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Little vegetation change during two decades in a dry grassland complex in the Biosphere Reserve Schorfheide-Chorin (NE Germany)

Nur unwesentliche Vegetationsveränderungen in einem Trockenrasenkomplex im Biosphärenreservat Schorfheide-Chorin (Nordost-Brandenburg) nach zwei Jahrzehnten

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Abstract

In many regions of Central Europe, semi-natural grasslands have experienced severe vegetation changes, e.g. compositional change and overall species loss, because of land use changes, atmospheric nitrogen input and also climate change. Here we analysed the vegetation change in a dry grassland complex (Gabower Hänge) in the Biosphere Reserve Schorfheide-Chorin (NE Brandenburg, Germany), one of the driest regions of the country. We resampled four 10 m² plots of each of four typical alliances (*Festucion valesiacae*, *Koelerion glaucae*, *Armerion elongatae*, *Arrhenatherion elatioris*) about 20 years after their original sampling with a recovery accuracy of approx. 10 m. The cover of vascular plants, bryophytes and lichens was recorded in both samplings. The overall compositional change was analysed with a detrended correpondence analysis (DCA). To interpret this change, we calculated unweighted mean Ellenberg indicator values for old and new plots. Furthermore we tested differences in constancy of individual species between old and new plots as well as differences in species richness, cover of herb and cryptogam layer, ecological indicator values and unweighted proportion of species groups (vascular plants, bryophytes, lichens), floristic status (native or not), life forms, CSR-strategy types and Red List species. The results of the ordination indicated no significant vegetation change, but revealed tendencies towards more nutrient-rich conditions. Ellenberg indicator values for nutrients and soil reaction were significantly correlated with the axes of the ordination. There were 28 species exclusively found in the new plots and 45 species of the old plots missing. While no species decreased significantly, there were seven species that increased significantly. Mean species richness was significantly increased in the new plots. There were no significant differences in mean Ellenberg indicator values. Proportions of vascular plants, neophytes, hemicryptophytes and CS-strategists decreased. We conclude that overall vegetation changes are small, indicating that the dry grassland complex at the Gabower Hänge is still in a good state and of high conservation value. This relative stability over time compared to the situation in many other dry grasslands throughout temperate Europe is likely attributable to low nitrogen deposition and the dryness of the local climate. However, the detected tendency towards more nutrient-rich conditions should be taken into account in future management.

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Keywords: *Armerion elongatae*, *Arrhenatherion elatioris*, CSR-strategy, Ellenberg indicator value, *Festucion valesiacae*, *Koelerion glaucae*, re-visitation study, semi-permanent plot, species richness, vegetation dynamics

Erweiterte deutsche Zusammenfassung am Ende des Artikels

1. Introduction

Most of the grasslands in Central Europe are semi-natural grasslands, which have developed from natural forest vegetation by low-intensity land use since the beginning of the Neolithic period (POSCHLOD et al. 2009). Today they are an essential part of the cultural landscape of Europe (DIERSCHKE & BRIEMLE 2002, DENGLER et al. 2014). In Central Europe such semi-natural grasslands contribute substantially to the biodiversity (DENGLER et al. 2014) and can reach exceptionally high species richness at small spatial scales (WILSON et al. 2012). Among them, the highest biodiversity is typically found in dry grasslands (HOBOHM 1998, JANIŠOVÁ et al. 2011, CHYTRÝ et al. 2015). Nowadays dry grasslands are threatened by agricultural intensification, land abandonment and atmospheric nitrogen input (DIERSCHKE & BRIEMLE 2002, JANIŠOVÁ et al. 2011, DENGLER et al. 2014), which makes them one of the most endangered habitats in Europe, whose conservation is of high priority (KORNECK et al. 1998, JANIŠOVÁ et al. 2011, EUROPEAN COMMISSION 2013).

Detecting vegetation change in grasslands to gain information on their condition is thus an important task. Three basic ways to analyse vegetation change have been described in the literature: (1) compare old and new records from permanent plots, (2) re-visitation studies: revisit historical phytosociological plots and compare old and new records and (3) compare large sets of old and new phytosociological records from the same area but different plots (CHYTRÝ et al. 2014). The advantage of re-visitation studies is that the phytosociological plots are established to describe vegetation types and not to document possible vegetation change. Thus there is no *a priori* expectation of future vegetation stability or change (CHYTRÝ et al. 2014). Re-visitation studies were shown to be robust to spatial heterogeneity within a stand of present vegetation (ROSS et al. 2010). Even when the original plot cannot be exactly recovered, no seeming historical change in vegetation is created, nor is the detection of an actual historic change precluded (ROSS et al. 2010, KOPECKÝ & MACEK 2015). Re-visitation studies are thus considered a reliable method to study vegetation change over decades (KOPECKÝ & MACEK 2015).

Productive semi-natural grassland sites are often threatened by intensification of land use. This includes application of artificial fertiliser and increased cutting frequency on meadows as well as increased stocking rate and resowing with agronomically valuable species on pastures (DIERSCHKE & BRIEMLE 2002, DENGLER et al. 2014). In contrast, semi-natural grasslands in less productive sites are prone to natural succession to shrublands or forests because of abandonment (DENGLER et al. 2014, TÄLLE et al. 2016). Another negative influence on semi-natural grasslands was found in atmospheric nitrogen deposition, which causes a loss of species richness and functional diversity (DUPRÈ et al. 2010, DIEKMANN et al. 2014). Using large vegetation databases, JANDT et al. (2011) found that many species in semi-dry basiphilous grasslands in Germany had consistent positive or negative developments over a 75-year period (1927–2003). Species with positive temporal trends had higher Ellenberg indicator values for moisture and nutrients compared to those with negative trends. This is likely to result from nitrogen deposition and land use changes (JANDT et al. 2011). Moreover, competitive species became more abundant. STEVENS et al. (2016) showed that

species composition of both acidic and calcareous grasslands has changed. WESCHE et al. (2012) reported a strong overall trend of decline in plot-scale plant species richness in Central European grasslands.

In our study we use a re-visitation approach to assess vegetation changes in a dry grassland complex, the Gabower Hänge in the Biosphere Reserve Schorfheide-Chorin. Due to the relatively dry, subcontinental climate, a large variety of different types of dry grasslands is widespread in the area (DENGLER 1994b). We took the opportunity of a detailed monograph of the Gabower Hänge (KRATZERT & DENGLER 1999) to resample some of the vegetation plots from the mid-1990s in 2015. We assumed that atmospheric nitrogen deposition as well as reduced land use has changed the species composition (see DIEKMANN et al. 2014). Specifically, we expected an increase in competitive generalist species and a loss of weak competitors (see JANDT et al. 2011), which in total should have led to a decrease in plot-scale species richness. Along with this we expected that the average Ellenberg indicator value for nutrients has increased during the two decades and that the average light indicator value has decreased because of a denser herb layer due to enhanced plant growth.

