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Diversity Increases but Community Specialists Decline Over Three Decades in Dry Grassland Communities of Central Germany

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ABSTRACT

Aim: Dry grasslands are vulnerable to climate and land-use change. Increasing temperatures, drought, grazing cessation and nitrogen deposition can all result in shifts in grasslands' taxonomic and functional composition. We tested the hypotheses that both species richness and diversity are decreasing at the scales of both the regional species pool of dry grasslands and for individual communities, with functional composition shifting towards more competitive traits and shortened live spans, and that these responses depend on species' functional characteristics and on drought stress levels to which communities are exposed.

Location: Semi-natural dry grasslands north-west of Halle (Saale), Central Germany.

Methods: In 2021/2022, a resurvey of vegetation was conducted in 131 relevés surveyed in 1992/1993 on 51 rocky hills, on which our focus was on six common grassland communities found along a gradient of increasing drought stress from harsh to more favourable conditions. Drought stress levels were quantified using slope, aspect, soil depth and soil texture, resulting in a sequence of communities on sun-exposed shallow soils to moister and deeper soils. Changes in taxonomic and functional composition were analysed and explored with paired *t*-tests, linear models, principal component analysis and (distance-based) redundancy analysis.

Results: The size of the regional species pool of the dry grasslands did not decrease over the last 30 years. Its functional turnover points to declining precipitation, longer growing seasons and an increasing frequency of drought events. In the resurveyed pool, a lower number of species flowering in mid summer and a higher number of early flowering species suggest a trend to avoidance of summer droughts and a response to warmer and moister spring conditions. At the community scale, species richness and alpha diversity increased, in spite of a decreasing plant cover over the investigation period. These increases were mainly caused by an increased abundance of annual plant species, as a response to cleared space through the decreasing cover of perennial plant species, pointing to drought avoidance as a successful survival strategy. The studied community types varied in the magnitude of diversity changes as well as in their species and functional responses, where changes in trait composition increased with increasing heat load on two of the community types.

Conclusions: Dry grassland communities undergo significant shifts in both species and functional composition, in favour of generalist species with faster life cycles, disadvantaging dry grassland specialist species. Given the predicted higher frequency of drought events in the future and the uncertainty of grazing resumption in the region, these changes can be expected to continue over the next decades. This underlines the importance of continuing locally adapted management practices for landscape-scale biodiversity conservation to compensate for climatic change.

1 | Introduction

Semi-natural dry grasslands are ecosystems that have been shaped by human activity (i.e., grazing or mowing), but still retain characteristics of natural dry grasslands. In Central Europe, they are hotspots for a variety of plant species (Habel et al. 2013) that can cope with warm and dry climatic conditions (Dengler et al. 2014; Feurdean et al. 2018). Small-scale micro-environmental variation contributes to the coexistence of numerous plant species with different ecological niches. Species richness is typically higher than 30 vascular species per square metre, but can reach values above 60 (Wilson et al. 2012; Bruelheide et al. 2020), which makes these habitats primary targets of biodiversity conservation (Carboni et al. 2015), as they are particularly vulnerable to climate change or land-use changes.

Although semi-natural dry grasslands are adapted to stressful conditions, they are still affected by climate change, especially by increasing temperatures and prolonged drought periods (Pötsch et al. 2011). A number of resurvey studies in recent years have documented vegetation change as a consequence of land-use and climate change, with habitat specialists declining and generalists increasing in cover and frequency (Diekmann et al. 2014; Jiménez-Alfaro et al. 2014; Diekmann et al. 2019; Janišová et al. 2023; Klinkovská et al. 2024). Unpredictable drought periods favour the expansion of ruderal species (Fischer et al. 2020), which thrive via rapid colonisation of open space created by drought, through their highly reproductive outputs and short life cycles (Evans et al. 2011; Fischer et al. 2020; Nabe-Nielsen et al. 2021). In addition, harsh microclimatic conditions which occur on steep and sun-facing slopes with shallow soils, can be expected to increase the impact of drought events on species composition (Mazalla et al. 2022). Variation of community trait combinations over time can be a useful indicator of possible drivers of environmental changes (Rosbakh et al. 2015; Luo et al. 2019). Recurring drought events, for example, could favour annual species that are able to complete their life cycle before the onset of drought and to survive dry periods as seeds, especially in summer (Chesson et al. 2004; Zeiter et al. 2016). Drought could also favour strategies to avoid desiccation and reduce above-ground biomass, for example, favouring plants with smaller, scleromorphic or circularly arranged leaves (Dostálek and Frantík 2011; Olsen et al. 2013; Tardella et al. 2016; Wehn et al. 2017).

The loss of habitat specialists can also be linked to grazing cessation (Giarrizzo et al. 2017; Harásek et al. 2023). In the absence of grazers, species with competitive strategies tend to become more frequent (Koch et al. 2017). For instance, grazing abandonment favours graminoids and geophytes, while disadvantaging species with traits adapted to grazing avoidance (Dupré and Diekmann 2001). Sheep grazing is known to enhance species richness in grasslands over time (Socher et al. 2013) and the widespread cessation of grazing over the past three decades could have negatively impacted species richness. Additionally, grazing abandonment influences plant trait variation, favouring growth forms and leaf traits associated with rapid growth and high-resource acquisition strategies, such as larger leaf area (Kahmen et al. 2002; Peco et al. 2012; Jarque-Bascuñana et al. 2022). Reduced herbivory pressure also leads to lower leaf dry matter content, indicating less tissue toughness (Targetti et al. 2013; Wehn et al. 2017; Helm et al. 2019; Al Hajj et al. 2024). Furthermore, the absence of grazers and therefore lack of removal of biomass leads to litter accumulation, which suppresses seedling establishment (Neuenkamp et al. 2016).

Besides climate change and land-use changes, increasing fertilisation through intensification and atmospheric nitrogen deposition further disadvantages specialist species and favours generalist species (Pakeman et al. 2017; Diekmann et al. 2019), which should be of greater impact in nutrient-poor dry grasslands. On the one hand, nutrient enrichment, especially nitrogen, shifts a community composition towards fast-growing, nitrophilous species, reflected, for example, in taller plants of rapid growth (Pierik et al. 2011). On the other hand, eutrophication leads to the loss of stress-tolerant and nutrient-efficient species that are replaced by more competitive nutrient-demanding species (Helsen et al. 2014), with even greater effects in acidic grasslands (Pannek et al. 2015). Hence, changes in the composition of ecological, phenological and morphological characteristics of a community could also link vegetation changes to either climate change or to land-use changes.

In Central Germany, under a continental climate with low precipitation, different dry grassland types reflect the fine-scale variation in geomorphology, soil characteristics and microclimate (Wesche et al. 2005), resulting in a localised mosaic of grassland communities. The most common plant communities (Appendix S1, Figure S1) range from short, open grasslands of siliceous rocks on southwest-(sun-)facing slopes and shallow soil (e.g., Thymo–Festucetum cinereae Mahn 1959), grasslands on gentle slopes with nutrient-poor and rather acidic soil (Galio veris-Agrostidetum tenuis Mahn 1965), and dense acidophilic dwarf-shrub heaths, prevailingly on cooler north-facing slopes (Euphorbio–Callunetum Schubert 1960), to dense continental dry grasslands on south-facing slopes (Festuco rupicolae–Brachypodietum pinnati Mahn 1965), very dense mesic grasslands on somewhat moister soil (Filipendulo vulgaris-Helictotrichetum pratensis Mahn 1965) and dense but disturbed ruderal grasslands on outcrop edges with nutrient-rich soil (Dauco–Arrhenatheretum, Tanaceto–Arrhenatheretum Fischer 1985). Each of these communities is characterised by a typical constellation of site factors (Schubert et al. 2010). Hence, this grassland mosaic provides an ideal platform for studying changes in community composition. This is particularly relevant given that, in addition to global climate change, significant

