absence of annuals in the *Sesleria* grassland in 1995 was nutrient limitation, as the soil was heavily eroded and skeletal (cf. Fig. 3a). This is because annual plants need sufficient nutrients (at least some humus enrichment) for their seed production. In general, airborne N deposition for the area was reported to be up to $10 \text{ kg per ha}^{-1} \times \text{year}^{-1}$, which is close to the critical nitrogen load of 14 and $25 \text{ kg ha}^{-1} \times \text{year}^{-1}$ for nutrient-poor grassland reported by DE JONG et al. (1998) and BOBBINK & HETTELINGH (2011). However, nitrogen inputs were high especially in the 1990s and have recently declined (FÖRSTER et al. 2017). The fact that winter annuals did not appear when N deposition was highest, but only when N deposition declined, can be explained by nutrient accumulation and by a threshold that nutrients first had to cross. We conclude that in the *Koeleria* and *Carex humilis* grasslands, winter annuals were mainly promoted by drought events and on the *Sesleria* grasslands by N deposition.

The increase in biennials, which are mainly sub-ruderals (cf. BRANDES & PFÜTZENREUTER 2013), was probably due to both factors, increased nutrients and stronger drought. However, the number of biennials in our study was low (only five species in total, of which only *Centaurea stoebe* was common), so the corresponding results are unreliable.

Summer annuals such as *Linum catharticum* or *Cuscuta epithymum* declined strongly in our study. This can be explained by the germination/establishment phase of summer annuals in early summer, when drought is often already severe. A strong decline of summer annuals in dry grasslands was also found by HAHN et al. (2013), RIDDING et al. (2020) and MEIER et al. (2021). In the Swiss Jura mountains, CHARMILLOT et al. (2021) found that *Linum catharticum* was the species with the greatest decline in meso-xeric grasslands.

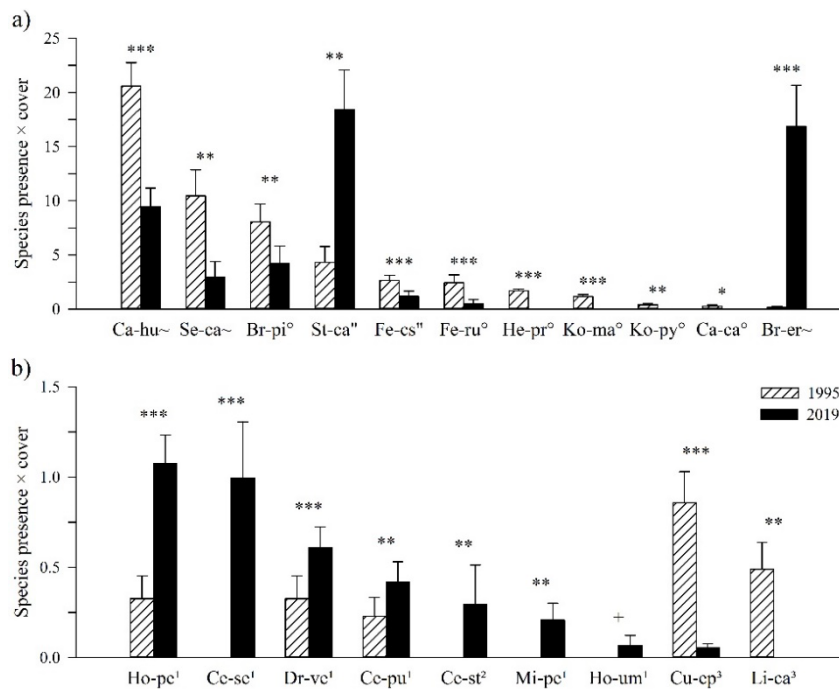


Fig. 9. The main **a)** short-lived species (¹ – winter annuals, ² – biennials, ³ – summer annuals) and **b)** graminoids (° – meso-xerophilic, " – xerophilic, and ~ – indifferent species) in the dry grasslands (all associations together) in 1995 and 2019 ($n = 46$, each). Mean values of presence $\times$ cover and 1 SE (for cover, the median percentage of the corresponding Braun-Blanquet class was taken). **a)** *Ce-pu* – *Cerastium pumilum* s. str., *Ce-se* – *Cerastium semidecandrum*, *Ce-st* – *Centaurea stoebe*, *Cu-ep* – *Cuscuta epithymum*, *Dr-ve* – *Draba verna*, *Ho-pe* – *Hornungia petraea*, *Ho-um* – *Holosteum umbellatum*, *Li-ca* – *Linum catharticum*, *Mi-pe* – *Microthlaspi perfoliatum*. **b)** *Br-er* – *Bromus erectus*, *Br-pi* – *Brachypodium pinnatum*, *Ca-ca* – *Carex caryophylla*, *Ca-hu* – *Carex humilis*, *Fe-cs* – *Festuca csikhegyensis*, *Fe-ru* – *Festuca rupicola*, *He-pr* – *Helictochloa pratensis*, *Ko-ma* – *Koeleria macrantha*, *Ko-py* – *Koeleria pyramidata*, *Se-ca* – *Sesleria caerulea*, *St-ca* – *Stipa capillata*. Order of species according decreasing presence $\times$ cover values in 1995, each. *** $p < 0.001$, ** $p < 0.01$, * $p < 0.05$, + $p < 0.1$.

Abb. 9. Die wichtigsten **a)** kurzlebigen Arten (¹ – Winterannuelle, ² – Bienne, ³ – Sommerannuelle) und **b)** Grasartigen (° – meso-xerophile, " – xerophile und ~ – indifferente Arten) in den Trockenrasen (alle Assoziationen zusammen) in den Jahren 1995 und 2019 (jeweils $n = 46$). Mittelwerte der Präsenz $\times$ Deckung mit einfachem Standardfehler (als Deckung diente in der Rechnung der Median des Prozentsatzes des entsprechenden Braun-Blanquet-Deckungsgrads). Die Bedeutung der Art-Kürzel geht aus der englischen Abbildungsunterschrift hervor. Die Arten sind jeweils nach abnehmender Präsenz $\times$ Deckung im Jahr 1995 sortiert. *** $p < 0,001$, ** $p < 0,01$, * $p < 0,05$, + $p < 0,1$.

5.3 Changes in graminoids

Most graminoids decreased, especially meso-xerophilic species like *Brachypodium pinnatum* but also xerophilic species like *Festuca csikhegyensis* and moisture indifferent (but xero-tolerant) species like *Carex humilis* and *Sesleria caerulea*. The somewhat meso-xerophilic *Helictochloa pratensis*, which was present in 70% of the plots in 1995, disappeared completely from the plots. The most likely reason for the general decline of

graminoids is again severe summer drought. Although xerophilic graminoids are generally well protected against drought, e.g. by small rolled-up leaves with wax coatings, these species seem to be more sensitive to drought in the root zone than many dicots, as they do not have thick storage roots protected by a periderm. Especially small-growing graminoids like *Koeleria macrantha* do not root deeply (KUTSCHERA & LICHTENEGGER 1982) and are therefore vulnerable to drought. In contrast, graminoids with deep roots did not decline in our study. Theoretically rooting up to 280 cm deep, *Stipa capillata* (KUTSCHERA & LICHTENEGGER 1982) increased mainly in cover, but also in abundance. *Stipa capillata* is both xerophilic and to some extent nitrophilic, which is why the species was probably promoted by N deposition in combination with drought. Nevertheless, drought seemed to be the determining factor, as nutrient supply alone tends to disadvantage *S. capillata* by increasing competition from mesic plants.

However, the main winner in our study was *Bromus erectus*, whose abundance increased by 933% (from 3 to 31 occupied plots) and whose coverage increased by 733% (on average from 3% to 25% coverage). *Bromus erectus* is currently invading many xeric and meso-xeric grasslands in Central Germany (BORNKAMM 2006, 2008, HEINRICH 2010, MEIER et al. 2021). On the Schafberg, its invasion has apparently started from the upper and lower edge. Here, in 1995, single tussocks of *B. erectus* grew scattered mainly in the *Koeleria* grassland at the back of the hill and in the *Carex humilis* grassland at the foot of the hill (cf. relevés in BECKER 1998b). The likely reasons for the success of the species are, in our opinion, in this order: The evergreen, sub-Mediterranean species benefits from climate change towards sub-Mediterranean climatic conditions mainly through (1) milder winters, which allow it to extend the growing season (BORNKAMM 2006), and (2) drier summers, which the species can cope with using its deep roots (up to at least 90 cm according to KUTSCHERA &

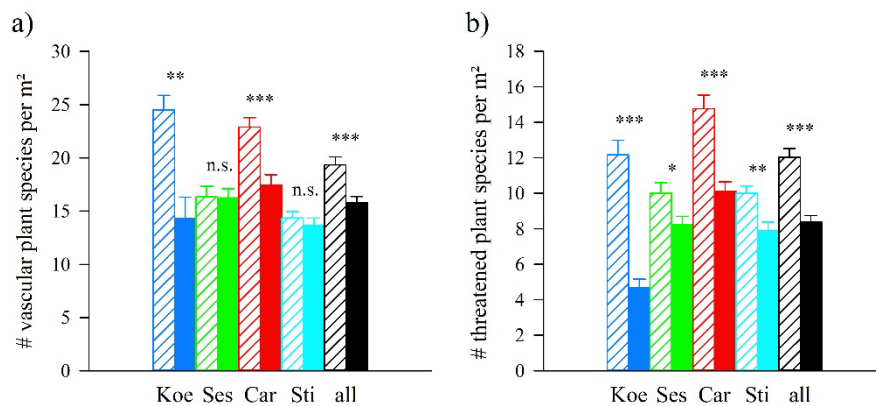


Fig. 10. Species richness (α diversity) of **a)** vascular plants and **b)** threatened vascular plants in four dry grassland associations separately and together: Car – *Carex humilis* grassland, Koe – *Koeleria* grassland, Ses – *Sesleria* grassland, Sti – *Stipa* grassland. Hatched bars: 1995, filled bars: 2019. Mean values and 1 SE. *** $p < 0.001$, ** $p < 0.01$, * $p < 0.05$, n.s. not significant.