2. Methods

2.1 Study sites

Our study was conducted in the dry grassland complex between the villages Gabow and Altglietzen ("Gabower Hänge") in NE Brandenburg, Germany (approx. 80 ha; 52.82° N, 14.08° E, 10–55 m a.s.l.; Fig. 1). The Gabower Hänge dry grassland complex is amongst the most prominent and largest areas of

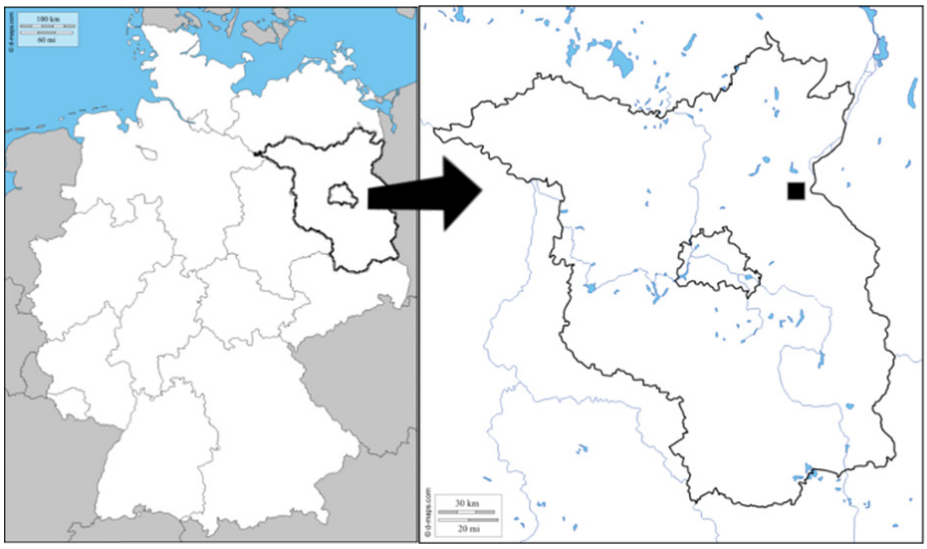


Fig. 1. Location of the study site "Gabower Hänge" in northeast Germany. Base map obtained from http://d-maps.com/carte.php?num_car=4690&lang=de and http://d-maps.com/carte.php?&num_car=6186&lang=de.

Abb. 1. Lage des Untersuchungsgebietes „Gabower Hänge" im Nordosten Deutschlands. Kartengrundlage entnommen aus http://d-maps.com/carte.php?num_car=4690&lang=de und http://d-maps.com/carte.php?&num_car=6186&lang=de.



Fig. 2. Landscape of the Gabower Hänge (Photo: J. Dengler, August 2015).

Abb. 2. Landschaft der Gabower Hänge (Foto: J. Dengler, August 2015).

dry grasslands in the Biosphere Reserve Schorfheide-Chorin (LUGV 2015, Fig. 2). This UNESCO Biosphere Reserve of 1,300 km² size was established in 1990 in the state of Brandenburg (NE Germany) in one of the least densely populated regions of the country (23 inhabitants km^{-2}). Schorfheide-Chorin is a young glacial landscape with many wetlands and extensive forests, but also a diverse agricultural landscape used at relatively low intensities. The Gabower Hänge form the southeastern edge of the so-called "Oderinsel" (Neuenhager Sporn) and decline steeply towards the Oderbruch (KRATZERT & DENGLER 1999, DENGLER et al. 2004). Geomorphologically the "Oderinsel" is a separate lobe of the main end moraine of the penultimate ice advance of the Weichsel glaciation (LUTZE 2014), surrounded by the "Oderbruch", the alluvial plain of the river Oder.

The site is located in the transition zone between the oceanic climate of northwest Germany and the subcontinental climate of Poland, exhibiting an annual temperature range of more than 19 K (KRATZERT & DENGLER 1999). With a mean annual precipitation of about or even below 500 mm and less than 300 mm during April to September, the Oderinsel belongs to the driest parts of Germany (KRATZERT & DENGLER 1999, KAPPAS et al. 2003). The Gabower Hänge are characterised by eroded summits and slopes with mainly sandy, calcareous substrates. However, local soils can be more acidic or loamy/clayey. The main soil types under grasslands according to AD-HOC-AG BODEN (2005) are pararendzina and regosol (KRATZERT & DENGLER 1999).

The study site is protected as Natura 2000 site DE 3150–303 "Gabower Hangkante". Dry grassland types, ruderal communities, shrublands and afforestations of *Pinus*, *Populus* and *Robinia* complete the habitat mosaic (see detailed vegetation map by KRATZERT & DENGLER 1999). During the last decades, low-intensity sheep grazing was the only management measure (LUGV 2015). Pasturing by tended sheep was practised for several days three times a year, and scrub clearance was performed from funds of the biosphere reserve in yearly changing intensity and extension. After a couple of years without any agricultural use in the 1990s, the pasturing was resumed and has been continued until today (LUGV 2015).

2.2 Vegetation sampling

To assess possible vegetation changes of the Gabower Hänge, we selected the four alliances of the xerothermic herbaceous vegetation that are the most widespread in the area (KRATZERT & DENGLER 1999, syntaxonomy according to BERG et al. 2004, habitat types according to EUROPEAN COMMISSION 2013):

- *Koelerion glaucae* Volk 1931 (*Sedo acris-Festucetalia* Tx. 1951 nom. invers. propos.; *Koelerio-Corynephoretea* Klika in Klika & V. Novák 1941): xeric continental grasslands on nutrient-poor, base-rich sands with *Festuca psammophila* and *Koeleria glauca* typically forming the matrix. Corresponds to the priority habitat type **6120 Xeric sand calcareous grasslands*.
- *Armerion elongatae* Pötsch 1962 (*Trifolio arvensis-Festucetalia ovinae* Moravec 1967; *Koelerio-Corynephoretea*): meso-xeric subcontinental grasslands on acidic to neutral, more developed sandy soils, with *Festuca brevipila*, *Agrostis capillaris*, *Carex praecox* and sometimes *Phleum phleoides* forming the matrix. Corresponds partly to the priority habitat type **6120 Xeric sand calcareous grasslands*.
- *Festucion valesiacae* Klika 1931 (*Festucetalia valesiacae* Br.-Bl. & Tx. ex Br.-Bl. 1950; *Festuco-Brometea* Br.-Bl. & Tx. ex Klika & Hadač 1944; Fig. 3): xeric, mostly base-rich continental grasslands, mainly occupying the steep south-facing slopes, with *Stipa capillata* and *Phleum phleoides* forming the matrix. Corresponds to the priority habitat type **6240 Sub-pannonic steppic grasslands*.
- *Arrhenatherion elatioris* W. Koch 1926 (*Arrhenatheretalia elatioris* Tx. 1931; *Molinio-Arrhenatheretea* Tx. 1937): mesic, nutrient-rich grasslands with *Arrhenatherum elatius*, *Dactylis glomerata* and *Festuca rubra* forming the matrix. Corresponds to the habitat type **6510 Lowland hay meadows (Alopecurus pratensis, Sanguisorba officinalis)*.