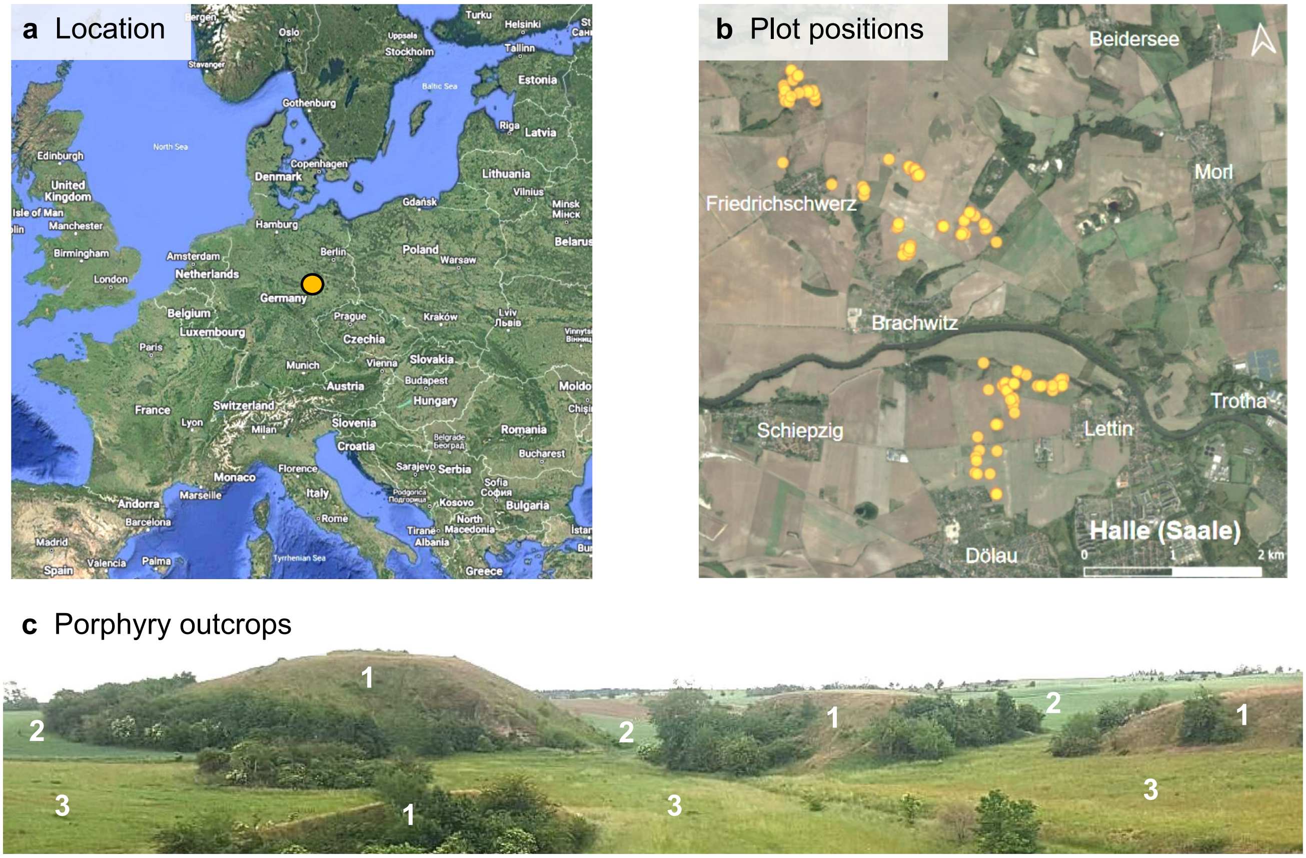


FIGURE 1 | Position of permanent vegetation plots in (a) Germany (yellow dot) and (b) the study area (yellow dots on Google satellite base map, 2022), and (c) the view over some porphyry outcrops (1) in June 2022, surrounded by mown meadow (2) and by agricultural crops (3). (Photo by Susanne Horka).

local land-use changes have occurred over the past 30 years, including agricultural intensification, widespread grazing abandonment after 1990 and the implementation of nature conservation management measures.

Previous studies of those dry grassland communities mentioned above have focused on phytosociological issues (e.g., Mahn 1965), with a first substantial survey in 1992/1993 by Partzsch and Krumbiegel (data not published). Partzsch (2003) reported increasing species richness on the smaller outcrops due to the invasion of ruderal and adventive species, while several formerly rare species decreased or disappeared. In a resurvey after two decades in the northern part of the porphyry landscape, Meier et al. (2021) found a lower floristic turnover in different functional groups in dry grassland compared to semi-dry grassland communities, with an overall increase in annuals and graminoids and a decline in endangered forbs. In 2021, we systematically revisited old vegetation plots after three decades, resurveyed the vegetation and arranged potential differences in community compositional changes along an environmental gradient. We hypothesised that (i) the regional species pool decreased and that within this species pool, the frequencies of strategy types and life-history traits became more competitive. To investigate changes in species composition across communities, we tested the hypothesis that (ii) local species diversity decreased and that the community trait composition changed to more short-living herbs, indicating increasing drought, higher temperatures and lower moisture levels as well as higher nutrient supply. To analyse community-specific responses along the topographic and drought-stress gradient on the outcrops, we further tested the hypothesis that (iii) the shifts in species composition and the shifts in trait composition were larger when a more severe drought stress level is experienced by a community type.

2 | Methods

2.1 | Study Site

The semi-natural dry grasslands north-west of Halle (Central Germany, 51°31 N to 51°34 N and 11°51 E to 11°53 E) comprise > 200 small habitat islands in a matrix of mostly intensively managed arable land (Figure 1). Regular low-intensity sheep grazing was abandoned after political changes in 1990, which resulted in changes in the vegetation that were accelerated by the fertilising effect of atmospheric nitrogen deposition decades ago, when the region was one of the most heavily industrialised parts of the former German Democratic Republic (Partzsch 2007; Wesche et al. 2005). Today, most of the grasslands are part of protected areas and, in addition, are protected under the European Habitat Directive (Council Directive 1992).

The habitat islands are of different shapes and sizes, traditionally called porphyry outcrops (which refers to the bedrock's visible porphyry texture). Their rhyolithic rocks have been formed by crystallisation of magma, followed by partial erosion through the Weichselian glacial period (15,000–57,000 years BC; Eissmann 2002). Aeolian loess deposits from the subsequent Pleistocene era were redistributed, mostly downhill, by further erosion. Due to the rain shadow of the adjacent Harz Mountains to the west, the mean annual precipitation is low, 450 mm (Fabig 2007), with a mean annual temperature of 10.6°C. Additionally, the region suffers from frequent, often lengthy drought events, especially in spring and summer, when prolonged rain-free periods coincide with high temperatures (Döring 2004).

The bedrock develops shallow, nutrient-poor and acidic topsoils, with coarse soil texture and a low water-holding capacity. Continuous eluviation and downslope transport processes result in the accumulation of soil material at lower slopes, the loss of basic cations, an increase in hydrogen ion concentration and the formation of distinct microsites. The outcrops show a clear top-to-bottom gradient of increasing pH, soil depth, water-holding capacity and nutrient availability. This gradient is further influenced by the size and height of the outcrops, as well as the steepness of slopes and their exposure to sunlight. These factors together create a wide range of microsite conditions for vegetation (Wesche et al. 2005; Partzsch 2007).

The outcrop vegetation (hereafter referred to as porphyry dry grasslands) developed through hundreds of years of sheep grazing, resulting in a prevalence of low-growing grasses and herbs, with a few shrubs and trees on the larger outcrops (Partzsch 2007). Many of the specialist plant species are acidophilic and xerophilic perennials that are able to cope with low pH and nutrient scarcity (e.g., *Calluna vulgaris*, *Thymus serpyllum*).