Abb. 10. Artenreichtum (α -Diversität) von **a)** allen Gefäßpflanzen und **b)** gefährdeten Gefäßpflanzen in vier Trockenrasenassoziationen einzeln und zusammen. Die Bedeutung der Kürzel geht aus der englischen Abbildungsunterschrift hervor. Schraffierte Balken: 1995, gefüllte Balken: 2019. Mittelwerte und einfache Standardfehler. *** $p < 0,001$, ** $p < 0,01$, * $p < 0,05$, n.s. nicht signifikant.

LICHTENEGGER 1982). Drought damage can also be easily regenerated due to the high regeneration potential of the species (PÉREZ-RAMOS et al. 2013). Apart from climate change, it is (3) nutrient input due to N deposition or low nutrient output due to low management intensity that enable the species (which is considered a CS strategist according to GRIME 2001) to reach full competitiveness when being dominant (ELLENBERG 1986: 655, WILLEMS 1987, NOWAK & SCHULZ 2002). On the other hand, historical reasons for the success of *B. erectus*, such as late recolonisation after a possible earlier extinction in the Pleistocene (HEINRICH 2010, SUTKOWSKA et al. 2013), are implausible, as common graminoids like *B. erectus* can usually build up high seed pressure and are therefore unlikely to be severely restricted in their dispersal. Following LEMMER et al. (2021) we therefore assume that in our study the main factor for the invasion of *B. erectus* is indeed climate change (i.e. drier summers and milder winters), while eutrophication also plays a role but is of secondary importance. If the tall species is dominant, it contributes to higher vegetation, which reduces the species richness of plants (MEIER et al. 2021, SPLITH et al. 2021) and insects (e.g. leafhoppers) (PONIATOWSKI et al. 2018). Overall, we expect *B. erectus* in particular to continue to increase on the Schafberg.

5.4 Changes in species richness and conservation value

In the 24 years covered by our study, all plots together lost 11.8% of their cumulative plant species richness and 13.3% of their cumulative number of threatened plant species. At the plot level, 18.1% of vascular plant species and 30.3% of threatened vascular plant species were lost. This indicates a disproportionate loss of threatened plants. The grassland had thus lost part of its conservation value. Other grassland resurvey studies also found disproportionate losses in threatened vascular plants, but no overall decline in species richness (e.g. DIEKMANN et al. 2019, MEIER et al. 2021, SCHÜLE et al. 2022). Only in the study by HAHN et al. (2013) from the neighbouring Kyffhäuser Mountains did threatened plant species increase, presumably because the Kyffhäuser grasslands had regenerated after decades of over-intensive use through grazing. In meso-xeric grasslands in north-western Germany, declining species richness was observed on south-exposed slopes after intense drought events between 2008 and 2019, while no negative trends were observed for ruderal species (MAZALLA et al. 2022).

5.5 Changes in homogenisation

While floristic homogenisation was found in forests in most resurvey studies (KEITH et al. 2009, REINECKE et al. 2014, HEINRICH & SCHMIDT 2017), the results for dry grasslands are ambiguous. Accordingly, no general trend was found in the meta-analysis by DIEKMANN et al. (2019) which includes six resurvey studies mainly on meso-xeric grassland. In our study, in three out of four associations (and in all associations combined) species dissimilarity of plot collectives increased over time, indicating reduced homogenisation and thus heterogenisation. This is a clear indication that the vegetation changes in our study were not primarily caused by N deposition or lower management intensity, but by increasing drought. N deposition and lower management intensity usually promote competitive species, leading to a lesser dissimilarity, i.e. homogenisation of vegetation, while disturbance by drought events usually leads to greater dissimilarity, i.e. heterogenisation (MCKINNEY & LOCKWOOD 1999).

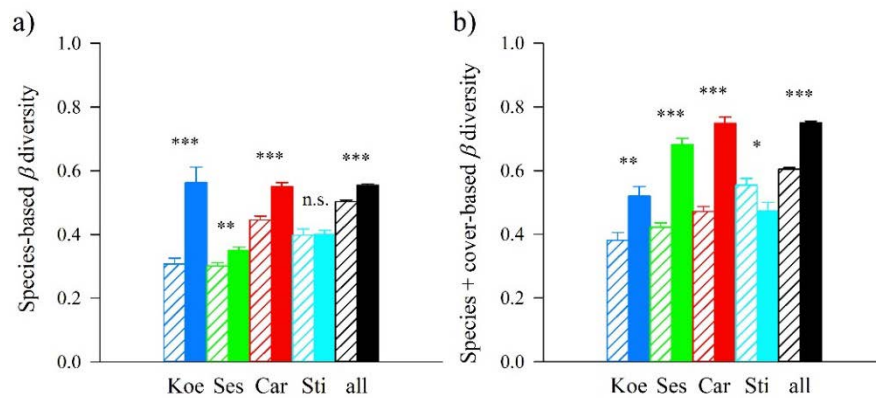


Fig. 11. Development of taxonomic β -diversity (Bray-Curtis) in four dry grassland associations alone and together over time (1995/2019). Decreased β -diversity means homogenisation and increased β -diversity heterogenisation. **a)** Species-based and **b)** species plus cover-based β -diversity. Car – *Carex humilis* grassland, Koe – *Koeleria* grassland, Ses – *Sesleria* grassland, Sti – *Stipa* grassland. Hatched and filled bars indicate β -diversity in 1995 and 2019, respectively. *** $p < 0.001$, ** $p < 0.01$, * $p < 0.05$, n.s. non-significant at $p < 0.05$.

Abb. 11. Entwicklung der taxonomischen β -Diversität (Bray-Curtis) von vier Trockenrasenassoziationen einzeln und zusammen über die Zeit (1995/2019). Abnehmende β -Diversität bedeutet Homogenisierung und zunehmende β -Diversität Heterogenisierung. **a)** Artbasierte und **b)** art- plus deckungs-basierte β -Diversität. Ein β -Diversitätswert von 1 bedeutet eine Unterschiedlichkeit von 100 %. Die Bedeutung der Kürzel geht aus der englischen Abbildungsunterschrift hervor. Mittelwerte und einfache Standardfehler. Schraffierte und gefüllte Balken zeigen die β -Diversität der Vegetation in 1995 bzw. 2019 an. *** $p < 0,001$, ** $p < 0,01$, * $p < 0,05$, n.s. nicht-signifikant bei $p < 0,05$.

This conclusion that management intensity has not decreased is consistent with our finding that the Schafberg has been adequately managed throughout the period, so management cannot be the reason for the change in vegetation. Another indication that management intensity has not decreased is that fringe species such as *Peucedanum cervaria* or *Inula hirta* have not increased; both species often become dominant in the Unstrut valley when the dry grasslands are abandoned (BECKER 1998b). The fact that dissimilarity increased is all the more remarkable as *Bromus erectus* became the dominant species in several plots and probably competes strongly with other species. This again indicates that the increasing dryness must have been the most important factor for the observed vegetation changes. Only the *Stipa* grassland was slightly homogenised. One possible explanation is that the *Stipa* grassland was already extremely dry in the past and contained many winter annuals, so that the corresponding tipping point could already have been reached before the first survey. We also found only weak heterogenisation in the *Sesleria* grassland. This can be explained by the extreme habitat conditions of the skeletal soil and the competitive, stress-tolerant species such as *Sesleria caerulea*, which may have prevented heterogenisation. Another explanation could be that this association in particular was heavily invaded by the competitive *Bromus erectus*, which may have counteracted heterogenisation.



Fig. 12. a) *Sesleria* grassland (*Carici-Seslerietum*) on the upper SW slope of the Schafberg in the transect area during the drought event 2018. In July, the vegetation was largely desiccated with exception of *Carex humilis*. This stand has been invaded by *Bromus erectus* (see dried flower shoots). **b)** The southwest slope of the Schafberg from the west. The transect went over the hilltop, in a direct line down along to the right of the single black pine to the foot of the hill (Photos: T. Meier, a) 10.07.2018, b) 08.07.2015).