From each of these target alliances, we selected four plots from the earlier study (DENGLER & KRATZERT 1999) conducted by J. Dengler in 1993 (DENGLER 1994a) and G. Kratzert in 1997 (KRATZERT 1998). We gave preference to plots whose location could be recovered relatively accurately and avoided to select plots of the same alliance that were too close together. Since the old plots were installed before cheap and accurate handheld GPS devices became available, they were marked on a copy of a topographical map at scale 1 : 10 000. The rugged terrain (reflected in the close contour lines), the many decaying steps of terraces from former arable fields and the location of tracks and forest patches allowed a relatively accurate recovery. We also used information on aspect and slope inclination of old plots to recover them. While we could not repeat the vegetation sampling at exactly the same location, we estimate that for the chosen 16 old plots, a maximum error of 10 m occurred. To allow future resampling with higher accuracy, we recorded the position of the new plots by taking the coordinates of their centres with a handheld GPS.

Both in the old and the new survey, square plots of 10 m² (3.16 m × 3.16 m) were used. Slope inclination and aspect were noted, and soil pH was measured electrochemically for a mixed sample of the uppermost 10 cm. All vascular plants as well as terricolous bryophytes and lichens were recorded with shoot presence. In the old sampling, the modified Braun-Blanquet scale by WILMANNS (1993) was used. For every class of the Braun-Blanquet scale, we calculated mean cover values in percent. For the new sampling, we estimated the cover directly in percent, accepting a minimum value of 0.001% per species. The new vegetation survey was conducted from 24 to 25 August 2015, while the old data were mainly recorded from May to October 1993, plus two plots in 1997.

The nomenclature of taxa follows JÄGER (2011) for vascular plants, HILL et al. (2006) for bryophytes and WIRTH et al. (2013) for lichens. We simplified the data for the analyses by merging *Poa angustifolia* with *P. pratensis* agg. and *Tragopogon dubius* and *T. pratensis* with *T.* spec. We excluded



Fig. 3. Stand of the *Potentillo arenariae-Stipetum capillatae* (*Festucion valesiacae*), which covers vast areas of the south-facing slopes of the Gabower Hänge with *Stipa capillata*, *Scabiosa canescens, Hieracium umbellatum* and *Dianthus carthusianorum* (Photo: J. Dengler, August 2015).

Abb. 3. Bestand des *Potentillo arenariae-Stipetum capillatae* (*Festucion valesiacae*), der die Südhänge der Gabower Hänge großflächig mit *Stipa capillata*, *Scabiosa canescens*, *Hieracium umbellatum* und *Dianthus carthusianorum* bedeckt (Foto: J. Dengler, August 2015).

Bryum spec., *Cladonia* spec. and "unidentified species (hairy leaf)" in plot T08 from the analysis. The vegetation table (Supplement E1) shows all taxa prior to the mentioned simplifications. In the following text "species" means "taxon" including also subspecies.

We included information on ecological indicator values (EIVs) of all species and life forms of vascular plants according to ELLENBERG et al. (2001), but only took the dominating life form into account, i.e. the first letter. Classifications of the Red List Germany refer to BFN (1996), Red List Brandenburg to LUGV (2006) (vascular plants), LUDWIG et al. (1996) (bryophytes) and OTTE & RÄTZEL (1998) (lichens). We did not consider species indicated with "V" (*Vorwarnstufe* ≈ near threatened) as Red List species. We retrieved the floristic status of vascular plants from WISSKIRCHEN & HAEUPLER (1998), while all occurring bryophytes and lichens were considered as native. We simplified the status "archaeophyte/native" to "native". We used CSR strategy types according to GRIME et al. (1988) for vascular plants from FRANK & KLOTZ (1990).

2.3 Statistical analyses

To recognise and assess possible differences between old and new plots qualitatively, we performed a nonmetric multidimensional scaling (NMDS) with the function *metaMDS* and default parameters in the R package *vegan* (OKSANEN et al. 2014). Because of the high stress value (0.16), we then conducted a detrended correspondence analysis (DCA) with the function *decorana*. Since the length of the gradient was more than four standard deviations and the DCA requires unimodal distribution of the species (LEYER & WESCHE 2007), we decided on the DCA as final ordination method. We tested the vegetation change between old and new plots along the first and second axis for significance by testing the scores of the DCA of old and new plots against each other.

To test a possible relationship between vegetation change and EIVs, we calculated unweighted mean ecological indicator values for each plot to avoid overweighing abundant species, e.g. grasses (TÖLGYESI et al. 2014). We used the function *envfit* to fit these to the ordination plot. We first performed a preliminary fit with all mean indicator values and checked for correlation between them. When the Pearson correlation coefficient was 0.8 or higher for pairs of indicator values, we only used the indicator value with higher r^2 in the preliminary fit for the final fit and excluded the other one. We performed 10,000 permutations to calculate a *p*-value and added indicator values that significantly correlated with the axes of the ordination plot.

To find species with significantly increasing or declining numbers, we performed a present-absent analysis with Fisher's exact test for count data. We tested for significant differences between old and new plots in species number, cover, EIVs and unweighted proportion of species groups (vascular plants, bryophytes, lichens), status, life forms, strategy types and Red List species by performing paired *t*-tests after we checked the data distribution visually and did not detect strong violations from the assumption of parametric models.

For all analyses we assumed a level of significance of $\alpha = 0.05$. All analyses were conducted in R (R CORE TEAM 2014).

3. Results

The ordination plot shows the alliances clearly separated from each other (Fig. 4). The mean indicator values for nitrogen and reaction were positively correlated with the axes of the ordination (N: $r^2 = 0.761$, $p < 0.001$, R: $r^2 = 0.753$, $p < 0.001$). We found no significant vegetation changes along the first and second axis of the DCA. Nevertheless, a trend can be assumed from the shifts of the centroids. This is most obvious for the alliance *Armerion elongatae* because the territory occupied in the ordination space by the new plots barely overlaps with that of the old plots. The shift of the centroids occurred towards a similar direction as the indicator values for nitrogen and reaction are pointing, indicating thatthis alliance developed towards more nutrient- and base-rich conditions. The territories occupied in the ordination space of old and new plots of the alliances *Festucion valesiacae* and *Arrhenaterion elatioris* have a large overlap, and the distance between the centroids is smaller, i.e. the vegetation change was small. The *Koelerion glaucae* shows vegetation change along the first axis in the same direction as the two other alliances by a larger distance between centroids and a smaller overlap in the ordination between old and new plots.

Overall, 113 taxa were recorded in the vegetation survey (Supplement E1). In the new plots, we recorded 28 species that were not present in the old plots (Supplement S1). Of those recorded in the old plots, we did not find again 45 species in the new plots (Supplement S1). None of the species decreased significantly, but seven species increased significantly (Table 1).