2.2 | Survey Method

In 2021/2022, we resurveyed 131 plots on 51 different outcrops that were randomly chosen from the dataset compiled by Partzsch and Krumbiegel in 1992/1993 (original survey). The results of the original surveys were at least partly published in summary tables (Partzsch 2007; Wesche et al. 2005). We have selected six of the most common dry grassland communities in the porphyry landscape (Appendix S1, Figure S1; full names in Section 1): Thymo-Festucetum (open silicate rock vegetation, $n=34$), Festuco-Brachypodietum (dense continental dry grassland, $n=21$), Galio-Agrostidetum (scattered acidic dry grassland, $n=16$), Filipendulo-Helictotrichetum (dense mesic dry grassland, $n=20$), Euphorbio-Callunetum (acidophilic dwarf-shrub heath, $n=22$) and Dauco- or Tanaceto-Arrhenatheretum (dense, disturbed ruderal grassland, $n=18$; herein after referred to as Arrhenatheretum in figures and tables). Plot positions of the original survey were relocated in the resurvey by on-site inspection and by comparing detailed hand-drawn maps and recent aerial photographs that showed permanent morphological outcrop characteristics. Once located, we established northwards-aligned plots of 3 × 3 m, determined site data (magnetic aspect and slope, in degrees using compass/inclinometer), measured soil depth (in cm, as mean of 5 probes per plot with a 10 mm rod), sampled soil material (200 cm^3, from 0 to 10 cm at the southwest corner of a plot) and estimated the cover (vertical projection of all plant parts of the same species onto the ground) for each vascular plant species identified (Müller et al. 2021). For more precise estimation of their coverage in view of potential future relevés, we refined the originally used Braun-Blanquet scale to the more detailed Londo scale (Appendix S1, Table S1). In this context, we also marked plot locations with permanent magnets, buried on opposite corners (NE and SW, at 10 cm depth).

2.3 | Data Preparation

Taxa were harmonised using the reference list GermanSL 1.4 (Jansen and Dengler 2008). Subspecies and variants were aggregated at species level or if necessary for taxonomic consistency between the surveys (as some species were not further distinguished in 1993) at aggregate level (e.g., *Achillea millefolium* agg.), using the R-package *Vegdata* (Jansen and Dengler 2010). To check the comparability of our survey times within the vegetation period, we tested for correlation of the calender day of both survey years with species richness (Vymazalová et al. 2012), which was not significant (data not shown). Taxonomic and functional changes between the two surveys were calculated using the package *Vegan* (Oksanen et al. 2022).

We compiled information on ecological and morphological traits relevant for the occurrence and persistence of dry grassland species from different databases (Table 1). Traits that were missing for a few species were substituted by trait values of congeners, i.e., for *Festuca csikhegyensis*, trait values of *Festuca pallens* were used. All non-numerical traits were transformed to sets of binary variables by creating categorical trait states. All trait values were expressed as community-weighted means (CWM) using percent cover as weights. Ellenberg indicator values (EIV), which are expert-based numerical assignments of species to their ecological optima on environmental gradients (represented as values for, e.g., moisture, soil reaction or nutrient levels), were taken from Tichý et al. (2023).

Soil texture was assessed by analysing particle size distribution, via laser diffraction sensoring (HELOS/KR, Sympatec GmbH, Germany), combined with a wet dispersion unit (QUIXEL, Sympatex GmbH, Germany). Particle sizes were categorised using the German classification of grain sizes into sand (2000–63 μm), silt (62–2 μm) and clay (< 2 μm).

To assess the influence of stress on grassland community differentiation, we combined two indices: a heat load index (HLI) reflecting solar exposure and a water supply index (WSI) representing the soil water retention capacity derived from soil texture.

The HLI estimates the relative exposure of the communities to solar radiation based on their aspect and slope (McCune and Keon 2002, originally published in Parker 1988). The usually required latitude was neglected in the small study area of the porphyry dry grasslands (< 10 km^2). To account for the maximum solar radiation on southwestern slopes at noon, we subtracted 225° from the aspects (−45° to make southwest slopes rather than the south-facing slopes the most exposed ones and another −180° to obtain maximum values for a high heat load when applying the cosine). Degrees were converted into radians before cosine transformation, thus ensuring a continuous

TABLE 1 | Considered numerical and categorical trait variables with units and factor levels, respectively, and their general or specific ecological function. A trait's code is used as its abbreviation in figures.

Trait variable	Unit/level	Ecological function	Code
Ellenberg indicator values[d] (numerical)	Light	Realised niche of preferred light conditions	Light
	Moisture	Realised niche of preferred soil moisture levels	Moist
	Nutrients	Realised niche of preferred soil nutrient levels	Nutri
	Soil reaction	Realised niche of preferred pH levels	Reac
	Temperature	Realised niche of preferred temperature conditions	Temp
Floristic status[a] (categorical)	Archaeophyte	Established early (< 1495)	Arch
	Indigenous	Native	Indig
	Neophyte	Established more recently (> 1495)	Neo
Leaf anatomy[a] (categorical)	Mesomorphic	Drought tolerance, water use efficiency and storage	Meso
	Scleromorphic		Scler
	Succulent		Succu
Leaf dry matter content[b,c] (numerical)	mg/g	Resource conservation, leaf longevity	LDMC
Life form[a] (categorical)	Geophyte	Drought tolerance, longevity, survival	Geoph
	Hemicryptophyte		Hemicr
	Herbaceous chamaephyte		herbCha
	Therophyte		Thero
	Woody chamaephyte		woodCha
Lifespan[a] (categorical)	Annual	Competitive ability, longevity	Annu
	Biennial		Bienn
	Perennial		Perenn
Phenological season[a] (categorical)	Early spring	Realised phenological niche	SpringE
	Mid spring		SpringM
	Early summer		SummE
	Mid summer		SummM
	Early autumn		Autumn
Reproduction type[a] (categorical)	Seeds	Dispersal, drought survival, regeneration	Seeds
	Seed and vegetative		SeedVege
	Vegetative		Vege
Rosette type[a] (categorical)	Rosette-less	Competitive ability, trampling and drought tolerance	noRos
	Semi-rosette		semiRos
	Whole rosette		wholeRos
Specific leaf area[b,c] (numerical)	mm^2/mg	Productivity, resource acquisition	SLA
Strategy type[a] (categorical)	Competitive	Competitive ability, stress tolerance, ruderal strategy	C
	Competitive-ruderal		CR
	Competitive-stress-ruderal		CSR
	Competitive-stress		CS
	Ruderal		R
	Stress		S
	Stress-ruderal		SR

Note: Data sources: [a]BiolFlor (Kühn et al. 2004), [b]FloraVeg (Chytrý et al. 2024), [c]TRY (Kattge et al. 2020) and [d]EBV (Tichý et al. 2023).

distribution of HLI values from low heat load (−1) on northeast-facing slopes to high heat load on southwest-facing slopes (+1). Since the steepness of a slope amplifies solar radiation effects, for example, steeper slopes that face the sun receive more solar radiation than those facing away, we multiplied the aspects by their slope (Equation 1), converting slope degrees to radians before tangent transformation, scaling the slopes from minimum (0° = 0) to maximum inclination (90° = 1).

The WSI expresses the influence of different soil textures on water availability (Equation 2), with sandier soils on top of the outcrops having lower water retention and higher drainage, thus experiencing higher drought stress. Therefore, sand, silt and clay proportions were summed and, to account for different water retention capacities, weighted by factors based on the typical available field capacity (e.g., determined for different soil types by Hohenbrink et al. 2023), as clay = 0.5 (high retention), silt = 0.3 (moderate retention) and sand = 0.1 (low retention). This was scaled by the inverse of soil depth (in cm), as the drought stress increases with decreasing soil depth.

The HLI (ranging −0.7–0.4) and WSI (0.1–3.7) were both rescaled (min–max normalisation) between 0 (least stressful) and 1 (most stressful) and combined in a composite drought stress index (DSI) by taking the mean of HLI and WSI (Equation 3).

$$\mathrm{HLI} = \cos\left(\mathrm{radians}\left(\mathrm{aspect}\ (\mathrm{in}^\circ) - 225^\circ\right)\right) \times \tan\left(\mathrm{radians}\left(\mathrm{slope}\right)\right) \tag{1}$$

$$\mathrm{WSI} = 1/\left[\left(\left(0.5\ \mathrm{Clay}\ (\mathrm{as}\%) + 0.3\ \mathrm{Silt}\ (\%) + 0.1\ \mathrm{Sand}\ (\%)\right)/100\right) \times \mathrm{soil\ depth}\ (\mathrm{cm})\right] \tag{2}$$

$$\mathrm{DSI} = 0.5\left(\mathrm{HLI} + \mathrm{WRI}\right) \tag{3}$$

2.4 | Data Analysis

Statistical analyses were performed in R open-source software, Version 4.2.2 (R Core Team 2021). We analysed the species and trait composition for the entire dataset and separately for each of the six dry grassland community types.