Abb. 12. a) Blaugras-Trockenrasen (*Carici-Seslerietum*) am oberen Südwesthang des Schafbergs im Bereich des Transekts während der Dürre 2018. Mit Ausnahme von *Carex humilis* war die Vegetation im Juli weitgehend vertrocknet. *Bromus erectus* (siehe die vertrockneten Blütenstände) hat den Bestand invadiert (Foto: T. Meier, 08.07.2015). **b)** Der Südwesthang des Schafbergs von Westen aus. Der Transekt verlief über die Kuppe, rechts von der einzelnen Schwarzkiefer entlang in direkter Linie nach unten (Fotos: T. Meier, a) 10.07.2018, b) 08.07.2015).

5.6 Treating associations individually or together

A special feature of our study is that we divided our grassland into four associations and analysed them both individually and together. Overall, the four associations differed greatly in their floristic composition. Of the total 38 species that changed significantly in at least one association after ISA, only seven species (19.4%) decreased in three or four associations, while 29 species (80.6%) changed in only one or two associations (two species changed only when all four associations were considered together). On the other hand, associations have often changed in parallel for common species. Only *Salvia pratensis* and *Teucrium chamaedrys* changed in opposite ways, i.e. they decreased in one association and increased in another. One could therefore argue that a distinction between associations would not have been necessary to detect most species changes. However, there were clear differences in the results of the individual associations. Evidence of eutrophication resulting, for example, from the colonisation of *Sesleria* grassland by winter annuals would not have been found if this grassland type had not been differentiated. The stronger changes in the meso-xeric *Koeleria* grassland correspond to results of MEIER et al. (2021) from the Kyffhäuser mountains where meso-xeric grasslands also changed more than xeric grasslands. We therefore conclude that distinguishing community types like associations, in addition to combining them, can be a suitable tool to obtain both detailed and general results on vegetation change.

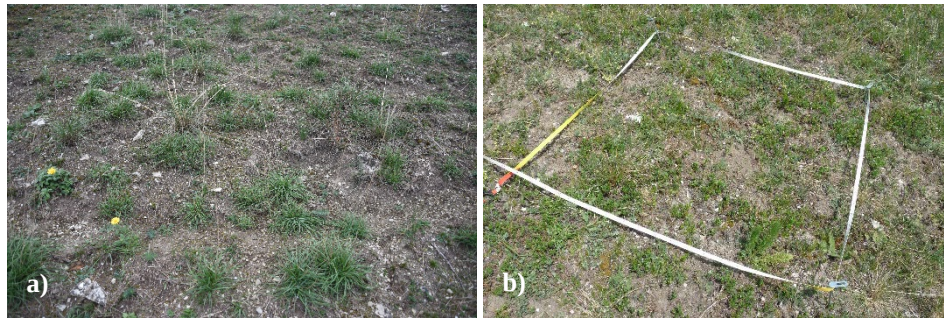


Fig. 13. a) Detail of the *Carex humilis* grassland (*Trinio-Caricetum*) on the upper SW slope of the Schafberg in October 2018 after severe drought. *Bromus erectus* (most tussocks) has already regenerated well despite the late season. **b)** Resurvey plot no. 20 in the *Carex humilis* grassland (*Trinio-Caricetum*) on the Schafberg SW middle slope in June 2019. More plants than expected survived the severe drought in previous year but vegetation was severely thinned. Visible are the dwarf shrubs *Teucrium chamaedrys* and *T. montanum* (in flower), the graminoids *Carex humilis* and *Stipa capillata* and the herbs *Adonis vernalis* and *Salvia pratensis*. Meso-xerophilic species like *Helictochloa pratensis* and *Hippocrepis comosa* had disappeared. This plot was still not invaded by *Bromus erectus* (Photos: T. Meier).

Abb. 13. a) Detail des Erdseggen-Trockenrasens (*Trinio-Caricetum*) am oberen Südwesthang des Schafbergs im Oktober 2018 nach schwerer Dürre. *Bromus erectus* (die meisten Horste) hat sich trotz fortgeschrittener Jahreszeit bereits gut regeneriert. **b)** Wiederholungsaufnahme fläche Nr. 20 im Erdseggen-Trockenrasen (*Trinio-Caricetum*) am mittleren Südwesthang des Schafbergs im Jahr 2019. Mehr Arten als erwartet hatten die schwere Dürre im Vorjahr überlebt, aber die Vegetation war stark ausgedünnt. Zu sehen sind die Zwergsträucher *Teucrium chamaedrys* und *T. montanum* (in Blüte), die Gräser *Carex humilis* und *Stipa capillata* und die Kräuter *Adonis vernalis* und *Salvia pratensis*. Meso-xerophile Arten wie *Helictochloa pratensis* und *Hippocrepis comosa* waren verschwunden. Diese Fläche war noch nicht von *Bromus erectus* invadiert (Fotos: T. Meier).

5.7 Study characteristics and limitations

Our study differs from other resurvey studies in four methodological points: the plot size was small, the plots were set up along a transect line, the study area was small, and the plots were relocated almost exactly (permanent plots). In general, very small plots are not necessarily representative. However, our 1 m² plots from 1995 contained an average of 20 vascular plant species, i.e. 63% of the number of species of the regular 20 m² plots recorded in the same year in the transect area on the Schafberg (cf. BECKER 1998b). We therefore conclude that our plots were sufficiently representative. Furthermore, we do not expect any negative effects of the transect approach. The 244 m transect encompassed the entire sequence of xeric and meso-xeric grassland types of the region compensating for the small study area, and the Schafberg dry grasslands were typical developed and thus representative. This is because the Schafberg was never used for viticulture/agriculture, i.e. the soil was never disturbed by terracing/ploughing, so that the dry grassland was ancient and completely preserved (BECKER 2010). The grassland was also managed throughout the study period and was in a good status of management during both surveys. However, local studies like ours are always associated with limitations related to the small size of the study area. *Helictochloa pratensis* and *Koeleria macrantha*, for example, declined at the Schafberg, but were constant in the Kyffhäuser Mountains between 1996 and 2018/2019



Fig. 14. *Carex humilis* grassland (*Trinio-Caricetum*) on the middle SW slope of the Schafberg in the transect area during the drought 2018. In August, with exception of *Vincetoxicum hirundinaria*, the above-ground vegetation was nearly completely dead (Photo: T. Meier).

Abb. 14. Erdseggen-Trockenrasen (*Trinio-Caricetum*) am mittleren Südwesthang des Schafbergs am Ende der Dürre 2018. Mit Ausnahme von *Vincetoxicum hirundinaria* war die Vegetation oberflächlich fast vollständig tot (Foto: T. Meier).

(MEIER et al. 2021). The same was found for *H. pratensis* on the Porphyry outcrops near Halle (Saale) between 2002 and 2018/2019 (MEIER et al. 2021). Furthermore, our approach of permanent plots led to a high data quality, i.e. pseudo-turnover by semi-permanent plots according to KAPFER et al. (2018) and VERHEYEN et al. (2018) were largely avoided. The high data quality also compensated for the relatively low number of plots in individual associations. We can also largely exclude out observer errors, which often result from the absence of inconspicuous species (MORRISON et al. 2020). At the beginning of our survey and resurvey, both observers were excellently trained by, among other things, recording many regular plots on the Schafberg. The absence of winter annuals in the non-*Stipa* grassland plots was also observed in the standard plots on the Schafberg in spring 1995, when these species were fully developed. Finally, in merging our data, taxonomic concepts were thoroughly harmonised and the error-prone division of taxa was avoided. We therefore conclude that our data was of high quality and our results were clear, consistent and plausible.

6. Conclusions

Our study shows that climate change (i.e. mild winters but especially the hot and dry summers since about 2015) as well as airborne nitrogen deposition are most likely the main drivers behind vegetation changes in a central German dry grassland between 1995 and 2019. At the same time, we were surprised by the strength of the changes after only 24 years,

i.e. we had expected fewer changes. In fact, most of our changes were shifts within existing species, which can happen relatively quickly. Annual plants, for example, can increase quickly due to their rapid reproduction, and perennials can die quickly during drought. However, the increase in *Stipa capillata* and *Bromus erectus* was not a short-term pattern, suggesting that climate change has been affecting the grassland for some time but was not properly recognised.

The observed vegetation changes were probably caused mainly by climate change, but partly also in interaction with N deposition. However, it is very likely that climate change has almost always been the driving force behind our patterns, because without climate change, N deposition would have led to more mesophilic grassland, i.e. the opposite pattern we have observed. For example, the increase in annual and biennial plants due to N deposition was only possible because drought had damaged the perennial plants, leaving open gaps. Only the colonisation of the *Sesleria* grassland by winter annuals can be attributed to N deposition alone, as this community already had many open gaps during the first survey but no winter annuals.

While MAZALLA et al. (2022) found evidence of climate change impacts for semi-dry (meso-xeric) grassland (i.e. a decline in species richness on south-facing slopes for all species groups except ruderal species), our study suggests for the first time, to our knowledge, such complex floristic changes for dry and semi-dry grassland that can be attributed to climate change. In our study, however, the mean indicator values for moisture and nutrients did not reflect any change in the factors concerned, which was due to their intercorrelation, i.e. mutual compensation. Such intercorrelation effects show limitations of indicator values which need to be taken more into account in resurvey studies.