The new plots had a mean species richness of 26.1 ± 7.0, which was significantly higher than in the old plots, where mean species richness was 22.4 ± 6.1 ($p = 0.047$, Fig. 5). The dry grassland alliances *Armerion elongatae*, *Koelerion glaucae* and *Festucion valesiacae* showed a trend towards higher species richness, whereas the mesic *Arrhenatherion elatioris* tended to have a lower species richness (Fig. 5).

None of the six ecological indicator values of ELLENBERG et al. (2001) showed significant differences between new and old plots, neither did percentage cover of herb or cryptogam layer.

In terms of species groups, old and new plots differed in proportion of vascular plants and bryophytes (Fig. 6A). The new plots had significantly smaller proportions of vascular plants ($p = 0.017$), which was, however, still the largest group with an average coverage of

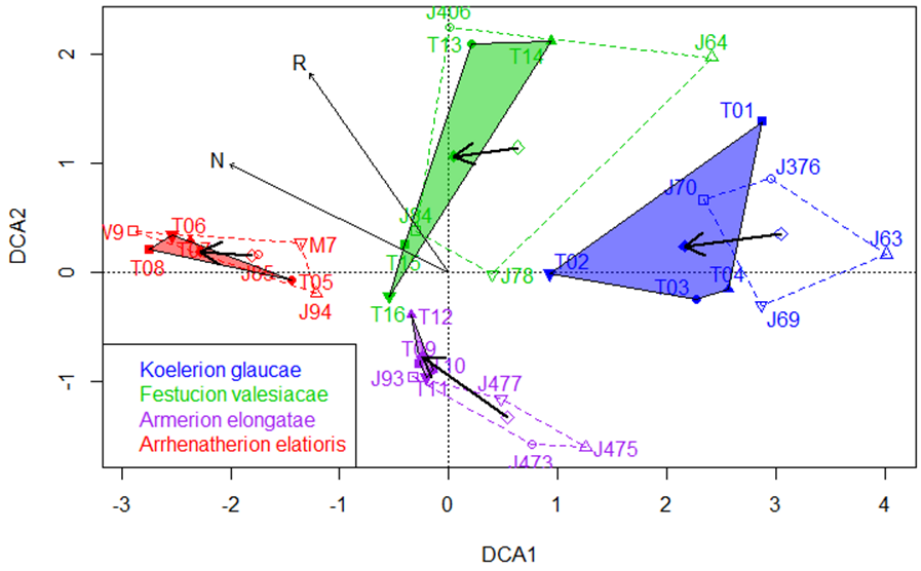


Fig. 4. Ordination (Detrended Correspondence Analysis, DCA) of old and new plots at the Gabower Hänge. Open symbols indicate old plots, filled symbols indicate new plots. Identic shape of symbols indicates which old and new plots of each alliance belong together. Polygons with dashed line indicate old plots, filled polygons new plots. Open diamonds indicate centroids (means) of old plots, filled diamonds centroids of new plots. The thick black arrows that connect the centroids of old and new plots indicate the mean vegetation change of the individual alliance. The thin black arrows indicate the mean fitted ecological indicator values. Only indicator values that were significantly correlated with the axes of the DCA ($p \leq 0.05$) are shown (permutation test with 10,000 repetitions. N: $r^2 = 0.761$, $p < 0.001$; R: $r^2 = 0.753$, $p < 0.001$).

Abb. 4. Ordination (Detrended Correspondence Analysis, DCA) von alten und neuen Vegetationsaufnahmen der Gabower Hänge. Offene Symbole stellen die alten Aufnahmen, gefüllte Symbole die neuen Aufnahmen dar. Die identische Form von Symbolen zeigt an, welche alten und neuen Aufnahmen jedes Verbandes zusammen gehören. Polygone mit gestrichelter Linie zeigen alte Aufnahmen, gefüllte Polygone neue Aufnahmen an. Offene Rauten zeigen die Zentroide (Mittelwerte) der alten Aufnahmen an, gefüllte Rauten die Zentroide der neuen Aufnahmen. Die dicken schwarzen Pfeile, die die Zentroide der alten und neuen Aufnahmen verbinden, repräsentieren die mittlere Vegetationsänderung des jeweiligen Verbandes. Die dünnen schwarzen Pfeile stellen die mittleren angepassten ökologischen Zeigerwerte dar. Nur Zeigerwerte, deren Korrelation mit den Achsen der DCA einen *p*-Wert von 0,05 oder weniger aufwies, sind dargestellt (Permutationstest mit 10.000 Wiederholungen. N: $r^2 = 0{,}761$; $p < 0{,}001$; R: $r^2 = 0{,}753$; $p < 0{,}001$).

88.4 ± 11.5% (old plots) and 81.6 ± 9.9% (new plots), respectively. The average proportion of bryophytes almost doubled from 7.2 ± 4.4% to 14.1 ± 8.6% ($p = 0.005$). The proportion of lichens did not change ($p = 0.940$).

The proportion of indigenous plant species and archaeophytes did not change significantly ($p = 0.091$ and $p = 0.267$), the proportion of neophytes, however, decreased significantly from 2.8 ± 3.7 % to 0.4 ± 1.2 % on average ($p = 0.035$, Fig. 6B).

The number of species listed on the Red List of Germany did not change significantly ($p = 0.348$) and was 3.4 ± 2.2 on average in the new plots. In contrast, the number of species on the Red List of Brandenburg increased significantly from 3.8 ± 3.3 to 5.6 ± 3.7 on aver-

Table 1. Taxa that increased significantly, with absolute constancy in 16 plots.

Tab. 1. Taxa, die signifikant zugenommen haben, mit absoluter Stetigkeit innerhalb der 16 Aufnahmen.

Taxon	Old plots	New plots	*p*-value from Fisher's test
Cladonia furcata	1	8	0.015
Cerastium semidecandrum	3	10	0.029
Bryum argenteum	0	5	0.043
Carex praecox	0	5	0.043
Syntrichia ruralis agg.	1	7	0.037
Tortula cf. lanceola	0	5	0.043
Trifolium arvense	1	7	0.037

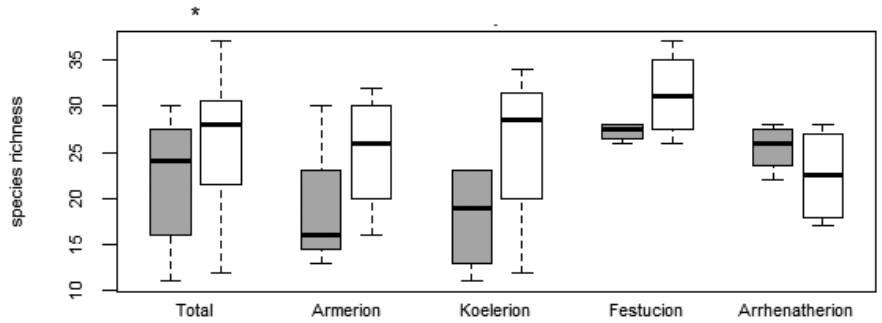


Fig. 5. Species richness of old (grey) and new (white) plots in the four alliances and in total. * indicates $p < 0.05$, "." indicates $p < 0.1$ (paired *t*-test). Whiskers indicate 1.5 × IQR.