To determine changes in the species composition within community types over time, we calculated means of species richness, Shannon index, Pielou evenness (Shannon/log(richness)) and total vegetation cover (summed cover of all species, which can exceed 100%) and tested the difference between surveys with paired *t*-tests or, in case of residuals not being normally distributed, Wilcoxon signed-rank tests. Cover changes were calculated assuming that the Braun-Blanquet classes of the historical samples were of the lowest values in the range of the respective Londo classes, to avoid potential pseudo-change of the species cover if a Braun-Blanquet class comprises more than one Londo class. Changes in state frequencies of categorical variables between the surveys were tested using the two proportions' *z*-test. The tests of each measure were adjusted for false discovery rates (Benjamini and Hochberg 1995).

Since our dataset consists of species abundance data across multiple sampling sites with limited heterogeneity, we conducted a detrended correspondence analysis (DCA) to assess the gradient length of the first ordination axis (0.7 for our dataset). A species turnover lower than one standard deviation suggests the appropriateness of using a linear method for modelling species–environment relationships. Thus, changes in species composition were analysed using distance-based redundancy analysis (RDA), using Bray–Curtis dissimilarity and time as the constraining variable. Changes in trait composition were analysed with ordinary RDA, again using time as the constraining variable. Significances of differences in species and trait composition between the surveys were calculated using permutational analysis of variance, which is based on reshuffling, respectively, either Bray–Curtis dissimilarities or the variance–covariance matrix for species and trait composition. Permutations were carried out using the plot ID as a block factor. To test the CWM values for significant shifts in time, numerical variables were scaled to a mean of 0 and a standard deviation of 0.5 (Gelman 2008) to allow for interpreting parameter estimates together with categorical variables and then tested using a paired *t*-test. Dissimilarities in species and trait composition were compared for average distances to the centroid (ADC), which can be interpreted as measures of beta diversity. In addition, we tested for significant differences of the CWM for every trait using paired *t*-tests. To relate the increases and decreases of all CWM trait values to each other and to the community types, the RDA factor loadings on Axis 1 were subjected to a principal component analysis (PCA). To link the compositional changes to environmental stress, RDA factor loadings of the species and the trait composition were correlated with the calculated DSI of each of the community types, ordered along increasing drought stress as follows: Galio-Agrostidetum, Dauco-/Tanaceto-Arrhenatheretum, Filipendulo-Helictotrichetum, Euphorbio-Callunetum, Festuco-Brachypodietum, Thymo-Festucetum (Appendix S2, Figure S2).

3 | Results

3.1 | Species Pool Remained Stable, Despite Shifts in Phenology and Life Forms

The regional species pool of the porphyry dry grasslands showed a nearly constant species number over time, with a total of 229 species in the original survey and 231 in the resurvey, with an overlap of only 182 species. About one-third of the species taxa differed between the surveys, with 49 species not being re-encountered and 47 species newly being found in the resurvey. The floristic status was nearly constant between the surveys, with 180 indigenous species in the original survey, 175 in the resurvey and 10 neophytes in both. In the original survey, 57 species were on the German Red List (RL), with 3 species of RL Category 1 (highly threatened), 16 species of Category 2 (threatened) and 38 species of Category 3 (nearly threatened). In the resurvey, there were 53 RL species, 4 species in Category 1, 13 in Category 2 and 36 in Category 3. Regarding shifts in strategy and life history for the regional species pool, trait state frequencies remained nearly constant for all analysed categories, with only a few significant changes in species numbers related to phenology and life form (Table 2). In the resurvey, we found 10 new early flowering species, but did not find again 20 mid-summer flowering species as well as 19 competitive-stress-ruderal (CSR) strategists.

3.2 | Richness and Diversity Increased, With Greater Shifts in Species Composition Than in Trait Composition

Comparing the plot pairs of the two surveys, for community data, the mean species richness increased from 20 to 28 species (Figure 2a), while the sum of covers decreased (94% to

TABLE 2 | Species' frequencies of the regional species pool per functional trait group for the original data (1993) and the resurvey (2021), including species not observed in 2021 (Not 2021) and only observed in 2021 (New 2021), with p-values (p) according to proportional z-tests, adjusted for false discovery rates (Benjamini and Hochberg 1995).

Functional trait	Trait level	1993	2021	p	Not 2021	New 2021	p
Strategy type	Competitivestress-ruderal	81	68	1	19	6	0.06
	Competitive	41	43	1	11	13	0.98
	Competitive-ruderal	33	32	1	6	5	0.99
	Competitive-stress	33	31	1	8	6	0.98
	Ruderal	22	28	1	3	9	0.28
	Stress-ruderal	15	20	1	1	6	0.28
	Stress	4	5	1	—	—	—
Life form	Hemicryptophyte	149	141	1	33	25	0.85
	Therophyte	66	73	1	13	20	0.85
	Geophyte	21	19	1	4	2	0.86
	Herbaceous chamaephyte	17	15	1	4	2	0.86
	Phanerophyte	7	8	1	3	4	0.99
	Woody chamaephyte	6	5	1	—	—	—
Life span	Perennial	165	153	0.88	37	25	0.4
	Annual	68	76	0.88	13	21	0.4
	Biennial	21	19	1	7	5	0.99
Phenology	Early spring	28	36	0.99	2	10	0.08
	Mid spring	38	37	1	8	7	0.99
	Early summer	87	93	0.77	16	22	0.51
	Mid summer	67	49	0.32	20	2	0.04

63%; Figure 2b). Even with the Braun-Blanquet cover values adjusted to the lowest of the applicable Londo classes, those trends in cover changes were still significant ($p < 0.001$; $n = 131$). The Shannon diversity index significantly increased (from 1.86 to 2.25; Figure 2c) as did species evenness (from 0.62 to 0.68; Figure 2d; test statistics in Appendix S3, Table S2). Species composition of the plot pairs changed significantly, as revealed by the RDA analysis (Figure 3a). Of the floristic variation in the resurveyed plots, 3.4% was explained by time (constrained axis, $p < 0.001$). Additionally, the species' dissimilarity (distance to centroids) of the plot pairs significantly decreased from 0.61 to 0.59 in the resurvey ($p < 0.01$). For the trait composition, a similar amount of variation was explained by time (4.2%; $p < 0.001$; Figure 3b). Significant decreases in trait values were found for leaf dry matter content (LDMC); EIVs for temperature, light, moisture and soil reaction; the numbers of hemicryptophytes, woody chamaephytes and geophytes as well as the possession of a perennial lifespan (Figure 4). Contrastingly, the number of therophytes increased, as did the specific leaf area (SLA), the use of seeds for reproduction and the possession of a ruderal life strategy, as well as the number of species blooming in early spring. However, trait dissimilarity of the plot pairs was constant, with an average distance of the plot scores to their centroid being 0.34 in both surveys ($p = 0.92$).

3.3 | Community Types Displayed Different Trends in Species Richness and Functional Composition

The dry grassland community types differed in shifts in species richness and diversity as well as shifts in taxonomic and functional composition (test statistics in Appendix S3, Tables S3 and S4). Large relative changes in species richness encountered for the Galio-Agrostidetum (+11 species on average) and the Euphorbio-Callunetum, similar to the Thymo-Festucetum (both +8 species). All community types showed a decrease in cover, with the most pronounced changes of more than one-third in the Euphorbio-Callunetum (−42.1% cover) and the Filipendulo-Helictotrichetum (−36.9% cover), while the cover of the Thymo-Festucetum decreased the least (−21.4% cover). Species diversity significantly increased in all of the community types except for the Filipendulo-Helictotrichetum. Highest diversity increases were found in the Dauco-/Tanaceto-Arrhenatheretum (+0.51), along with the Galio-Agrostidetum and the Thymo-Festucetum (both +0.49). Significant changes in species evenness occurred in the Dauco-/Tanaceto-Arrhenatheretum (+0.11) and the Thymo-Festucetum along with the Galio-Agrostidetum (both +0.08).