Erweiterte deutsche Zusammenfassung

Einleitung – Trockenrasen haben durch Nutzungsintensivierung und -aufgabe einen starken Rückgang erfahren und zählen daher zu den wertvollsten Habitaten in Mitteleuropa (JANSSEN et al. 2016). Selbst in Schutzgebieten wird ihr Naturschutzwert jedoch durch inadäquate Pflege, atmosphärische Stickstoffeinträge (BOBBINK et al. 1998) und Fragmentierung (COUSINS 2009) weiter reduziert. Eine neue Gefahr für Trockenrasen bildet der Klimawandel. Da Trockenrasen grundsätzlich an Hitze und Trockenheit angepasst sind, könnte man eine gewisse Resilienz gegenüber Temperaturerhöhung und zunehmender Trockenheit erwarten; konkret sind sowohl positive als auch negative Effekte denkbar. Positiv wäre es, wenn der Klimawandel durch Trockenheit die Stickstoffdepositionen kompensieren und so auch die Sukzession der Bestände verlangsamen würde (ELLENBERG & LEUSCHNER 2010: 949). Negativ wären irreversible Hitze- und Trockenschäden. Die Faktoren (Treiber), welche Vegetationsveränderungen bewirken, können mit Hilfe von ökologischen Zeigerwerten sowie Zeigerarten detektiert werden. Winterannuelle zeigen in Trockenrasen z.B. starke Sommertrockenheit an, die zu Vegetationslücken führt, welche die konkurrenzschwachen Winter-einjährigen benötigen. Grasartige dagegen haben in Trockenrasen als aufbauende Arten eine Bedeutung und sind gleichzeitig oftmals ökologisch eng eingenischt und daher oft gute Indikatoren. Die relativ wenigen vorliegenden Studien zu Vegetationsveränderungen in Trockenrasen fanden oft eine Abnahme seltener und gefährdeter Arten, seltener eine Abnahme der Gesamtartenzahl, sowie eine Zunahme an Nährstoffzeigern und teilweise auch eine Abnahme an Störungszeigern (z.B. PARTZSCH 2000, HAHN et al. 2013, DIEKMANN et al. 2014, 2019, CHARMILLOT et al. 2021, MEIER et al. 2021). Halbtrockenrasen hatten sich meist stärker verändert als Volltrockenrasen (z.B. MEIER et al. 2021). Lediglich MAZALLA et al. (2022) beobachteten in Halbtrockenrasen negative Effekte von Dürre auf den Artenreichtum. Wir untersuchten Vegetationsveränderungen in einem Trockenrasen am Schafberg im unteren Unstruttal über einen Zeitraum von 24 Jahren (1995–2019). In dieser Zeit gab es v. a. zum Ende hin vier schwere Dürren (BOERGENS et al. 2020), welche mit dem Klimawandel in Verbindung gebracht

werden. Daher fragen wir, ob bzw. wie sich die Trockenrasen zwischen 1995 und 2019 durch diese klimawandelassoziierten Dürren aber auch den Temperaturanstieg sowie Stickstoffdepositionen verändert haben. Zur Beantwortung dieser Fragen untersuchten wir neben Veränderungen in der Gesamtartenkombination eine Reihe von Merkmalen, die in der Vegetationsanalyse erprobt und verbreitet sind und speziell auf veränderte Trockenheit oder Nährstoffversorgung reagieren: Ökologische Zeigerwerte nach Ellenberg, Anteile xerophiler und meso-xerophiler Pflanzenarten, Raunkiaer-Lebensformen, CSR-Strategietypen und die β -Diversität der Vegetation als Maß für eine mögliche Homogenisierung. Innerhalb der Arten fokussierten wir uns besonders auf kurzlebige Pflanzenarten und Graminoide. Tabelle 1 fasst unsere einzelnen Hypothesen zusammen.

Untersuchungsgebiet – Die Studie wurde am Schafberg bei Zscheiplitz im unteren Unstruttal (Sachsen-Anhalt) durchgeführt (Abb. 1). Der Untergrund besteht hier aus Unterem Muschelkalk und das Klima war mit ca. 550 mm Jahresniederschlag immer schon sehr trocken (BECKER 1998b). Bei der Erstaufnahme im Jahr 1995 wuchs am Nordhang des Schafbergs ein *Gentiano-Koelerietum* und an dem großen Südwesthang auf Steinböden ein *Carici-Seslerietum*, auf mittelgründigen Lehm Böden ein *Trinio-Caricetum humilis* und auf flachgründigen Lehm Böden ein *Festuco-Stipetum* (BECKER 1998a). Abbildung 2–3 zeigt die Rasen im Jahr der Erstaufnahme und Abbildung 12–14 im Jahr der Wiederaufnahme.

Methoden – Bei der Erstaufnahme im Jahr 1995 wurden entlang einer 244 m-Transektlinie von der Rückseite des Berges (Nordhang) über den Südwesthang bis zum Bergfuß 46 Dauerflächen von je 1 m² eingemessen und aufgenommen (BECKER 1998b). Die Wiederaufnahme erfolgte im Juni 2019 in gleicher Weise. Aus den Vegetationsdaten wurden folgende Variablen pro Fläche und Jahr berechnet: (1) Artumsatz in den Aufnahmepaaren nach Bray-Curtis, (2) mittlere Zeigerwerte nach Ellenberg, (3) Anteile und Summen der xerophilen und meso-xerophilen Arten, (4) Anteile der Lebensformen nach Raunkiaer einschließlich winter- und sommerannueller sowie biennier Arten, (5) Anteile der wichtigsten CSR-Strategietypen, (6) Veränderung der wichtigsten Grasartigen als Produkt ihrer Präsenz und ihres ordinal-transformierten Deckungsgrades, (7) Artenreichtum (α -Diversität) und Anzahl gefährdete Arten, (8) Homogenisierung/Heterogenisierung als Veränderung der β -Diversität der Vegetation. Unterschiede in den Mittelwerten der Variablen nach Assoziationen getrennt und zusammen wurden mit *t*-Tests und Unterschiede zwischen Assoziationen mit einfaktorieller ANOVA und anschließend Tukey-post-hoc-Test analysiert. Arten mit signifikanter Zu- (Gewinner) oder Abnahme (Verlierer) wurden mit Hilfe von Zeigerartanalyse (ISA) determiniert. Eine Ordinationsanalyse (NMDS) diente zur Extraktion und Visualisierung des floristischen Gradienten der Veränderung. Zusammenhänge zwischen diesem Gradienten und Umweltvariablen wurden mithilfe von Pearson-Korrelationen analysiert.

Ergebnisse – Die meisten Assoziationen waren bei ihrer Wiederaufnahme noch erkennbar vorhanden. Lediglich das *Gentiano-Koelerietum* am Nordhang hatte sich in ein *Onobrychido-Brometum* gewandelt und das *Trinio-Caricetum humilis* entsprach nicht mehr der meso-xerischen Subassoziation *cirsietosum*, sondern eher der xerischen Subassoziation *typicum* (Anhang E1). Der Artumsatz innerhalb der Flächenpaare auf Basis der Präsenz/Absenz der Arten betrug über alle vier Assoziationen 50 % (Abb. 4). In der NMDS-Ordination wurde die Vegetation der beiden Jahre entlang der zweiten Achse voneinander getrennt, die mit der Zeit korrelierte (Abb. 5). Der mittlere Ellenberg-Zeigerwert für Temperatur nahm zu und der für Kontinentalität ab, während die Zeigerwerte für Nährstoffe und Feuchte keine signifikante Veränderung zeigten (Abb. 6a). Die Ellenberg-Zeigerwerte für Nährstoff und Feuchte waren eng miteinander korreliert (Abb. 6b). Der Anteil meso-xerophiler Arten nahm ab und der Anteil xerophiler Arten zu (Abb. 6c). Winterannuelle hatten stark zugenommen, die wenigen Sommerannuellen dagegen stark abgenommen und die ebenfalls wenigen Biennen zugenommen (Abb. 7). CS- und CSR-Strategen hatten ab- und SR-Strategen zugenommen (Abb. 8). Insgesamt standen neun Gewinnerarten 29 Verliererarten gegenüber (Tabelle 2). 31 % der Verliererarten waren Grasartige, darunter die dominanten *Carex humilis*, *Sesleria caerulea* und *Brachypodium pinnatum*. Auch typische kleinwüchsige Horstgräser (z. B. *Festuca csikhegyensis*) hatten abgenommen oder waren

verschwunden (*Helictochloa pratensis*) (Abb. 9a). *Stipa capillata* und vor allem *Bromus erectus* hatten dagegen zugenommen. Der Gesamtartenreichtum pro Quadratmeter hatte von 19,3 auf 15,8 (-18 %) und der Artenreichtum gefährdeter Arten von 12,0 auf 8,4 abgenommen (-30 %) (Abb. 10). Die Vegetation war insgesamt heterogener geworden (Abb. 11).