Abb. 5. Gesamtartenanzahl und Artenzahl in den vier Verbänden von alten (grau) und neuen (weiß) Aufnahmen. * zeigt $p < 0{,}05$ an, „." zeigt $p < 0{,}1$ an (gepaarter *t*-Test). Die Whisker zeigen 1,5 × IQR an.

age ($p = 0.019$). The number of species in threat categories "1" (≈ CR/critically endangered) and "2" (≈ EN/endangered) did not change significantly ($p = 0.333$ and $p = 0.545$, respectively), while the number of species in threat category "3" (≈ VU/vulnerable) increased significantly from 3.4 ± 2.7 to 5.0 ± 3.3 ($p = 0.034$).

Out of the four examined life forms, only the proportion of hemicryptophytes decreased significantly ($p = 0.004$, Fig. 6C). This group made up the largest share with an average proportion of 54.3 ± 14.8 % in the old plots and 45.4 ± 10.3% in the new plots. The proportions of the clearly less frequent chamaephytes ($p = 0.069$), therophytes ($p = 0.554$) and geophytes ($p = 0.056$) did not change significantly.

When comparing strategy types, we only found differences between the proportions of CS-strategists ($p = 0.025$, Fig. 6D). Their average proportion decreased from 17.6 ± 10.3% in the old plots to 12.6 ± 7.1% in the new plots. The largest share in both old and new plots had CSR-strategists.

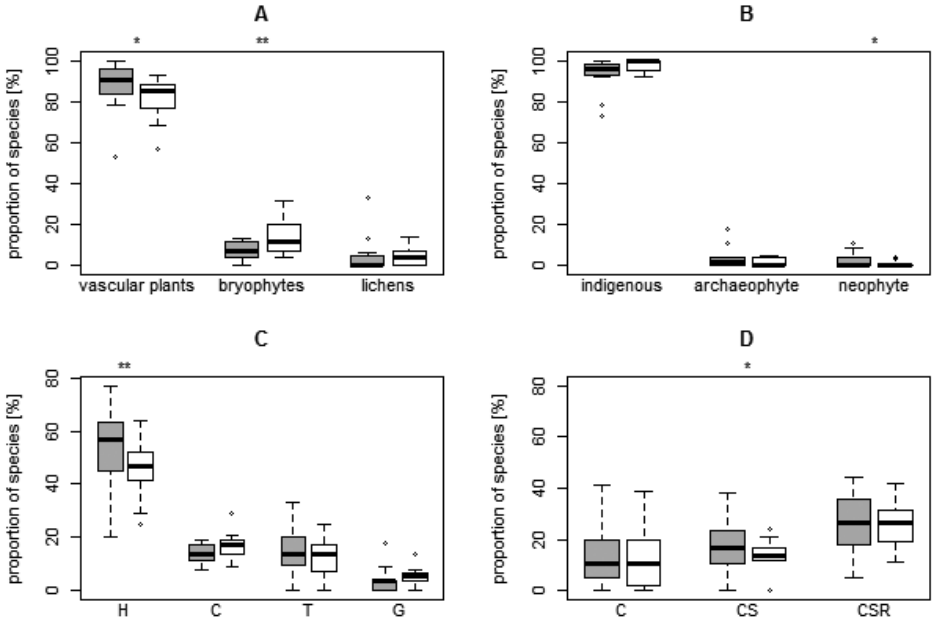


Fig. 6. Comparison of old and new plots concerning A: proportion of species groups in total species number; B: proportion of status in total species number; C: proportions of life forms in total species number; D: proportions of main strategy types according to GRIME (1988) in total species number (strategies with proportions less than 5% are not shown). Grey: old plots. White: new plots. H, hemicryptophytes; C, chamaephytes; T, therophytes; G, geophytes. C, competitors; CS, stress-tolerant competitors; CSR, CSR strategists. * indicates $p < 0.05$, ** indicates $p < 0.01$ (Fisher's exact test for count data). Whiskers indicate 1.5 × IQR.

Abb. 6. Vergleich von alten und neuen Vegetationsaufnahmen hinsichtlich A: Anteile der Artengruppen an der Gesamtartenzahl; B: Anteile der Florenstatus an der Gesamtartenzahl; C: Anteile der Lebensformen an der Gesamtartenzahl; D: Anteile der Hauptstrategietypen nach GRIME (1988) an der Gesamtartenzahl (Strategietypen mit Anteilen von weniger als 5 % sind nicht dargestellt). Grau: alte Aufnahmen. Weiß: neue Aufnahmen. H, Hemikryptophyten; C, Chamaephyten; T, Therophyten; G, Geophyten, C, Konkurrenzstrategen; CS, stress-tolerante Konkurrenzstrategen; CSR, CSR-Strategen. * zeigt $p < 0{,}05$ an, ** zeigt $p < 0{,}01$ an (Exakter Test nach Fisher). Die Whisker zeigen 1,5 × IQR an.

4. Discussion

4.1 Changes and their causes

We did not find significant changes in species composition between old and new plots. However, single alliances showed trends. We consider the tendency of the *Armerion elongatae* towards more nutrient-rich conditions as problematic because these communities are particularly endangered by eutrophication (SCHUBERT et al. 2001).

Aside from these trends, our expectations regarding the EIVs for nutrients were not met since the average EIV for nutrients did not change, as also observed elsewhere (STEVENS et al. 2016). Probably, the study site is only relatively little affected by eutrophication, as nitrogen surplus in the region is low (UMWELTBUNDESAMT 2014). The mean EIV for light did not change significantly either.

Average bryophyte richness per plot increased since both total richness and bryophyte proportion increased. This might be due to better light conditions because of a less dense herb layer. However, because neither cover of herbs or bryophytes nor mean EIV for light has changed significantly, this needs further testing. TÖLGYESI et al. (2016) observed similar changes in their study of vegetation changes in a dry sandy grassland complex in Hungary over 13 years. While their vegetation remained rather stable, an increase of cryptogams and ephemerals indicated that the vegetation became more open. From a conservation perspective, the significantly higher mean species richness is a positive trend. Particularly positive is that the number of Red List species of Brandenburg increased and the proportion of neophytes decreased.

Life forms showed little overall changes. Although the proportion of hemicryptophytes decreased, this life form was still by far the most frequent one. Hemicryptophytes regenerate from buds close to the ground in spring and after mowing or pasturing. They account for the largest part of life forms in temperate grasslands, whereas therophytes, chamaephytes and geophytes are less relevant (DIERSCHKE & BRIEMLE 2002). The proportions of the latter life forms, however, did not increase significantly. Similarly, the proportion of CS-strategists decreased, which indicates that disturbances may have increased, but neither the proportion of R-strategists nor of the other life strategies changed significantly. In both cases, changes were probably too small to be statistically significant.