The turnover in species composition explained by time was significant for each community type (Figure 5a; $p < 0.001$). The

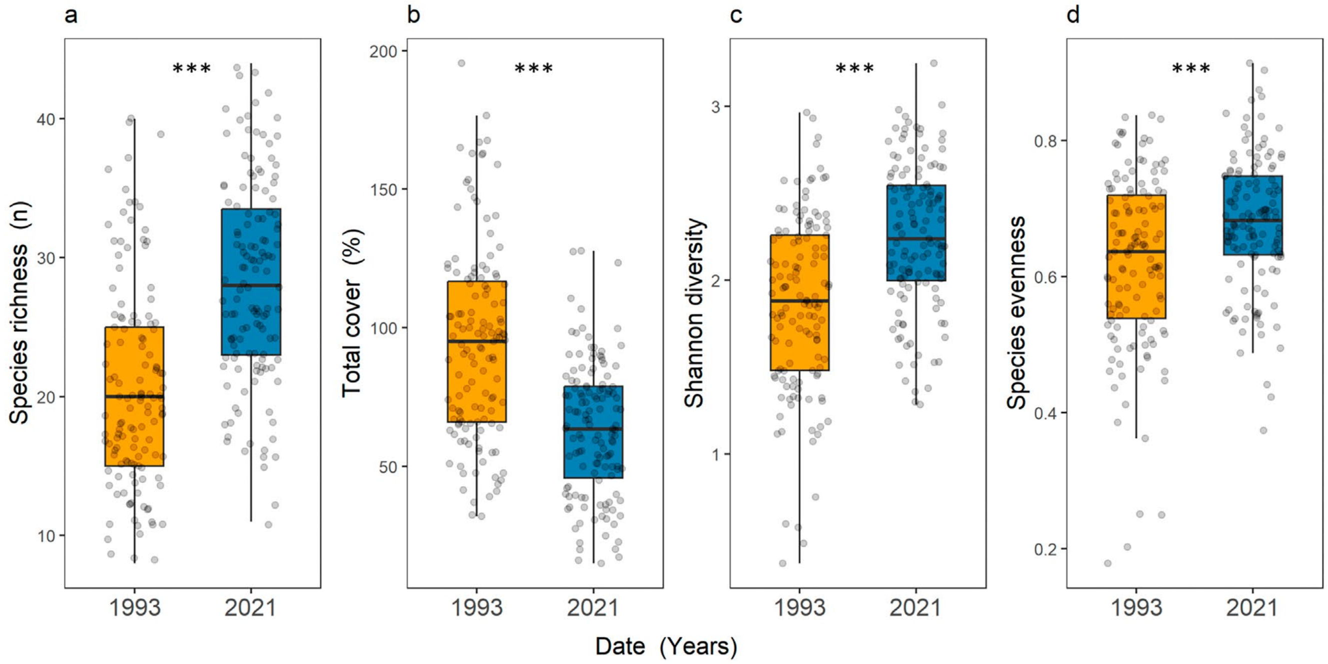


FIGURE 2 | Differences in taxonomic diversity measures between the original survey (yellow, 1993) and the resurvey (blue, 2021) for (a) species richness, (b) total cover values of all species, (c) Shannon diversity and (d) species evenness, with points from each plot jittered for visibility. Differences between the survey and resurvey were compared with paired *t*-tests (with df = 130, $p < 0.001$).

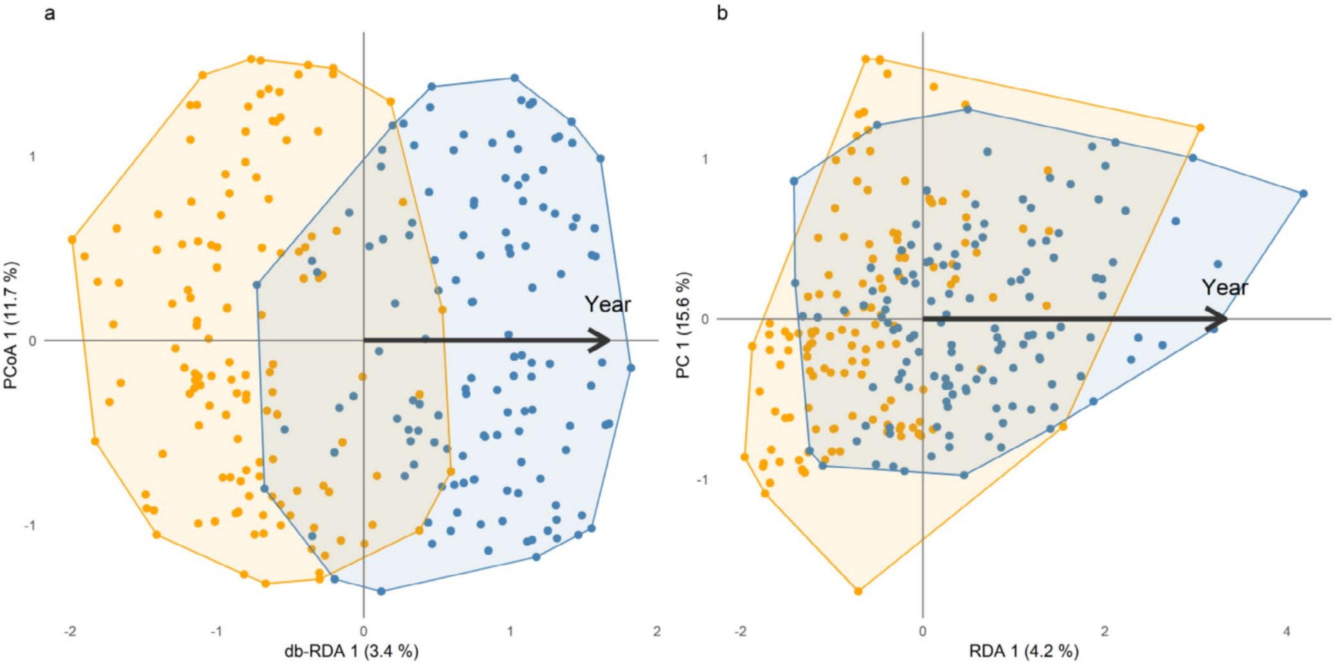


FIGURE 3 | Differences in (a) species composition, analysed with distance-based RDA and using Bray–Curtis dissimilarities, and in (b) trait composition, analysed with ordinary RDA, both between the original survey (yellow, 1993) and the resurvey (blue, 2021). The constraining variable (arrow) in both ordinations was the year of survey.

amount of floristic variation differed between community types, being highest in the Galio-Agrostidetum (20.9%), followed by the Dauco-/Tanaceto-Arrhenatheretum (17%) and the Euphorbio-Callunetum (15.1%), and was 7%–10% in the other communities. Contrary to the slight decrease in the regional species pool, the ADC values, measuring beta diversity, increased significantly in the resurvey, except for the Thymo-Festucetum. ADC values increased the most in the Dauco-/Tanaceto-Arrhenatherum (+0.19) and the least in the Filipendulo-Helictotrichetum (+0.07). However, species beta diversity of the regional species pool showed the opposite trend, with a slight but significant decrease (−0.02).

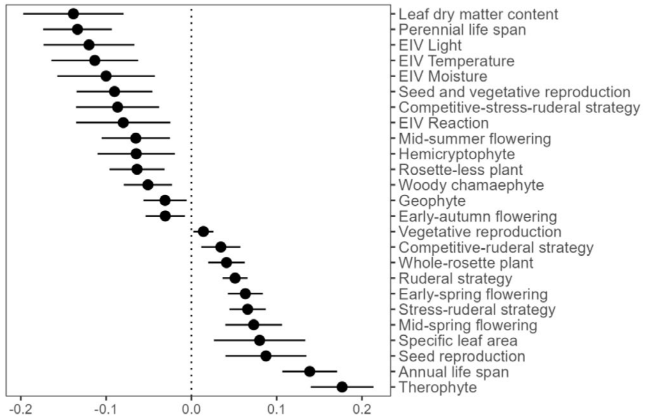


FIGURE 4 | Differences in CWM trait values, between the original survey (1993) and the resurvey (2021), displayed from the largest negative to the largest positive CWM difference. Only traits with a significant difference are shown ($p < 0.05$, according to *t*-test), with error bars indicating standard errors.