Diskussion – Vor dem Hintergrund unserer Hypothese bzw. anderen Ergebnisse, dass der Klimawandel und atmosphärische Stickstoffdepositionen die wichtigsten Treiber der Vegetationsveränderungen waren, waren wir überrascht, dass der mittlere Zeigerwert für Nährstoffe (N-Wert) nicht signifikant zu- und insbesondere der für Feuchte (F-Wert) nicht signifikant abnahm. Dies kann durch die starke Interkorrelation der beiden Zeigerwerte erklärt werden, die dazu führte, dass zunehmende Trockenheit den Anstieg der N-Werte und Eutrophierung das Absinken der F-Werte verhindert hat – obwohl Eutrophierung und Austrocknung tatsächlich stattfanden. Vor diesem Hintergrund interpretieren wir die nicht signifikant veränderten N- und F-Werte als Anzeichen für stärkere Trockenheit und Eutrophierung. Ein weiteres Indiz für stärkere Trockenheit war die Zu- bzw. Abnahme der Anteile der xerophilen bzw. meso-xerophilen Arten, was v.a. durch die überproportionale Abnahme meso-xerophiler Arten bedingt war, die offenbar vertrocknet waren. Der verringerte Zeigerwert für Kontinentalität kann als Indiz für ein weniger kontinentales und stärker mediterranes (nicht ozeanisches) Klima gewertet werden. Tatsächlich standen sechs Gewinnerarten mit submediterraner Verbreitung zwei Gewinnerarten mit kontinentaler Verbreitung gegenüber. Unter den Ersteren waren fünf Winterannuelle (u.a. *Cerastium pumilum* s. str., *C. semidecandrum*, *Hornungia petraea*), die in der Erstaufnahme noch auf die *Stipa*-Rasen (*Festuco-Stipetum*) beschränkt waren, wo sie in Vegetationslücken wuchsen, während sie in den anderen Rasentypen aus Mangel an Vegetationslücken fehlten. Bei der Wiederaufnahme in 2019 waren die Winterannuellen dann in allen Assoziationen häufig vertreten, was wir auf mildere Winter aber v.a. die Ausdünnung der Vegetation durch die Sommerdürren zurückführen (vgl. Abb. 12a und 14). Nur in den *Sesleria*-Rasen (*Carici-Seslerietum*) griff diese Erklärung nicht, da es dort früher schon zahlreiche Vegetationslücken gab, aber keine Winterannuellen. Hier nehmen wir an, dass die Winterannuellen früher aus Nährstoffmangel fehlten, der dann durch die Stickstoffdepositionen überwunden wurde. Die starke Abnahme der Sommerannuellen wie *Linum catharticum* oder *Cuscuta epithymum* lässt sich dagegen durch deren Keim- und Etablierungsphase im Frühsommer erklären, wenn oftmals bereits Dürre herrscht. Auch den starken Rückgang der Graminoiden führen wir auf die jetzt stärkere Trockenheit zurück. Denn obwohl sich xerophytische Graminoide grundsätzlich vor Trockenheit schützen können, reagieren sie auf andauernde tiefe Bodentrockenheit anscheinend empfindlicher als viele Dikotylen mit ihren Speicherwurzeln mit Periderm. Dies gilt v. a. für kleinwüchsige Gräser wie *Koeleria*- oder *Festuca*-Arten, die eher flach wurzeln (KUTSCHERA & LICHTENEGGER 1982). Graminoide mit tiefreichenden Wurzeln wie *Stipa capillata* und *Bromus erectus* hatten dagegen zugenommen. Letzterer hatte die Rasen regelrecht invadiert. Hauptgrund dieser Invasion dürfte ebenfalls der Klimawandel sein, der mit trockeneren Sommern (welche die Art toleriert bzw. deren Schäden sie schneller als andere Arten regeneriert) und v.a. milderen Wintern (in denen die Art effektiv produziert) die Klimaansprüche der submediterranen Art bedient (LEMMER et al. 2021). Unterstützend dürften aber auch Stickstoffdepositionen gewirkt haben, welche die wuchskräftig-konkurrenzstarke Art insgesamt fördern (LEMMER et al. 2021). Insgesamt haben sich die Trockenrasen des Schafbergs während nur 24 Jahren nicht nur deutlich verändert, sondern auch einen Teil ihres Naturschutzwertes eingebüßt, wie die abgenommene Artendiversität und der überproportional starke Rückgang der gefährdeten Arten zeigen. Andere Wiederholungsstudien im Grasland fanden ebenfalls über-proportionale Verluste gefährdeter Arten, aber keinen generellen Rückgang des Artenreichtums (z. B. DIEKMANN et al. 2019, MEIER et al. 2021, SCHÜLE et al. 2022). Insgesamt bewerten wir in unserer Studie den Klimawandel mit v.a. Sommerdürren aber auch milden Wintern als die treibende und Stickstoffdepositionen als untergeordnete (aber dennoch wichtige) Kraft. Denn ohne den Einfluss des Klimawandels hätten die Stickstoffdepositionen zu entgegengesetzten Ergebnissen führen müssen, nämlich einer mehr mesophilen und dichteren Vegetation. Nutzungsänderungen als Grund für unsere Vegetationsveränderungen können wir weitgehend ausschließen; in beiden Jahren war der Pflegezustand der Rasen gut und es gab keine Anzeichen einer Verbrachung. Unseres Wissens zeigt unsere Studie erstmals die

beginnenden Auswirkungen des Klimawandels auf Trockenrasen auf breiter Ebene. Außer der Studie von MAZALLA et al. (2022) sind uns überhaupt keine weiteren Untersuchungen bekannt, die wie wir die Vegetationsveränderungen in Trocken- oder Halbtrockenrasen mit dem Klimawandel in Zusammenhang bringen können.

Schlussfolgerung – Unsere Ergebnisse indizieren, dass mitteleuropäische Trockenrasen gegen den Klimawandel nicht resilient, sondern teilweise davon in vielfältiger Weise bereits betroffen und dadurch gefährdet sind.

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Author contribution statement

The vegetation was surveyed by T.B. and resurveyed by T.M. within his PhD project supervised by I.H. and M.P. T.B. and T.M. performed data analysis and drafted the manuscript. All authors revised the draft and agreed with the final manuscript for publication.

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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. Biological/ecological characteristics of studied species.

Anhang E1. Biologisch-ökologische Eigenschaften der untersuchten Arten.

Supplement E2. Synoptic table of the dry grassland communities in 1995 und 2019.

Anhang E2. Übersichtstabelle der Trockenrasengesellschaften in den Jahren 1995 und 2019.

Supplement E3. (Table 2 continued) Constant vascular plant species or species that are too rare for assessing their change.

Anhang E3. (Fortsetzung Tabelle 2) Konstante Gefäßpflanzenarten oder Arten, die zu selten sind, um ihre Veränderung zu bemessen.

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Supplement E1. Biological/ecological characteristics of studied species. Threat categories according to the RL G – Red List of Germany (METZING et al. 2018) and RL SA – Red List of Saxony-Anhalt (FRANK et al. 2020): 1 – critically endangered, 2 – endangered, 3 – vulnerable, V – near-threatened. § – protected after national species protection ordinance. Life forms (LF) according to ELLENBERG et al. (2001): C – herbaceous chamaephyte, G – geophyte, H – hemicryptophyte, N – nano-phanerophyte, P – phanerophyte, T – therophyte. Sub-life forms of short-lived species according to KLOTZ et al. (2002) and own observations: sum – summer annuals, win – winter annuals, bien – biennials (monocarpic-perennial). CSR strategy types according to KLOTZ et al. (2002): CS – competition/stress strategy, CSR – competition/stress/ruderal strategy, SR – stress/ruderal strategy. Moisture behaviour types according to BECKER (1998b): *xero* – xerophilic, *meso-xero* – meso-xerophilic, × – indifferent behaviour. Mean Ellenberg indicator values according to ELLENBERG et al. (2001) for: L – light, T – temperature, K – continentality, F – moisture, R – soil reaction, N – nutrients.

Anhang E1. Biologisch-ökologische Eigenschaften der untersuchten Arten. Gefährdung nach der RL G – Roten Liste Deutschlands (METZING et al. 2018) und RL SA – Roten Liste Sachsen-Anhalts (FRANK et al. 2020). Die Gefährdungskategorien sind: 1 – vom Aussterben bedroht, 2 – stark gefährdet, 3 – gefährdet, V – Vorwarnliste. § – geschützt nach Bundesartenschutzverordnung. Lebensformen (LF) nach ELLENBERG et al. (2001): C – krautige Chamaephyten, G – Geophyten, H – Hemikryptophyten, N – Nano-Phanerophyten, P – Phanerophyten, T – Therophyten. Sub-Lebensformen kurzlebiger Arten nach KLOTZ et al. (2002) und eigenen Beobachtungen: sum – sommer-annuell, win – winter-annuell, bien – zweijährig (mehrjährig-monokarp). CSR-Strategietypen nach KLOTZ et al. (2002): CS – Konkurrenz/Stress-Strategie, CSR – Konkurrenz/Stress/Ruderal-Strategie, SR – Stress/Ruderal-Strategie. Feuchteverhalten nach BECKER (1998b): *xero* – xerophil, *meso-xero* – meso-xerophil, × – indifferentes Verhalten. Mittlere Ellenberg-Zeigerwerte nach ELLENBERG et al. (2001): L – Licht, T – Temperatur, K – Kontinentalität, F – Feuchte, R – Bodenreaktion, N – Nährstoff.