We are aware that differences between old and new plots might not result from temporal changes, but from spatial changes due to uncertain plot recovery, so-called pseudo-turnover (FISCHER & STÖCKLIN 1997, CHYTRÝ et al. 2014). We estimate that there is a plot recovery error of up to 10 metres in our resurvey. However, KOPECKÝ & MACEK (2015) showed that studying temporal vegetation change by revisiting historical plots is robust to uncertain recovery of plots. Therefore, observed changes are unlikely to be heavily influenced from inaccurate plot recovery. In particular the recovery error in space should be more or less random, thus producing some noise in the data, which rather can hide temporal trends, but not create the impression of directed change when there was no change.

Other biases may have resulted from temporal pseudo-turnover, such as seasonal and observer differences (KIRBY et al. 1986, CHYTRÝ et al. 2014). Old plots were mainly examined from May to October, while we inspected the new ones in August, so that the observed changes could result from phenological differences. Indeed, a few, particular annual, plants might not have been (well) visible very early and late in the year, which could partly explain higher observed richness values in 2015. There could also be temporal pseudo-differences through subjective cover estimation, plant misidentification or overlooking (CHYTRÝ et al. 2014). However, this effect is likely to be rather small because the same botanist (J. Dengler) was the (main) observer for all old and new plots, except for two *Arrhenatherion elatioris* plots of 1997.

4.2 Comparison with other studies

Little overall changes and even a significantly higher mean species richness are a positive trend compared to other studies, which found a constant species loss over time in grasslands (FREDE 1999, KRAUSE et al. 2014). Our findings are consistent with the results of DIEKMANN et al. (2014), who examined calcareous grasslands in NW Germany over the last 70 years by compiling over 1,000 historic and over 100 new plots. They found that atmospheric N deposition had no or even a slight positive effect on species richness. The authors conclude that atmospheric nitrogen input has little impact on the species richness in calcare-

ous grasslands because of high soil pH. In contrast to acidic grasslands, where nitrogen deposition leads to acidification and increased ammonium contents or higher ammonium/nitrate ratios, the soils of calcareous grasslands have a large buffering capacity against acidification, and N is predominantly mineralised as nitrate (DIEKMANN et al. 2014). Moreover, the study region is within Germany among those with the lowest N surplus (UMWELTBUNDESAMT 2014).

However, changes in the species composition of dry grasslands across Germany are at least equally attributable to cessation of traditional land use (mowing or grazing) and atmospheric nitrogen deposition, typically with very similar consequences for species composition. DIEKMANN et al. (2014) report that species with a negative trend were small, light-demanding, wintergreen or evergreen dry grassland specialists with smaller seeds and sclera-morphic leaves. Similarly, JANDT et al. (2011) in their analysis of a large vegetation-plot database found for calcareous grasslands a decrease in frequency mainly of low-growing species, while competitive tall grasses, typical forbs of forest edges (class *Trifolio-Geranietea*) and phanerophytes increased. These general trends across Central Europe were also very well matched by a re-visitation study by PLESS (1994) on continental dry grasslands at the margin of the Oder valley, just about 50 km SE of our site, 40 years after the original sampling. He studied stands of the *Festucion valesiacae* and the *Cirsio-Brachypodion pinnati* on (mostly) loamy soils. While the author did not conduct statistical analyses, his synoptic tables indicate that in both community types relatively tall and competitive grasses (*Arrhenatherum elatius*, *Dactylis glomerata*, *Brachypodium pinnatum*, *Bromus erectus* and *B. inermis*) increased in frequency and cover. Moreover, in the *Festucion valesiacae*, many ruderal, often annual, species were more frequent in the more recent survey. By contrast, in the *Cirsio-Brachypodion*, *Trifolio-Geranietea* species (e.g. *Hypericum perforatum*, *Vicia tenuifolia*, *Viola hirta*) increased, while some, often small, typical *Festuco-Brometea* species (e.g. *Trifolium montanum*, *Oxytropis pilosa*, *Viola rupestris*) decreased. HAHN et al. (2013) found similar vegetation change by doing a revisitation study of dry grassland in the Kyffhäuser mountain area, Central Germany. The climate of the Kyffhäuser is almost identical to that of our study site and that of PLESS (1994), i.e. continental climate with ca. 500 mm of annual precipitation. Overall vegetation change at the Kyffhäuser study site was stronger than in our study, in particular annual plants decreased and hemicryptophytes increased.

None of these patterns could be detected in the dry grassland complex of the Gabower Hänge, in particular no encroachment of tall competitive grasses or shrubs/trees. On the contrary, the seven significantly increased species are all small, including several annual ones (*Cerastium semidecandrum*, *Trifolium arvense*, the moss *Tortula lanceola*; Table 1). Why are the Gabower Hänge so different from the rest of Central Europe and even from the Oder valley further south although today the grazing on the "Oderinsel" is certainly also less regular and less intensive than in the past and has even been interrupted for several subsequent years? We assume that the main factor for this very slow succession in our study area is the combination of very low annual precipitation and soils that are mostly pure sands and thus prone to edaphic drought. This combination of factors makes the site more extreme in terms of drought stress than most other dry grasslands in Central Europe, even compared to the sites analysed by PLESS (1994) and HAHN et al. (2013), which have a similarly low precipitation, but mostly loamy soils and thus higher water holding capacity. This proneness to drought apparently prevents the encroachment of more mesophytic species over longer periods. Perhaps even more important than average years are those with particularly low precipitation. During one summer essentially none of the thousands of *Stipa capillata* individuals of

the site had set flowers because of a very dry spring (unpubl. observation, J. Dengler). When even a species perfectly adapted to drought like *Stipa capillata* is so strongly affected, the impact is likely to be fatal for more mesophytic species, which might have established there in preceding years with above-average precipitation. Such temporal processes could explain why we found some typical annual dry grassland species more often in 2015 than two decades before: A strong drought in one of the previous years might have created the necessary gaps in the perennial sward for them to establish.

5. Outlook

In summary, we found astonishingly little vegetation change in the dry grassland complex of the Gabower Hänge, and we found that it remained in a similarly good condition as in the years 1993−1997 (KRATZERT & DENGLER 1999). This relative stability together with the large expanse of several included EU priority habitat types (LUGV 2015) and supraregionally significant populations of rare and endangered species (KRATZERT & DENGLER 1999) highlight the outstanding nature conservation value of the site. Further studies with a larger number of plots and analyses are needed to verify the indicated tendencies. Also, separate analyses for different vegetation types would be preferable to assess possible divergent developments. The sample size of our study was not sufficient for that, but we still achieved results that allow first conclusions about the development and state of the dry grassland in the focal area. If there have been vegetation changes at all, these could have been only small since changes where non-significant and effects were minute. The observed trends toward more nutrient-rich conditions should be carefully observed, and appropriate management should be implemented. The assumption that the unexpected stability is due to the particularly dry conditions (lowest precipitation of the region combined with soils of a particularly low water holding capacity) should be tested in the future by resampling other dry grasslands studied earlier by DENGLER (1994a, b) in the Biosphere Reserve where the local precipitation is higher and the soils are richer in silt and clay.