The turnover in trait composition explained by time ranged between 6.4% and 19.1% (Figure 5b). The temporal shift was significant for all community types ($p < 0.001$), with the highest explained variation in the Galio-Agrostidetum (19.1%), Dauco-/Tanaceto-Arrhenatheretum (15.8%) and Euphorbio-Callunetum (15.5%), and lower amounts in the other communities (6%–9%). The negative changes in the Galio-Agrostidetum and the Dauco-/Tanaceto-Arrhenatheretum indicate that the number of decreasing trait values exceeded that of increasing ones, contrary to the predominant increase of the traits in other community types. ADC values significantly increased in three community types and were highest in the Galio-Agrostidetum (+0.14) and Dauco-/Tanaceto-Arrhenatheretum (+0.16) and lowest in the Filipendulo-Helictotrichetum (+0.06), while no such trend was observed for trait beta diversity in the regional species pool.

The community types differed not only in the amount of functional change but also in traits ($p < 0.05$) that changed most (Figure 6). The first axis of the PCA explained 45.6% of the variation, separating the community types into two groups: the Thymo-Festucetum, Euphorbio-Callunetum, Festuco-Brachypodietum and Filipendulo-Helictotrichetum with many traits increasing over time (e.g., increasing annuals and therophytes, increasing seed reproduction, ruderality and early spring flowering), but also some decreasing frequencies (e.g., of perennials and hemicryptophytes or a decrease in mid-summer flowering), while the Galio-Agrostidetum and Dauco-/Tanaceto-Arrhenatheretum showed the opposite trend. The second axis (19.4%) slightly separated the Filipendulo-Helictotrichetum from the other communities, that is, by its vegetation being more sclerophyllic.

The trait shifts were even more pronounced in the different community types than for the regional species pool, showing greater changes and more shifted traits in the less stressed community types (Appendix S2, Figure S3). While the trend of increasing therophytes, ruderals and annuals in the regional species pool continued across all community types, other trait shifts showed opposite trends. In the Thymo-Festucetum, the community type with the highest initial drought stress and decreasing EIVs for temperature, soil reaction and light might point to declining specialists, which here would be the woody chamaephytes with scleromorphic leaf anatomy adapted to drought and acidic soil conditions. The Filipendulo-Helictotrichetum showed a decreasing EIV for moisture, which might have affected the hemicryptophytes that were sensitive to drought. Surprisingly, in the Festuco-Brachypodietum, increasing EIVs for moisture and light point to improved conditions for competitors, probably through declining perennials in this rather grass-dominated community type. Major trait shifts were observed for the Galio-Agrostidetum, with all EIVs and SLA decreasing, maybe pointing to the decline of drought-sensitive hemicryptophytes, which would be the mid-summer flowering perennials representing the majority of species in that community type. In contrast to all other community types, the Dauco-/Tanaceto-Arrhenatheretum was characterised by an increase in the EIV for nutrients, but decreasing EIVs for reaction, temperature and light, pointing to an increase in more productive and less drought-tolerant species, while scleromorphic leaf anatomy also became more common. In the Euphorbio-Callunetum, the increasing EIVs for moisture and light together with decreases in LDMC, scleromorphic leaf anatomy and autumn-flowering woody chamaephytes might also point to the decline of community specialists.

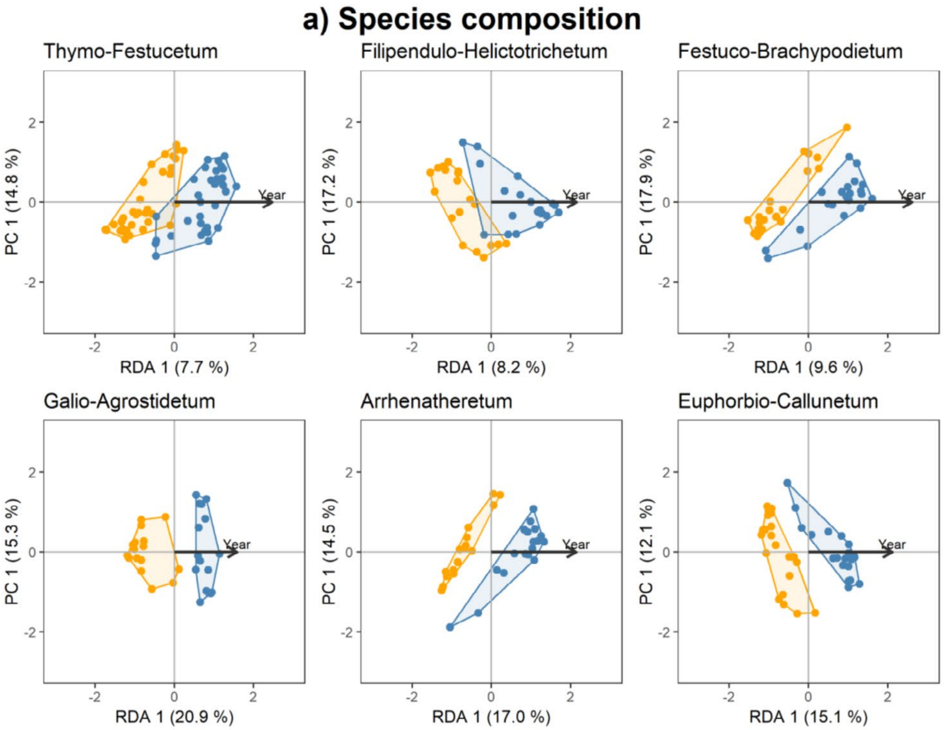
Although the community types differed in the amount and direction of changes, for both the species composition and the trait composition, these shifts were not correlated to the DSI and neither to the HSI or WSI (Appendix S2, Figure S4). However, among the community types, the HLI was significantly correlated to the amount of changes in the Festuco-Brachypodietum ($R^2 = 0.29$, $p < 0.05$) and in the Euphorbio-Callunetum ($R^2 = 0.21$, $p < 0.05$), indicating that their changes in trait composition between the surveys were greater with increasing heat load (Appendix S2, Figure S5). Although the WSI better differentiated between community types (Appendix S2, Figure S2), also accounting for most of the observed variation in the DSI, the magnitude of vegetation changes in terms of both species and trait composition was more closely related to the DSI than to the HLI (Appendix S2, Figures S4 and S5). This suggests that the HLI may influence vegetation dynamics in interaction with water availability, highlighting the importance of water-related stress gradients in driving functional and compositional shifts.

4 | Discussion

Our resurvey of 131 vegetation plots first surveyed in 1992/1993 in the species-rich porphyry dry grasslands showed that neither the regional nor the plot-scale diversity of vascular plant species has decreased over the last 30 years, though species turnover was substantial. Community composition shifted towards a higher abundance of therophytes and grass species, at the expense of perennials and of total vegetation cover. The magnitude of these shifts varied among the six investigated community types and was related to the amount of topography-induced drought stress in two of the six community types.

4.1 | Changes in Functional Composition Are Not Connected to the Size of the Species Pool

The size of the regional species pool of the porphyry dry grasslands did not decrease over the last 30 years, rejecting our



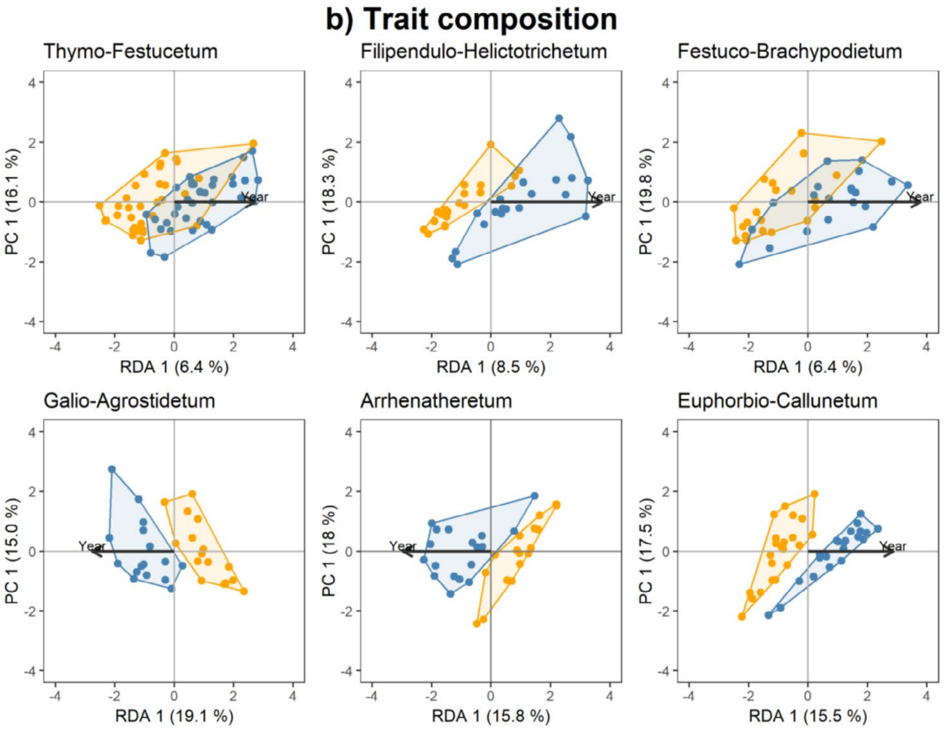


FIGURE 5 | Differences for the six dry grassland community types in (a) species composition, analysed with distance-based RDA and using Bray–Curtis dissimilarities, and (b) trait composition, analysed with ordinary RDA, between the original survey (yellow, 1993) and the resurvey (blue, 2021). The constraining variable (arrow) was the year of survey, showing positive (mainly increasing) or negative (mainly decreasing) trends of species for trait values in the plots (dots) over time.

