Received: 29 May 2023 | Revised: 17 April 2024 | Accepted: 23 April 2024

DOI: 10.1111/gcb.17315

RESEARCH ARTICLE

Global Change Biology WILEY

Large-scale remote sensing analysis reveals an increasing coupling of grassland vitality to atmospheric water demand

Katja Kowalski[1] | Cornelius Senf[2] | Akpona Okujeni[1,3] | Patrick Hostert[1,3]

[1]Geography Department, Humboldt-Universität zu Berlin, Berlin, Germany

[2]School of Life Sciences, Earth Observation for Ecosystem Management, Technical University of Munich, Freising, Germany

[3]Integrative Research Institute of Transformations of Human-Environment Systems (IRI THESys), Humboldt-Universität zu Berlin, Berlin, Germany

Correspondence
Katja Kowalski, Geography Department, Humboldt-Universität zu Berlin, Unter den Linden 6, 10099 Berlin, Germany.
Email: katja.kowalski@tum.de

Present address
Katja Kowalski, School of Life Sciences, Earth Observation for Ecosystem Management, Technical University of Munich, Hans-Carl-von-Carlowitz-Platz 2, 85354, Freising, Germany

Funding information
Bundesministerium für Bildung und Forschung, Grant/Award Number: 031B0734I; Einstein Foundation Berlin and Berlin University Alliance, Grant/Award Number: ERU-2020-609

Abstract

Grasslands provide important ecosystem services to society, including biodiversity, water security, erosion control, and forage production. Grasslands are also vulnerable to droughts, rendering their future vitality under climate change uncertain. Yet, the grassland response to drought is not well understood, especially for heterogeneous Central European grasslands. We here fill this gap by quantifying the spatiotemporal sensitivity of grasslands to drought using a novel remote sensing dataset from Landsat/Sentinel-2 paired with climate re-analysis data. Specifically, we quantified annual grassland vitality at fine spatial scale and national extent (Germany) from 1985 to 2021. We analyzed grassland sensitivity to drought by testing for statistically robust links between grassland vitality and common drought indices. We furthermore explored the spatiotemporal variability of drought sensitivity for 12 grassland habitat types given their different biotic and abiotic features. Grassland vitality maps revealed a large-scale reduction of grassland vitality during past droughts. The unprecedented drought of 2018–2019 stood out as the largest multi-year vitality decline since the mid-1980s. Grassland vitality was consistently coupled to drought (R^2 = .09–.22) with Vapor Pressure Deficit explaining vitality best. This suggests that high atmospheric water demand, as observed during recent compounding drought and heatwave events, has major impacts on grassland vitality in Central Europe. We found a significant increase in drought sensitivity over time with highest sensitivities detected in periods of extremely high atmospheric water demand, suggesting that drought impacts on grasslands are becoming more severe with ongoing climate change. The spatial variability of grassland drought sensitivity was linked to different habitat types, with declining sensitivity from dry and mesic to wet habitats. Our study provides the first large-scale, long-term, and spatially explicit evidence of increasing drought sensitivities of Central European grasslands. With rising compound droughts and heatwaves under climate change, large-scale grassland vitality loss, as in 2018–2019, will thus become more likely in the future.

KEYWORDS
drought, EUNIS, habitat, Landsat, Sentinel-2, time series, Vapor Pressure Deficit