Erweiterte deutsche Zusammenfassung

Einleitung –Heute sind viele Trocken- und Magerrasen durch intensive Landwirtschaft, Nutzungsaufgabe und atmosphärischen Stickstoffeintrag bedroht (DIERSCHKE & BRIEMLE 2002, DENGLER et al. 2014). Ein Verlust an Arten- und funktioneller Vielfalt, Verbuschung aufgrund von Sukzession und Veränderungen der Artzusammensetzung sind die Folgen. Magerrasen gehören zu den am stärksten bedrohten Habitaten in Europa; ihr Schutz hat daher hohe Priorität (KORNECK et al. 1998, EUROPEAN COMMISSION 2013). Es ist deshalb wichtig, Vegetationsveränderungen in Magerrasen zu untersuchen, etwa durch die Wiederholung historischer pflanzensoziologischer Aufnahmen. Diese Methode hat den Vorteil, dass die alten Aufnahmen frei von *a priori*-Annahmen sind, da die Aufnahmen ursprünglich nicht mit dem Ziel durchgeführt wurden, Vegetationsänderungen zu dokumentieren. Solche Wiederholungsaufnahmen liefern selbst dann zuverlässige Ergebnisse, wenn die Aufnahmeflächen nicht exakt wieder gefunden werden können, und sie gelten daher als eine robuste Methode um Vegetationsänderungen über Jahrzehnte zu untersuchen (ROSS et al. 2010, KOPECKÝ & MACEK 2015). In dieser Arbeit nutzen wir das Verfahren, um Vegetationsveränderungen der Gabower Hänge, einem Trockenrasenkomplex im Biosphärenreservat Schorfheide-Chorin (Nordostbrandenburg), zu untersuchen.

Methoden – Die Gabower Hänge sind ein Komplex verschiedener Trockenrasen zwischen den Dörfern Gabow und Altglietzen (ca. 80 ha, 52,82° N, 14,08° O, 10–55 m ü. NN, Abb. 1). Sie bilden den südöstlichen Rand der „Oderinsel“ (Neuenhager Sporn) und fallen steil zum Oderbruch hin ab (KRAT-

ZERT & DENGLER 1999). Das Klima liegt in der Übergangszone zwischen dem ozeanischen Klima Nordostdeutschlands und dem subkontinentalen Klima Polens. Die mittlere Jahrestemperaturspanne beträgt über 19 K und der mittlere Jahresniederschlag nur etwa 500 mm. Die Gabower Hänge zeichnen sich durch erodierte Kuppen und Hänge mit überwiegend sandigen, kalkhaltigen Substraten (Geschiebesande) aus (Abb. 2). Die Hauptbodentypen sind Pararendzina und Regosol. Das Untersuchungsgebiet ist als Natura 2000 Gebiet DE3150–303 "Gabower Hangkante" geschützt. In den letzten Jahrzehnten bestand die einzige Landschaftspflege in extensiver Beweidung mit Schafen und Maßnahmen zur Entbuschung, war aber zwischenzeitlich mehrere Jahre unterbrochen (LUGV 2015).

Wir wiederholten jeweils vier 10 m²-Aufnahmen von vier typischen Verbänden (*Festucion valesiacae* – Abb. 3, *Koelerion glaucae*, *Armerion elongatae*, *Arrhenatherion elatioris*) ca. 20 Jahre nach der ursprünglichen Vegetationsuntersuchung (vgl. KRATZERT & DENGLER 1999) mit einer ungefähren Relokalisierungs-Genauigkeit von 10 m. In beiden Aufnahmeperioden wurden die Deckung der Gefäßpflanzen, Moose und Flechten aufgenommen. Die Gesamtänderung der Artenzusammensetzung wurde mit einer Detrended Correspondence Analysis (DCA) analysiert. Um die Vegetationsänderungen interpretieren zu können, berechneten wir ungewichtete mittlere Ellenberg-Zeigerwerte für die alten und neuen Aufnahmen. Wir testeten mit gepaarten *t*-Tests Unterschiede in der Stetigkeit der einzelnen Arten zwischen alten und neuen Aufnahmen sowie Unterschiede in Artenanzahl, Deckung von Kraut- und Kryptogamenschicht, ökologischen Zeigerwerten und in den ungewichteten Anteilen taxonomischer Hauptgruppen (Gefäßpflanzen, Moose, Flechten), Florenstatus (einheimisch oder nicht), Lebensformen, CSR-Strategietypen und Rote Liste-Arten.

Ergebnisse – Die Verbände waren im Ordinationsplot deutlich voneinander getrennt (Abb. 4). Die mittlere Stickstoff- und Reaktionszahl waren positiv mit den Achsen der Ordination korreliert. Wir fanden keine signifikanten Vegetationsveränderungen entlang der ersten und zweiten Achse der DCA, allerdings deutete sich eine Tendenz zu nährstoffreicheren und basenreicheren Bedingungen an, da die Verschiebung der Zentroide in eine ähnliche Richtung wie die Zeigerwerte für Stickstoff und Reaktion weist. Insgesamt wurden 113 Taxa aufgenommen (Anhang E1). In den neuen Aufnahmen fanden wir 28 Arten, die in den alten Aufnahmen fehlten (Anhang S1). Von den Arten aus den alten Aufnahmen fehlten 45 in den neuen Aufnahmen (Anhang S1). Es nahmen keine Arten signifikant ab, aber sieben Arten nahmen signifikant zu (Tab. 1). Die neuen Aufnahmen hatten mit 26,1 ± 7,0 eine signifikant höhere durchschnittliche Artenzahl als die alten Aufnahmen mit 22,4 ± 6,1 (Abb. 5). Keiner der sechs ökologischen Zeigerwerte nach ELLENBERG et al. (2001) war zwischen alten und neuen Aufnahmen signifikant verschieden. Ebenso gab es keine Unterschiede in der Deckung der Kraut- und Kryptogamenschicht. Die neuen Aufnahmen hatten einen signifikant geringeren Artenanteil von Gefäßpflanzen und einen fast doppelt so hohen von Moosen (Abb. 6A), während jener der Flechten gleich blieb. Der Anteil an einheimischen Arten und Archäophyten änderte sich nicht, hingegen nahm der Anteil der Neophyten signifikant von 2,8 ± 3,7 % auf 0,4 ± 1,2 % ab (Abb. 6B). Die Anzahl der Rote Liste-Arten Deutschlands änderte sich nicht; der Anteil der Rote Liste-Arten Brandenburgs nahm jedoch signifikant zu. Von allen Lebensformen änderte sich nur der Anteil der Hemikryptophyten signifikant. Diese nahmen signifikant ab (Abb. 6C), waren aber nach wie vor die häufigste Lebensform. Die CS-Strategen nahmen signifikant ab, während sich der Anteil der übrigen Strategietypen nicht veränderte. Sowohl bei den alten als auch den neuen Aufnahmen war der Anteil der CSR-Strategen am größten.