hypothesis that the species pool became smaller. Our finding of substantial species turnover changes, which were not connected to species richness trends, supports results from other studies that found species turnover to be more influenced by changes in abundance and dominance of resident species than extinction or colonisation (Hillebrand et al. 2018). However, the nature of functional turnover indicates changing precipitation patterns and an increasing frequency of drought events over the study period, thus confirming our hypothesis that the frequency of occurrence of strategy types and life-history traits is trending to more competitiveness, more or less across all community types. The lower number of species that flower in summer and

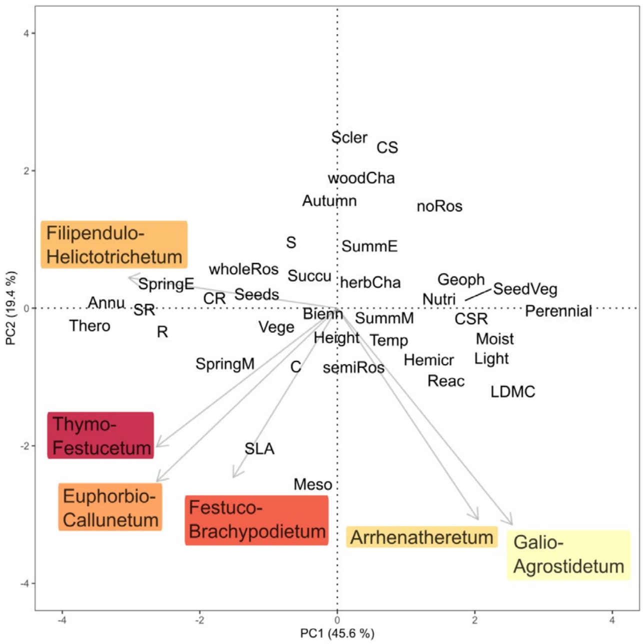


FIGURE 6 | Principal component analysis (PCA) of factor loadings of CWM trait value changes (from RDA) for the six dry grassland community types that are coloured according to their drought stress level from low (yellow) to high (red), showing which traits increased or decreased with time in the respective community type. Codes are as specified in Table 1.

autumn, together with the higher number of (early) spring-flowering species, indicates a lengthened growing season with a shift towards warmer and moister winter and spring conditions and an avoidance of summer droughts. According to meteorological data for this particular region, in the past 30 years, the mean annual temperature increased from 9.7°C to 10.6°C (German Weather Service, April 2023). While slightly decreasing rainfall during summer was not found to be significant for Germany, the number of rainless days in a row, meaning more than 30°C for a duration of at least 14 days, tripled over the past 70 years. Fischer et al. (2020) have found species' responses to seasonal weather fluctuations to vary with their different life histories and ecology, with annuals benefitting from wet springs, while perennials are sustained by wet summers. Although more annual species were counted in our resurvey at the community scale, their number did not increase significantly at the level of the species pool, as most species were already present. Hence, the increasing frequency of prolonged summer drought events in the porphyry dry grasslands seems to be acting as a filter at the scale of the species pool, reducing the cover of perennial species. As a result, the declining abundance of perennials is clearing space for the establishment of annual species (Fischer et al. 2020). Vacant soil patches, together with the presence of soil moisture, are the principal resources for the establishment of annual seedlings, while a warm temperature is the key environmental condition. In this context, having seed dormancy could provide a competitive advantage in periods of extreme drought, mainly benefitting annual species. Doležal et al. (2022) have reported species-specific responses linking precipitation to root length and seed mass of annuals in temperate grasslands, as the recruitment of deep-rooted, heavy-seeded species was improved by both winter and spring precipitation. Despite being part of the regional species pool, ruderals are regarded as potentially problematic species that have become newly established at many sites, where their increasing cover indicates either improved dispersal in the absence of grazing or decreasing habitat quality, brought about by an increased nutrient supply from agriculture (Valcheva et al. 2021; Klinkovská et al. 2024). This increase of ruderals seems to be independent of the protection status of those grasslands (Harásek et al. 2023). For instance, even in the inner Tyrolean Alps, ruderals (e.g., *Convolvolus arvensis*) have migrated into the alpine steppe vegetation (Lübben and Erschbamer 2021). Consistent with literature findings, in three of our community types the number of ruderals increased, comprising habitats with strongly divergent environmental conditions, in particular with respect to soil reaction and nutrient content (for an overview on our soil conditions, see Wesche et al. 2005). For example, Krumbiegel et al. (1998) have stated that ruderals were not able to survive the harshest conditions in the porphyry outcrops, which are on the south-westerly exposed shallow soils characteristic of the Thymo-Festucetum. In contrast, in our resurvey, ruderal annuals, e.g., *Senecio vernalis*, *Papaver argemone* or *Trifolium* spp., were common new colonisers in the Thymo-Festucetum. The EIV for nutrients indicates improved soil conditions since the first survey on their originally nutrient-poor sites, which, besides nitrogen deposition, are further enriched through N_2-fixation by newly colonising Fabaceae species (i.e., *Trifolium dubium*, *Trifolium campestre, Trifolium arvense*), as reported for dry grasslands in Western and Central Europe (Diekmann et al. 2019; Mitchell et al. 2017; Schüle et al. 2023). In addition, Schüle et al. (2023) have found that species of earlier successional stages of grasslands were declining (e.g., *Aira caryophyllea*, *Corynephorus canescens*), along with stress-tolerant ruderals and stress-tolerant competitors (e.g., *Sedum sexangulare*), which also declined in our resurvey. Succession might also have contributed to the changes observed in the porphyry dry grasslands in the last decades, particularly on bigger outcrops, where the lack of grazing benefits shrub encroachment. This might exacerbate in the future, as long as there are only occasionally some management measures initiated by associations for ecological conservation on a few big outcrops, such as occasional sheep grazing or manual clearing of shrubs.

4.2 | Taxonomic and Functional Shifts Reflect Increasing Drought Stress and Nitrogen Deposition

At the community scale, species richness and diversity increased over 30 years in the porphyry dry grasslands, in spite of decreasing plant cover, thus showing the opposite trend to that hypothesised. This trend might be the result of the increasing number of annuals and ruderals in all communities, compared to the lower number of declining specialists in the overall richness balance. This increase was mainly caused by annual plant species increasing their cover following phenological shifts and spreading across the plots, for example, species flowering earlier in the season, such as *Arabidopsis thaliana*, *Spergula morisonii*, *Cerastium pumilum*, *Erophila verna*, *Holosteum umbellatum* and *Senecio vernalis*, supporting our hypothesis of a shift towards more short-living life forms. The reason for that spread might be due to better seedling survival under the moister and warmer conditions now occurring in winter and spring as well as the lack of sheep trampling to which these small species would be sensitive. Increased seed reproduction and ruderality is reflected in the increasing proportion of therophytes, which indicates that drought avoidance is a successful survival strategy (Hofer et al. 2016; Griffin-Nolan et al. 2019), as occurs in other types of dry grasslands (Diekmann et al. 2019; Fischer et al. 2020; Scherrer et al. 2022; Klinkovská et al. 2024). Similarly, that increase in therophytes explains the increase in archaeophytes, which generally are often non-native arable weeds that were introduced with agriculture.