1 | INTRODUCTION

Grasslands are one of the largest biomes globally, covering up to 40% of the terrestrial land area (O'Mara, 2012) and providing livelihood to millions of people (Gibson, 2009). They further are important carbon sinks (Chang et al., 2015; Dangal et al., 2020), as well as global hotspots of biodiversity (Mittermeier et al., 2011; Wilsey, 2018). One region with particular high abundance and diversity of semi-natural and agriculturally improved grasslands is Central Europe. The grassland systems of Central Europe deliver essential resources for livestock farming (Bengtsson et al., 2019), are rich biodiversity reservoirs (Habel et al., 2013; Wilson et al., 2012), and are important features of local cultural landscapes (Pellaton et al., 2022). Despite their importance, grasslands in Central Europe are already facing increasing pressures from meteorological extreme events, such as droughts (Ciais et al., 2005; Fu et al., 2020), which are expected to further accelerate under climate change (Hari et al., 2020; Spinoni et al., 2018). The years 2018 to 2020, for instance, have been characterized by extreme drought conditions across large parts of Central Europe, which were unprecedented in the last 250 years (Hari et al., 2020; Rakovec et al., 2022). This recent drought episode has substantially affected grassland productivity (Bastos et al., 2021) and impacts on grasslands have likely been amplified by anthropogenic warming through a higher atmospheric water demand resulting from simultaneously low water availability and high temperatures (i.e., “hotter drought”; Samaniego et al., 2018; Teuling, 2018; Yin et al., 2023). For the second half of the 21st century, such compounding drought and heatwave events are expected to affect up to 60% of Central European grasslands (Hari et al., 2020), highlighting the need for a well-founded and detailed understanding of how grasslands respond to drought under climate change.

Droughts, here defined as periods of unusually low water availability relative to the long-term average (Sheffield & Wood, 2011), can have significant impacts on the functioning of grasslands (Fu et al., 2020; Reichstein et al., 2007). Droughts, for instance, can change grassland community structure and diversity (Reynaert et al., 2021), decrease carbon uptake and thus grassland productivity (Felton & Goldsmith, 2023), and ultimately lead to hydraulic failure and plant mortality (Grossiord et al., 2020; Volaire, 2018). Grasses and forbs have a comparably low rooting depth, preventing them from reaching moisture in deeper soil layers during drought (Jackson et al., 1996) and they reduce transpiration later than other vegetation types (e.g., trees), causing accelerated soil water depletion under continuous drought conditions (Teuling et al., 2010; Wolf et al., 2013). In experimental studies, declining productivity and plant mortality was frequently observed under different levels of precipitation exclusion (Gilgen & Buchmann, 2009; Hovenden et al., 2017; Mackie et al., 2019; Stampfli et al., 2018), and high temperatures additionally exacerbated plant mortality during long-lasting drought periods (Reynaert et al., 2021). High air temperatures have an amplifying effect on droughts, because evaporative demand increases, leading to faster depletion of soil moisture (Miralles et al., 2014). This, in turn, creates a feedback mechanism further increasing air temperatures (Teuling, 2018), which has already been observed under past summer droughts (Teuling et al., 2010). Recent research highlights the important role increasing temperatures might play for drought impacts on grasslands under climate change. Yet, while those past studies have substantially improved our understanding of drought impacts on grassland systems, it is still unclear how well conclusions from those mostly experimental studies translate to real-world grassland systems, covering heterogeneous biophysical and land use conditions (Knapp et al., 2018; Kröel-Dulay et al., 2022). In fact, the response of grassland systems to drought might be modulated by a multitude of environmental factors, including precipitation gradients (Huxman et al., 2004; Maurer et al., 2020), soil properties (Luna et al., 2023), topography (Buttler et al., 2019; Gharun et al., 2020), land management (Bütof et al., 2012; Karlowsky et al., 2018; Stampfli et al., 2018; Vogel et al., 2012), or the site-specific community composition of grassland habitats (Wellstein et al., 2017). To better understand the potentially complex impacts of past and future droughts on grassland systems, it is hence necessary to characterize drought impacts on grasslands over long time periods and across large environmental gradients, complementing recent insights from controlled experiments.