	Threat and protection			Raunkiaer life form	Short-lived life form	CSR strategy	Moisture behaviour	Ellenberg indicator value					
	RL G	RL SA	§					L	T	K	F	R	N
Graminoids													
<i>Agrostis gigantea</i>	–	–	–	H	–	C	meso-xero	7	5	3	8	7	6
<i>Avenula pubescens</i>	–	–	–	H	–	C	meso-xero	5	×	3	3	×	4
<i>Bothriochloa ischoemum</i>	3	V	–	H	–	CSR	xero	9	7	6	3	8	3
<i>Brachypodium pinnatum</i>	–	–	–	G, H	–	CS	meso-xero	6	5	5	4	7	4
<i>Briza media</i>	–	3	–	H	–	CSR	meso-xero	8	×	3	×	×	2
<i>Bromus erectus</i>	–	–	–	H	–	CS	×	8	5	2	3	8	3
<i>Carex caryophyllea</i>	V	–	–	G, H	–	CSR	meso-xero	8	×	3	4	×	2
<i>Carex humilis</i>	V	V	–	H	–	CSR	×	7	6	5	2	8	3
<i>Dactylis glomerata</i>	–	–	–	H	–	C	meso-xero	7	×	3	5	×	6
<i>Festuca csikhegyensis</i>	3	–	–	H	–	CS	xero	9	7	4	2	8	1
<i>Festuca rupicola</i>	V	–	–	H	–	CS	meso-xero	9	7	7	3	8	2
<i>Festuca valesiaca</i>	3	V	–	H	–	CSR	xero	8	7	7	2	7	2
<i>Helictochloa pratensis</i>	V	V	–	H	–	CS	meso-xero	7	6	4	3	×	2
<i>Koeleria macrantha</i>	V	–	–	H	–	CS	meso-xero	7	6	7	3	8	2
<i>Koeleria pyramidata</i>	V	–	–	H	–	CS	meso-xero	7	6	4	4	7	2
<i>Poa badensis</i>	2	3	–	H	–	CSR	xero	8	7	4	3	8	1
<i>Sesleria caerulea</i>	–	–	–	H	–	CS	×	7	3	2	4	9	3
<i>Stipa capillata</i>	3	V	§	H	–	CS	xero	8	7	8	2	8	2
<i>Stipa pulcherrima</i>	2	2	§	H	–	CS	xero	9	8	7	1	8	1
Herbs													
<i>Achillea millefolium</i> agg.	V	–	–	H	–	CS	×	7	7	6	3	6	2
<i>Adonis vernalis</i>	3	3	§	H	–	CSR	meso-xero	7	6	7	3	7	2
<i>Agrimonia eupatoria</i>	–	–	–	H	–	C	meso-xero	7	6	4	4	8	4
<i>Allium lusitanicum</i>	3	3	§	G	–	CSR	xero	9	×	5	2	6	2
<i>Anthericum ramosum</i>	V	3	§	H	–	CSR	meso-xero	7	5	4	3	7	3
<i>Anthyllis vulneraria</i>	–	–	–	H	–	CSR	meso-xero	8	6	3	3	7	2
<i>Arabis hirsuta</i>	V	V	–	H	bien	CSR	meso-xero	7	5	3	4	8	×
<i>Arenaria serpyllifolia</i>	–	–	–	H, T	sum/win	R	xero	8	×	×	4	7	×
<i>Asparagus officinalis</i>	–	–	–	G	–	CS	×	6	6	7	3	×	4
<i>Asperula cynanchica</i>	V	3	–	H	–	CSR	meso-xero	7	×	5	3	8	3
<i>Astragalus danicus</i>	3	3	–	H	–	CSR	meso-xero	8	7	7	3	9	2
<i>Bupleurum falcatum</i>	V	–	–	H	–	CSR	meso-xero	6	6	6	3	9	3
<i>Campanula rotundifolia</i>	–	–	–	H	–	CSR	meso-xero	7	5	×	×	×	2
<i>Carlina acaulis</i> subsp. <i>simplex</i>	V	3	§	H	–	CSR	meso-xero	9	×	4	4	×	2
<i>Carlina vulgaris</i>	–	–	–	H, T	bien	CSR	meso-xero	7	5	3	4	7	3
<i>Centaurea scabiosa</i>	–	–	–	H	–	C	meso-xero	7	×	3	3	8	4
<i>Centaurea stoebe</i>	–	–	–	H, T	bien	CSR	xero	8	7	6	2	8	3
<i>Cerastium pumilum</i> s. str.	–	–	–	T	win	SR	xero	8	7	4	2	8	2
<i>Cerastium semidecandrum</i>	–	–	–	T	win	R	xero	8	6	3	3	6	×
<i>Cirsium acaulon</i>	V	V	–	H	–	CSR	meso-xero	9	5	4	3	8	2
<i>Cuscuta epithymum</i>	3	3	–	T	sum	-	×	×	×	5	×	×	2
<i>Daucus carota</i>	–	–	–	H	–	CR	meso-xero	8	6	5	4	×	4
<i>Draba verna</i>	–	–	–	T	win	SR	xero	8	6	3	×	×	2
<i>Echium vulgare</i>	–	–	–	H	bien	CR	xero	9	6	3	4	8	4
<i>Eryngium campestre</i>	V	–	–	H	–	CS	×	9	7	5	3	8	3
<i>Euphorbia cyparissias</i>	–	–	–	H	–	CSR	×	8	×	4	3	×	3
<i>Falcaria vulgaris</i>	–	–	–	H	–	CS	xero	7	7	6	3	9	×
<i>Filipendula vulgaris</i>	3	V	–	H	–	CSR	meso-xero	7	6	5	3	8	2
<i>Fragaria viridis</i>	–	–	–	H	–	CSR	meso-xero	7	5	5	3	8	3
<i>Galatella linosyris</i>	3	3	–	H	–	CSR	xero	8	7	5	2	8	2
<i>Galium glaucum</i>	V	V	–	H	–	CSR	xero	8	7	6	2	9	2
<i>Galium verum</i>	–	–	–	H	–	CS	meso-xero	7	6	×	4	7	3
<i>Globularia bisnagarica</i>	3	3	§	H	–	CSR	xero	8	6	5	2	9	2
<i>Helianthemum canum</i>	3	3	§	C	–	CS	xero	8	7	4	2	9	1
<i>Hieracium pilosella</i>	–	–	–	H	–	CSR	meso-xero	7	×	3	4	×	2
<i>Hippocrepis comosa</i>	V	V	–	C, H	–	CSR	×	7	5	2	3	7	2
<i>Holosteum umbellatum</i>	–	–	–	T	win	SR	xero	8	6	5	3	×	2
<i>Hornungia petraea</i>	2	3	–	T	win	SR	xero	8	7	2	2	9	1
<i>Hypericum elegans</i>	2	1	–	H	–	CS	xero	7	7	6	3	9	2
<i>Hypericum perforatum</i>	–	–	–	H	–	C	meso-xero	7	6	5	4	6	4
<i>Inula hirta</i>	3	3	–	H	–	CS	xero	7	6	6	3	8	3
<i>Linum catharticum</i>	–	V	–	T	sum	SR	meso-xero	7	×	3	×	7	2
<i>Lotus corniculatus</i>	–	–	–	H	–	CSR	meso-xero	7	×	3	4	7	3
<i>Medicago falcata</i>	–	–	–	H	–	CS	×	8	6	7	3	9	3
<i>Medicago lupulina</i>	–	–	–	H	–	CSR	meso-xero	7	5	×	4	8	×
<i>Microthlaspi perfoliatum</i>	–	–	–	T	win	SR	xero	8	6	5	4	8	2
<i>Ononis spinosa</i> agg.	–	–	–	C, H	–	CS	meso-xero	8	6	5	4	7	3
<i>Orchis purpurea</i>	V	3	§	G	–	CSR	meso-xero	5	7	4	4	8	3
<i>Peucedanum cervaria</i>	V	3	–	H	–	CS	×	7	6	4	3	7	3
<i>Pimpinella saxifraga</i>	–	–	–	H	–	CS	meso-xero	7	×	5	3	×	2
<i>Plantago lanceolata</i>	–	–	–	H	–	CSR	meso-xero	6	×	3	×	×	×
<i>Plantago media</i>	–	–	–	H	–	CSR	meso-xero	7	×	7	4	7	3
<i>Potentilla heptaphylla</i>	V	–	–	H	–	CSR	meso-xero	7	5	4	3	9	2
<i>Potentilla incana</i>	V	–	–	H	–	S	xero	9	7	6	1	8	1
<i>Potentilla verna</i>	–	–	–	H	–	CSR	meso-xero	8	6	4	3	7	2
<i>Prunella grandiflora</i>	V	3	–	H	–	CSR	meso-xero	7	×	5	3	8	3
<i>Pulsatilla vulgaris</i>	3	2	§	H	–	CSR	meso-xero	7	6	5	2	7	2
<i>Reseda lutea</i>	–	–	–	H	bien	CSR	xero	7	6	3	3	8	5
<i>Salvia pratensis</i>	V	–	–	H	–	CSR	×	8	6	4	3	8	4
<i>Sanguisorba minor</i>	–	–	–	H	–	CSR	meso-xero	7	6	5	3	8	2
<i>Scabiosa canescens</i>	3	3	–	H	–	CSR	xero	7	7	6	3	8	3
<i>Scabiosa ochroleuca</i>	3	–	–	H	–	CSR	meso-xero	8	5	2	3	8	3
<i>Securigera varia</i>	–	–	–	H	–	C	meso-xero	7	6	5	4	9	3
<i>Seseli hippomarathrum</i>	2	3	–	H	–	CS	xero	9	8	6	2	9	1
<i>Silene latifolia</i>	–	–	–	H	–	C	meso-xero	8	6	×	4	×	7
<i>Stachys recta</i>	V	V	–	H	–	CSR	xero	7	6	4	3	9	2
<i>Taraxacum</i> sect. <i>Erythrosperma</i>	–	–	–	H	–	CSR	×	8	6	5	3	7	2
<i>Teucrium chamaedrys</i>	–	–	–	C	–	CSR	xero	7	6	4	2	8	1
<i>Teucrium montanum</i>	V	–	–	C	–	CSR	xero	8	5	4	1	9	1
<i>Thesium linophyllum</i>	3	3	–	G	–	CSR	meso-xero	8	7	5	2	8	1
<i>Thymus praecox</i>	–	3	–	C, H	–	CSR	×	8	6	5	3	8	1
<i>Trifolium pratense</i>	–	–	–	H	–	C	meso-xero	7	×	3	5	×	×
<i>Veronica praecox</i>	V	3	–	T	win	SR	xero	8	8	5	2	8	1
<i>Veronica spicata</i>	3	3	§	H	–	CSR	meso-xero	7	7	6	3	7	2
<i>Vincetoxicum hirundinaria</i>	–	–	–	H	–	CS	×	6	5	5	3	7	3
<i>Viola hirta</i>	–	–	–	H	–	CSR	meso-xero	6	5	5	3	8	3
<i>Viola rupestris</i>	2	3	–	H	–	CSR	meso-xero	6	5	7	3	8	2
Woody plants													
<i>Cornus sanguinea</i> juv.	–	–	–	N	–	C	×	7	5	4	5	7	×
<i>Prunus spinosa</i> juv.	–	–	–	N	–	C	×	7	5	5	4	7	×
<i>Rosa canina</i> juv.	–	–	–	N	–	C	×	8	5	3	4	×	×
<i>Rosa elliptica</i> juv.	3	–	–	N	–	C	×	8	6	4	3	8	3
<i>Rosa rubiginosa</i> juv.	–	–	–	N	–	C	×	7	6	2	3	8	3