In the porphyry dry grasslands, those archaeophytes have become more dominant, for example, brome grasses, such as the perennial *Bromus erectus*, which most likely benefits from the mild winters (Meier et al. 2021, 2022), or the annual *Bromus hordeaceus* and *Bromus sterilis*, the last of which was the species with the greatest increase in abundance and cover in the resurveyed plots. Having been a weed problem in agriculture since the 1970s, *Bromus sterilis* is a strong competitor that exploits unused soil resources and thrives well in dense stands (Fenesi et al. 2011). Moreover, *Robinia pseudoacacia* (an increasing neophyte in the porphyry dry grasslands) is associated with the dominance of *Bromus sterilis*, which is tolerant to *Robinia's* allochemicals (Fenesi et al. 2011). However, so far *Robinia pseudoacacia* does not play a big role in the grasslands as long as they are not affected by the encroachment of shrubs. As a consequence of the intensification of agricultural management with herbicides, typical crop weeds (e.g., *Consolida regalis*, *Centaurea cyanus*, *Papaver argemone*) have mostly disappeared from the surrounding mosaic of arable fields, but still find marginally suitable habitats at the edges of the porphyry outcrops (Deák et al. 2020), contributing to an increase in the overall biodiversity of the resurveyed plots.

In contrast to our hypothesis of increasing nutrient supply through nitrogen deposition, the EIV for nutrients did not increase. One explanation might be reduced nitrogen mineralisation rates during drought, which are reported to limit the nitrogen uptake by roots along with decreased microbial biomass (Schaeffer et al. 2017; Fuchslueger et al. 2019; Yang et al. 2020). Thus, nitrogen fertilisation does not affect grassland productivity, diversity or phenology under severe and prolonged drought (Carlsson et al. 2017; Nogueira et al. 2017).

Along with the observed increases of generalists in the porphyry dry grasslands, specialists decreased. The decline of habitat specialists, such as heliophilic, thermophilic and acidophilic species, is reflected in lower EIVs for soil reaction, light and temperature, as reported also from other dry grasslands (Diekmann et al. 2019; Klinkovská et al. 2024; Finderup Nielsen et al. 2021). Declining specialists often are indigenous chamaephytes, such as *Calluna vulgaris*, *Thymus serpyllum* or *Helianthemum nummularium*. Their decline is probably the reason for the decrease of total cover in the resurveyed plots and also explains the decrease in LDMC over the years, as all those species are woody chamaephytes. This indicates a decreasing general stress tolerance of the resident species. While chamaephytes have been reported to survive repeated drought events without suffering severe damage at older ages (Barros et al. 2017), juveniles might lack the necessary capacity to re-sprout after drought-caused damage. For the chamaephytes in the porphyry dry grasslands, it is likely that both the prolonged and repeated drought events of the recent years and the coincidence of short or missing recovery phases have decreased the population sizes of those specialists. Geophytes were also negatively affected, surprisingly including drought-adapted perennial grasses with rhizomes, such as *Poa angustifolia* or *Brachypodium pinnatum*, as well as rare species with bulbs, such as *Muscari tenuiflorum* or *Anacamptis morio*. Fang et al. (2024) reported drought as one of many perturbations that negatively affect the bud bank density of geophytes, which might also explain the decrease of geophytes in the porphyry dry grasslands.

4.3 | Shifts in Species Composition and Functional Traits Are Greater in Less Drought-Stressed Community Types

The investigated community types varied in species richness and diversity and in their functional responses. The increase of generalists indicates a tendency towards biotic homogenisation across the community types, as reported for other grassland types (Ross et al. 2012; Watts et al. 2022). Against our third hypothesis that greater heat and drought stress among the communities would result in greater shifts along with the decreased cover, diversity increases were unrelated to the magnitude of drought stress. However, greater changes in richness and composition occurred in community types with less stressful conditions, such as the Galio-Agrostidetum and Dauco-/Tanaceto-Arrhenatheretum. An explanation might be that fewer species, mostly specialists, can occur in the most stressful conditions, whereas less stressful conditions can be used by more and more different species. Moreover, the community types with larger changes were probably affected by other factors than those captured by our DSI.

Rather than climate change, land-use is often mentioned as a main driver of changes in the taxonomic (Schils et al. 2022) and functional composition of grasslands (Allan et al. 2015), being even more pronounced in combination with drought (Stampfli et al. 2018; Schüle et al. 2023). Changes that are caused by altered land-use might vary with the local species pool, as the species composition often reflects shifts in competitive dynamics rather than a response to environmental stress. In addition, the shifts in community composition might lag behind environmental changes (Conradi and Kollmann 2016). In particular, species' responses to stressors might be affected by interactions with other species, including competition and facilitation as well as herbivory, either through resumed sheep grazing on some outcrops (feeding mainly on Poaceae) or through feral deer browsing on preferred plants (e.g., *Anthericum liliago*). Moreover, habitat alteration in various ways, such as abandonment and shrub encroachment, can lead to local extinctions of vascular plants (Auffret et al. 2018; Geppert et al. 2020), which on the heterogeneously managed or partly abandoned porphyry outcrops is apparent, where some specialist populations have already completely disappeared by the time of the resurvey on some of the outcrops (e.g., *Thymus serpyllum*, *Calluna vulgaris*, *Anthoxanthum odoratum*). This indicates that land-use is another driver for vegetation changes in the porphyry dry grasslands.

Our results suggest that the causes for changes in taxonomic and functional composition are not generalisable across the dry grassland community types. However, since all communities have been affected and even drought-adapted grassland communities showed small compositional changes, it is likely that some community types will survive future climate change better than others, depending on the species' ability to recover from drought stress or to cope with the changing nutrient status in soil. The goal of reverting changed dry grassland communities to their initial states is a complex management challenge. For example, the high cover loss in the Euphorbio-Callunetum is caused by decreased *Calluna vulgaris*, which is adapted to acidic and nutrient-poor soil conditions. But a recovery of *Calluna* populations is difficult, as the seedlings are highly sensitive to drought during germination and seedling stages (Meyer-Grünefeldt et al. 2015; Birkeli et al. 2023). In general, the anthropic reintroduction of perennials in dry grasslands is complex, as the establishment and survival of seedlings depend on the presence of appropriate environmental conditions (Kövendi-Jakó 2017), on both temporal and spatial scales as well as on the species pool (Waldén et al. 2017) on local management adaptations, for example, the grazing period and grazing intensity (Buisson et al. 2015; Dostálek and Frantík 2012; Elias et al. 2018; Gilhaus et al. 2017). Ongoing management of those areas can help compensate for climatic and land-use changes (Harásek et al. 2023). This underlines the contribution of long-term monitoring as the logical basis of future management decisions in grassland and also other ecosystems (Bauer and Albrecht 2020).

5 | Conclusions

Using a historic dataset from one of the driest regions in Central Europe, we show that dry grassland community types, occurring under different levels of environmental stress, have undergone significant shifts in both species and functional composition, in favour of generalist species with faster life cycles at the expense of local specialists. While a significant species turnover and functional change but no richness change was observed at the regional species pool level, the analysis of changes at the community level revealed more nuanced changes with overall local richness increase and plot cover decrease. Changes can be expected to accelerate over the next decades, due to a predicted higher frequency of drought events (Spinoni et al. 2017), but could be counteracted by the resumption of grazing as a positive management strategy for these grasslands, as it would reduce the spread of generalists while creating small-scale disturbances and keeping the landscape open for the regeneration and reestablishment of dry grassland specialists in wetter years. This also underlines the importance of locally adapted management practices and highlights the need to include future monitoring in the evaluation of the success of such management actions.

Author Contributions

Susanne Horka conducted the resurvey together with Ute Jandt. All authors analysed the data. Susanne Horka wrote the initial draft of the manuscript. All authors contributed to the final manuscript.

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Conflicts of Interest

The authors declare no conflicts of interest.

Data Availability Statement

Data is openly accessible at the Data Repository of the German Centre for Integrative Biodiversity Research (iDiv, https://doi.org/10.25829/IDIV.3590-53np94) Halle-Jena-Leipzig and ReSurveyGermany (Horka et al. 2025).

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Supporting Information

Additional supporting information can be found online in the Supporting Information section.