Satellite remote sensing is a key tool for understanding impacts of climate extremes on ecosystems across large scales (Felton & Goldsmith, 2023; Senf, 2022; West et al., 2019). In the case of grasslands, using dense time series of optical data covering several decades has been shown to be a promising approach for assessing drought impacts at national or even continental scales (Henebry, 2019), with coarse-scale remote sensing analyses revealing an immediate drought response of grasslands in Europe during recent drought periods (Chen et al., 2022, 2023; Ivits et al., 2014; Reinermann et al., 2019). Yet, the exact functional relationship between drought and grassland vegetation conditions remains still not empirically quantified, especially with respect to different drought indices, compounding drought and heatwave events, and grassland habitats in variable environmental conditions. Remote sensing-based vegetation indices such as the Normalized Difference Vegetation Index or Enhanced Vegetation Index were often used to analyze drought responses of ecosystems, including grasslands (Ivits et al., 2014; Reinermann et al., 2020). While those simple indices are practical proxies of photosynthetic activity, they suffer from several drawbacks such as saturation effects and difficult interpretability (Huete et al., 2002; Montandon & Small, 2008). More recently, ground cover percentages of green (i.e., photosynthetically active) vegetation, dry (i.e., non-photosynthetic) vegetation, and soil have proven to be interpretable, physical measures of grassland conditions (Guerschman et al., 2020; Lewińska et al., 2020, 2021). Based on these ground cover types, Kowalski et al. (2022, 2023) developed a grassland monitoring framework using dense intra-annual Sentinel-2 time series at 10 m spatial resolution, providing physical quantities related to grassland vitality loss during drought. Grassland vitality loss is thereby defined as high percentage of dry, non-photosynthetic vegetation (NPV) representing tissue dieback and a decrease in biomass growth. A high ground cover of photosynthetically active vegetation (PV), in turn, indicates sustained biomass growth during the active growing season, which we define as grassland vitality gain. The original approach by Kowalski et al. (2022) based on Sentinel-2 time series has recently been adopted to combined Sentinel-2 and Landsat time series (Okujeni et al., 2024), which creates novel opportunities for quantifying grassland vitality over several decades (Landsat provides data at 30 m spatial resolution since the 1980s) and across large spatial extents (e.g., national scale). Tapping into this data archive offers great potential for empirically quantifying how past droughts impacted grasslands in Central Europe, and thus to derive insights into the potential impacts of future droughts under climate change.

Here, our aim was to assess the spatiotemporal sensitivity of grasslands to meteorological drought over four decades and at national scale using a unique remote sensing product of grassland vitality (Okujeni et al., 2024). Our first objective was to map and quantify seasonal grassland vitality from 1985 to 2021 across all of Germany, where grasslands cover 4.7 million ha (DESTATIS, 2022) and are important from a social, ecological, and economic perspective (Huyghe et al., 2014). The second objective was to empirically quantify the sensitivity of grassland vitality to drought by (i) comparing a set of common drought indices for explaining the spatiotemporal variability in grassland vitality and by (ii) testing whether the link between grassland vitality and drought varies temporally, i.e., over the past four decades and spatially, i.e., across different grassland habitats. Our expectation was that meteorological conditions associated with drought were the dominant drivers of seasonal grassland vitality in the past four decades, with indices of atmospheric water demand having the strongest effect on grassland vitality compared to indices quantifying solely low water availability. We also presumed that the most extreme drought seasons have the strongest influence on grassland vitality and that the drought sensitivity of grasslands would show an increasing trend over the past four decades. Moreover, we expected that drought effects vary among grassland habitats, with an increasing sensitivity from wet to mesic to dry grassland habitats.