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Supplement E3. Constant vascular plant species or species that are too rare for assessing their change. Frequencies (constancies) in percent and mean percent cover values in uppercase. All comparisons shown are not significant (*n.s.*) at $p > 0.1$.

Anhang E3. Konstante Gefäßpflanzenarten oder Arten, die zu selten sind, um ihre Veränderung zu bemessen. Prozentstetigkeiten und mittlere Prozentdeckungen (hochgestellt). Alle gezeigten Vergleiche sind nicht signifikant (*n.s.*) bei $p > 0,1$.

	<i>Koe</i> (<i>n</i> = 6)			<i>Ses</i> (<i>n</i> = 12)			<i>Car</i> (<i>n</i> = 17)			<i>Sti</i> (<i>n</i> = 11)			<i>all</i> (<i>n</i> = 46)		
	1995	2019		1995	2019		1995	2019		1995	2019		1995	2019	
Graminoids															
<i>Agrostis gigantea</i>	17 ³	0 ⁻	<i>n.s.</i>	—	—		—	—		—	—		2 ³	0 ⁻	<i>n.s.</i>
<i>Bothriochloa ischoeum</i>	—	—		—	—		18 ³	12 ³	<i>n.s.</i>	18 ⁶	27 ³	<i>n.s.</i>	11 ⁴	11 ³	<i>n.s.</i>
<i>Briza media</i>	100 ¹⁰	67 ⁷	<i>n.s.</i>	—	—		18 ⁸	12 ³	<i>n.s.</i>	9 ³	9 ³	<i>n.s.</i>	22 ⁸	15 ⁵	<i>n.s.</i>
<i>Dactylis glomerata</i>	—	—		—	—		6 ^{0.5}	0 ⁻	<i>n.s.</i>	—	—		2 ^{0.5}	0 ⁻	<i>n.s.</i>
<i>Festuca valesiaca</i>	—	—		—	—		6 ³	0 ⁻	<i>n.s.</i>	—	—		2 ³	0 ⁻	<i>n.s.</i>
<i>Avenula pubescens</i>	50 ³	0 ⁻	<i>n.s.</i>	—	—		—	—		—	—		7 ³	0 ⁻	<i>n.s.</i>
<i>Poa badensis</i>	0 ⁻	17 ³	<i>n.s.</i>	0 ⁻	8 ³	<i>n.s.</i>	—	—		—	—		0 ⁻	4 ³	<i>n.s.</i>
<i>Stipa pulcherrima</i>	—	—		0 ⁻	17 ¹	<i>n.s.</i>	0 ⁻	6 ^{0.5}	<i>n.s.</i>	—	—		0 ⁻	7 ¹	<i>n.s.</i>
Herbs															
<i>Achillea millefolium</i> agg.	67 ³	17 ³	<i>n.s.</i>	—	—		18 ³	24 ¹	<i>n.s.</i>	—	—		15 ³	11 ¹	<i>n.s.</i>
<i>Agrimonia eupatoria</i>	0 ⁻	33 ¹	<i>n.s.</i>	—	—		6 ³	0 ⁻	<i>n.s.</i>	—	—		2 ³	4 ¹	<i>n.s.</i>
<i>Allium lusitanicum</i>	—	—		8 ³	0 ⁻	<i>n.s.</i>	—	—		—	—		2 ³	0 ⁻	<i>n.s.</i>
<i>Anthericum ramosum</i>	—	—		25 ⁵	33 ⁴	<i>n.s.</i>	29 ²	29 ¹	<i>n.s.</i>	0 ⁻	9 ^{0.1}	<i>n.s.</i>	17 ³	22 ²	<i>n.s.</i>
<i>Arabis hirsuta</i>	—	—		—	—		24 ²	35 ^{0.2}	<i>n.s.</i>	9 ³	18 ^{0.1}	<i>n.s.</i>	11 ²	17 ^{0.2}	<i>n.s.</i>
<i>Arenaria serpyllifolia</i>	—	—		—	—		—	—		18 ³	0 ⁻	<i>n.s.</i>	4 ³	0 ⁻	<i>n.s.</i>
<i>Asparagus officinalis</i>	—	—		—	—		6 ³	0 ⁻	<i>n.s.</i>	0 ⁻	9 ^{0.1}	<i>n.s.</i>	2 ³	2 ^{0.1}	<i>n.s.</i>
<i>Astragalus danicus</i>	17 ³	50 ²⁰	<i>n.s.</i>	—	—		—	—		—	—		2 ³	7 ²⁰	<i>n.s.</i>
<i>Bupleurum falcatum</i>	—	—		—	—		18 ⁴	12 ^{0.3}	<i>n.s.</i>	—	—		7 ⁴	4 ^{0.3}	<i>n.s.</i>
<i>Campanula rotundifolia</i>	33 ²	0 ⁻	<i>n.s.</i>	—	—		—	—		—	—		4 ²	0 ⁻	<i>n.s.</i>
<i>Carlina acaulis</i>	17 ³	0 ⁻	<i>n.s.</i>	8 ^{0.5}	0 ⁻	<i>n.s.</i>	—	—		—	—		4 ²	0 ⁻	<i>n.s.</i>
<i>Carlina vulgaris</i>	—	—		—	—		12 ²	0 ⁻	<i>n.s.</i>	—	—		4 ²	0 ⁻	<i>n.s.</i>
<i>Centaurea scabiosa</i>	—	—		—	—		18 ⁴	18 ^{0.9}	<i>n.s.</i>	—	—		7 ⁴	7 ^{0.9}	<i>n.s.</i>
<i>Cirsium acaulon</i>	50 ⁵	50 ⁵	<i>n.s.</i>	17 ⁶	25 ¹	<i>n.s.</i>	18 ³	12 ^{0.1}	<i>n.s.</i>	—	—		17 ⁴	17 ²	<i>n.s.</i>
<i>Daucus carota</i>	17 ³	0 ⁻	<i>n.s.</i>	—	—		—	—		—	—		2 ³	0 ⁻	<i>n.s.</i>
<i>Echium vulgare</i>	0 ⁻	17 ^{0.1}	<i>n.s.</i>	—	—		0 ⁻	6 ³	<i>n.s.</i>	—	—		0 ⁻	4 ¹	<i>n.s.</i>
<i>Eryngium campestre</i>	—	—		—	—		24 ⁹	6 ³	<i>n.s.</i>	0 ⁻	9 ³	<i>n.s.</i>	9 ⁹	4 ³	<i>n.s.</i>
<i>Falcaria vulgaris</i>	—	—		—	—		0 ⁻	6 ^{0.1}	<i>n.s.</i>	—	—		0 ⁻	2 ^{0.1}	<i>n.s.</i>
<i>Filipendula vulgaris</i>	—	—		—	—		0 ⁻	6 ^{0.1}	<i>n.s.</i>	0 ⁻	18 ^{0.5}	<i>n.s.</i>	0 ⁻	7 ^{0.4}	<i>n.s.</i>
<i>Fragaria viridis</i>	17 ³	17 ^{0.5}	<i>n.s.</i>	—	—		6 ¹⁰	0 ⁻	<i>n.s.</i>	—	—		4 ⁶	2 ^{0.5}	<i>n.s.</i>