Diskussion – Wir fanden keine signifikanten Unterschiede in der Artenzusammensetzung zwischen alten und neuen Aufnahmen, allerdings gab es Tendenzen zu nährstoffreicheren und basenreicheren Bedingungen. Die durchschnittliche Anzahl an Moosarten pro Aufnahme nahm zu, da sowohl Gesamtartenzahl als auch der Moosanteil anstieg. Dies könnte auf bessere Lichtbedingungen aufgrund einer weniger dichten Krautschicht zurückzuführen sein. Aus Sicht des Naturschutzes ist es positiv, dass die Artenzahl und die Anzahl an Rote Liste-Arten Brandenburgs zunahm und der Anteil der Neophyten zurückging. Methodische Einschränkungen unserer Studie könnten beobachtete Vegetationsänderungen aufgrund von Pseudo-Turnover sein, wenn die neuen Aufnahmen nicht an der exakten Position der alten Aufnahmen aufgenommen wurden (CHYTRÝ et al. 2014). Allerdings zeigten KOPECKÝ & MACEK (2015), dass solche „revisitation studies" diesbezüglich robust sind. Da die Ungenauigkeit im Auffin-

den der alten Plots außerdem zufällig sein sollte, gehen wir davon aus, dass es dadurch zwar Rauschen in den Daten gibt, aber kein falscher Eindruck einer gerichteten Vegetationsänderung entstand. Dagegen könnte es zu einem gewissen zeitlichen Pseudo-Turnover gekommen sein, da die alten Aufnahmen von Mai bis Oktober und die neuen Aufnahmen nur im August erfolgten.

Während andere Studien einen Artenverlust in Grasländern im Laufe der Zeit fanden (FREDE 1999, KRAUSE et al. 2014), nahm in unserem Fall die Artenzahl zu. Übereinstimmend stellten DIEKMANN et al. (2014) fest, dass atmosphärischer Stickstoffeintrag in basenreichen Grasländern keinen oder sogar einen leicht positiven Einfluss auf die Artenzahl hatte. Unser Untersuchungsgebiet liegt zudem in einer Region mit besonders niedrigem Stickstoffüberschuss innerhalb Deutschlands (UMWELTBUNDESAMT 2014). Änderungen der Artenzusammensetzung von Trockenrasen werden mindestens genauso stark von der Aufgabe traditioneller Landnutzung (Mahd oder Beweidung) beeinflusst. DIEKMANN et al. (2014) berichten, dass Arten mit negativem Trend klein, lichtbedürftig, winter- oder immergrüne Trockenrasenspezialisten mit kleineren Samen und skleromorphen Blättern waren. JANDT et al. (2011) stellten fest, dass in kalkreichen Grasländern v.a. niedrigwüchsige Arten abnahmen, während konkurrenzstarke, hohe Gräser, typische Saumarten und Phanerophyten zunahmen. Diese allgemeinen Tendenzen wurden auch von PLESS (1994) an kontinentalen Trockenrasen am Rand des Odertals, nur etwa 50 km von unserem Untersuchungsgebiet entfernt, nach 40 Jahren bestätigt. Keines dieser Muster konnten wir bei den Trockenrasen der Gabower Hänge erkennen, v. a. kein Vordringen von hohen konkurrenzstarken Gräsern oder Sträuchern/Bäumen. Vielmehr sind die sieben Arten, die signifikant zugenommen haben, klein und einige davon annuell (Tab. 1). Wir vermuten, dass der Hauptfaktor für die langsame Sukzession im Untersuchungsgebiet außergewöhnliche Trockenheit ist, die aus dem sehr niedrigen Jahresniederschlag in Kombination mit den überwiegend sandigen Böden resultiert.

Insgesamt fanden wir erstaunlich geringe Vegetationsveränderungen und stellen damit fest, dass sich das Untersuchungsgebiet in einem ähnlich guten Zustand wie in den Jahren 1993–1997 befindet (KRATZERT & DENGLER 1999). Die relative Stabilität der Vegetation und die vorhandenen Populationen von seltenen und bedrohten Arten von überregionaler Bedeutung verdeutlichen den Wert des Untersuchungsgebietes für den Naturschutz.

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Supplements

Supplement S1. Taxa found only in new plots or only in old plots. In brackets, the absolute constancy among 16 plots is given; * indicates a significant change (Fisher's exact test; $p < 0.05$).

Anhang S1. Taxa, die nur in den neuen (Only new) oder nur in den alten Aufnahmen (Only old) gefunden wurden. In Klammern ist die absolute Stetigkeit in 16 Aufnahmen angegeben; * steht für eine signifikante Häufigkeitsänderung (Exakter Test nach Fisher, $p < 0{,}05$).

Only new: *Bryum argenteum* (5)*, *Carex praecox* (5)*, *Tortula* cf. *lanceola* (5)*, *Petrorhagia prolifera* (3), *Bryum dichotomum* (2), *Calamagrostis epigejos* (2), *Chenopodium album* (2), *Cladonia rangiformis* (2), *Euphorbia esula* (2), *Hylotelephium maximum* (2), *Koeleria macrantha* (2), *Myosotis stricta* (2), *Phleum pratense* (2), *Silene latifolia* subsp. *alba* (2), *Arabidopsis thaliana* (1), *Artemisia vulgaris*

(1), *Barbula convoluta* (1), *Bryum caespiticium* (1), *Didymodon fallax* (1), *Digitaria ischaemum* (1), *Echium vulgare* (1), *Homalothecium lutescens* (1), *Myosotis arvensis* (1), *Papaver argemone* (1), *Placynthiella* spec. (1), *Plagiomnium undulatum* (1), *Thuidium assimile* (1), *Verbascum densiflorum* (1).

Only old: *Achillea* cf. *pannonica* (4), *Sanguisorba minor* subsp. *minor* (3), *Falcaria vulgaris* (2), *Holcus lanatus* (2), *Medicago falcata* (2), *Medicago lupulina* (2), *Medicago minima* (2), *Papaver dubium* (2), *Silene chlorantha* (2), *Anchusa officinalis* (1), *Berteroa incana* (1), *Bromus tectorum* (1), *Carex hirta* (1), *Centaurea jacea* (1), *Conyza canadensis* (1), *Cynoglossum officinale* (1), *Draba verna* agg. (1), *Erodium cicutarium* (1), *Fragaria viridis* (1), *Holosteum umbellatum* (1), *Lotus corniculatus* (1), *Pimpinella saxifraga* agg. (1), *Populus* ×*canadensis* (1), *Potentilla argentea* (1), *Salsola tragus* (1), *Scorzoneroides autumnalis* (1).

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. Vegetation table of old and new relevés and coordinates of the new relevés.

Anhang E1. Vegetationstabelle der alten und neuen Vegetationsaufnahmen sowie Koordinaten der neuen Vegetationsaufnahmen.

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