<i>Galatella linosyris</i>	—	—		8 ^{0.5}	33 ¹	<i>n.s.</i>	41 ⁶	35 ²	<i>n.s.</i>	—	—		17 ⁵	22 ²	<i>n.s.</i>
<i>Galium glaucum</i>	—	—		—	—		6 ³	0 ⁻	<i>n.s.</i>	—	—		2 ³	0 ⁻	<i>n.s.</i>
<i>Galium verum</i>	—	—		—	—		24 ³	29 ²	<i>n.s.</i>	0 ⁻	9 ³	<i>n.s.</i>	9 ³	13 ²	<i>n.s.</i>
<i>Globularia bisnagarica</i>	—	—		—	—		—	—		0 ⁻	9 ^{0.1}	<i>n.s.</i>	0 ⁻	2 ^{0.1}	<i>n.s.</i>
<i>Hieracium pilosella</i>	33 ³	50 ¹	<i>n.s.</i>	33 ³	33 ²	<i>n.s.</i>	24 ³	0 ⁻	<i>n.s.</i>	—	—		22 ³	15 ¹	<i>n.s.</i>
<i>Holosteum umbellatum</i>	—	—		—	—		—	—		0 ⁻	27 ¹	<i>n.s.</i>	0 ⁻	7 ¹	<i>n.s.</i>
<i>Hypericum elegans</i>	—	—		—	—		6 ³	0 ⁻	<i>n.s.</i>	—	—		2 ³	0 ⁻	<i>n.s.</i>
<i>Hypericum perforatum</i>	—	—		—	—		6 ³	0 ⁻	<i>n.s.</i>	—	—		2 ³	0 ⁻	<i>n.s.</i>
<i>Inula hirta</i>	—	—		—	—		12 ²	18 ⁴	<i>n.s.</i>	—	—		4 ²	7 ⁴	<i>n.s.</i>
<i>Medicago falcata</i>	17 ³	0 ⁻	<i>n.s.</i>	—	—		6 ³	0 ⁻	<i>n.s.</i>	—	—		4 ³	0 ⁻	<i>n.s.</i>
<i>Medicago lupulina</i>	17 ³	0 ⁻	<i>n.s.</i>	—	—		—	—		—	—		2 ³	0 ⁻	<i>n.s.</i>
<i>Ononis spinosa</i> agg.	—	—		—	—		0 ⁻	6 ^{0.5}	<i>n.s.</i>	—	—		0 ⁻	2 ^{0.5}	<i>n.s.</i>
<i>Orchis purpurea</i>	0 ⁻	17 ^{0.1}	<i>n.s.</i>	—	—		6 ³	0 ⁻	<i>n.s.</i>	0 ⁻	9 ^{0.5}	<i>n.s.</i>	2 ³	4 ^{0.3}	<i>n.s.</i>
<i>Peucedanum cervaria</i>	—	—		8 ^{0.5}	17 ^{0.3}	<i>n.s.</i>	47 ⁶	47 ⁵	<i>n.s.</i>	9 ³	27 ¹⁹	<i>n.s.</i>	22 ⁵	28 ⁸	<i>n.s.</i>
<i>Plantago lanceolata</i>	17 ^{0.5}	0 ⁻	<i>n.s.</i>	—	—		—	—		—	—		2 ^{0.5}	0 ⁻	<i>n.s.</i>
<i>Plantago media</i>	67 ¹¹	67 ²	<i>n.s.</i>	8 ³	0 ⁻	<i>n.s.</i>	6 ³	0 ⁻	<i>n.s.</i>	—	—		13 ⁸	9 ²	<i>n.s.</i>
<i>Prunella grandiflora</i>	—	—		—	—		29 ¹⁷	18 ³	<i>n.s.</i>	—	—		11 ¹⁷	7 ³	<i>n.s.</i>
<i>Pulsatilla vulgaris</i>	0 ⁻	17 ^{0.1}	<i>n.s.</i>	—	—		—	—		—	—		0 ⁻	2 ^{0.1}	<i>n.s.</i>
<i>Reseda lutea</i>	—	—		—	—		0 ⁻	6 ^{0.5}	<i>n.s.</i>	0 ⁻	9 ^{0.1}	<i>n.s.</i>	0 ⁻	4 ^{0.3}	<i>n.s.</i>
<i>Scabiosa canescens</i>	83 ¹⁶	50 ¹⁷	<i>n.s.</i>	17 ³	0 ⁻	<i>n.s.</i>	29 ⁶	47 ⁵	<i>n.s.</i>	9 ^{0.5}	0 ⁻	<i>n.s.</i>	28 ⁹	24 ⁸	<i>n.s.</i>
<i>Scabiosa ochroleuca</i>	67 ⁶	50 ¹⁴	<i>n.s.</i>	—	—		24 ²	24 ³	<i>n.s.</i>	—	—		17 ⁴	15 ⁷	<i>n.s.</i>
<i>Securigera varia</i>	0 ⁻	50 ²⁶	<i>n.s.</i>	—	—		6 ¹⁰	0 ⁻	<i>n.s.</i>	—	—		2 ¹⁰	7 ²⁶	<i>n.s.</i>
<i>Silene latifolia</i>	—	—		—	—		0 ⁻	60 ^{.1}	<i>n.s.</i>	—	—		0 ⁻	2 ^{0.1}	<i>n.s.</i>
<i>Stachys recta</i>	—	—		—	—		12 ³	18 ¹	<i>n.s.</i>	9 ³	0 ⁻	<i>n.s.</i>	7 ³	7 ¹	<i>n.s.</i>
<i>Thesium linophyllum</i>	—	—		8 ³	33 ¹⁰	<i>n.s.</i>	41 ³	35 ²	<i>n.s.</i>	—	—		17 ³	22 ⁵	<i>n.s.</i>
<i>Trifolium pratense</i>	0 ⁻	17 ^{0.5}	<i>n.s.</i>	—	—		—	—		—	—		0 ⁻	2 ^{0.5}	<i>n.s.</i>
<i>Veronica praecox</i>	—	—		—	—		—	—		9 ^{0.5}	0 ⁻	<i>n.s.</i>	2 ^{0.5}	0 ⁻	<i>n.s.</i>
<i>Veronica spicata</i>	33 ²	17 ^{0.1}	<i>n.s.</i>	—	—		—	—		—	—		4 ²	2 ^{0.1}	<i>n.s.</i>
<i>Vincetoxicum hirundinaria</i>	0 ⁻	17 ^{0.1}	<i>n.s.</i>	—	—		6 ³	29 ^{0.4}	<i>n.s.</i>	0 ⁻	9 ^{0.1}	<i>n.s.</i>	2 ³	15 ^{0.3}	<i>n.s.</i>
<i>Viola hirta</i>	—	—		—	—		12 ²	0 ⁻	<i>n.s.</i>	—	—		4 ²	0 ⁻	<i>n.s.</i>
<i>Viola rupestris</i>	17 ³	0 ⁻	<i>n.s.</i>	0 ⁻	8 ^{0.1}	<i>n.s.</i>	6 ³	0 ⁻	<i>n.s.</i>	—	—		4 ³	2 ^{0.1}	<i>n.s.</i>
Woody species															
<i>Cornus sanguinea</i> juv.	0 ⁻	17 ^{0.5}	<i>n.s.</i>	—	—		—	—		—	—		0 ⁻	2 ^{0.5}	<i>n.s.</i>
<i>Rosa canina</i> juv.	—	—		—	—		29 ^{0.5}	6 ³	<i>n.s.</i>	—	—		11 ^{0.5}	2 ³	<i>n.s.</i>
<i>Rosa elliptica</i> juv.	—	—		8 ^{0.5}	0 ⁻	<i>n.s.</i>	18 ¹	0 ⁻	<i>n.s.</i>	—	—		9 ¹	0 ⁻	<i>n.s.</i>
<i>Rosa rubiginosa</i> juv.	0 ⁻	17 ^{0.1}	<i>n.s.</i>	42 ⁵	33 ^{0.9}	<i>n.s.</i>	35 ⁵	18 ²	<i>n.s.</i>	—	—		28 ⁴	24 ¹	<i>n.s.</i>

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