2 | MATERIAL AND METHODS

2.1 | Grassland vitality from Landsat/Sentinel-2 time series

To assess seasonal grassland vitality and its relation to meteorological drought, we used satellite-based time series of green vegetation, dry vegetation, and soil ground cover percentages for Germany. This fractional cover dataset was based on all available Sentinel-2 and Landsat data at 10 and 30 m spatial resolution, respectively; and included all stable grassland pixels in Germany from 1985 to 2021 (Okujeni et al., 2024). Ground cover percentages provide a quantitative measure of the main grassland components and reflect changes of grassland condition over time. Processes of land management, such as mowing or grazing, are captured as short-term decrease of the green vegetation cover with a quick recovery within a few days to weeks. During periods of limited water availability, the grassland response is captured by decreasing green vegetation fraction and simultaneous increase of dry vegetation and soil fractions (depending on vegetation cover density) over periods of several weeks to months (Kowalski et al., 2022, 2023). Based on ground cover percentages, we derived time series of the Normalized Difference Fraction Index (NDFI) for all grasslands in Germany. The NDFI was specifically developed to capture changes in grassland ground cover (Kowalski et al., 2022). By contrasting dry vegetation and soil relative to green vegetation, the NDFI provides a physically grounded indicator of grassland vitality over the growing season. The NDFI varies between −1 and 1. Positive NDFI values correspond to dominant dry vegetation or soil cover indicating low grassland vitality, whereas negative values indicate predominantly vital vegetation cover. As the NDFI introduced by Kowalski et al. (2022) requires a seasonal parameter which cannot be reliably derived for each year due to low observation frequencies of Landsat time series, we used a simplified version of the NDFI:

$$NDFI = \frac{f_{NPV} + f_{soil} - f_{PV}}{f_{NPV} + f_{PV} + f_{soil}},$$

where f_{NPV}, f_{soil}, and f_{PV} are the ground cover percentages between 0% and 100% for dry, non-photosynthetic vegetation (NPV); soil; and green, photosynthetically active vegetation (PV), respectively (Kowalski et al., 2022). The NDFI was calculated for each pixel observation in the time series.

To derive grassland vitality from NDFI time series, we first resampled all NDFI images from Sentinel-2 with 10 m spatial resolution to 30 m Landsat resolution. Next, we interpolated the NDFI time series to monthly time steps using Radial Basis Function Kernels. The interpolation step preserved temporal variation of grassland vitality within the growing season while also filling observation gaps in years with lower observation frequencies (Schwieder et al., 2016). As the number of cloud-free observations varied with space and time (Okujeni et al., 2024) and single observations can be influenced by grassland management, we used only grassland pixels with a minimum of two cloud-free observations between June and September. We defined grassland vitality as the average anomaly in NDFI between June and September. We chose this period to capture the response of grassland vitality to summer drought representing the dominant drought type in Central Europe (Markonis et al., 2021). Based on our definition, grassland vitality expresses the seasonal deviation from average conditions, thereby accounting for variability in phenological development and productivity of different grasslands. Positive deviations represent a seasonal grassland vitality loss (i.e., higher than average soil and dry vegetation cover) and negative deviations represent a seasonal vitality gain (i.e., higher than average green vegetation cover):

$$grassland\ vitality_t = \frac{1}{k}\sum_{m=1}^{k} NDFI_{t,m} - NDFI_{base_m},$$

where *grassland vitality* for year *t* is defined as the average monthly difference between *NDFI* and the long-term (1985–2021) average conditions $NDFI_{base}$ of month *m*, including $k=4$ months from June to September of year *t*.

2.2 | Meteorological data

We downloaded ERA5-Land monthly averaged data from the Copernicus Climate Change Service (C3S) for the years 1985 to 2021 (Muñoz Sabater, 2019). We obtained time series of temperature, dewpoint temperature, total precipitation, potential evaporation, and volumetric soil water. Based on these datasets, we derived anomalies of temperature, precipitation, soil moisture (average volumetric soil water for the three layers from 0 to 100 cm weighted by layer depth), Climatic Water Balance (CWB; calculated as the difference between precipitation and potential evaporation), and Vapor Pressure Deficit (VPD; capturing the atmospheric water demand based on air temperature and dewpoint temperature, calculated following Barkhordarian et al. (2019)). We obtained time series of monthly anomalies by subtracting the mean of the average monthly time series from 1985 to 2021 from each monthly value and dividing by the standard deviation of the entire monthly time series (i.e., *z*-transformation). We calculated seasonal anomalies for each growing season as the mean of the monthly anomalies from June to September. Seasonal anomaly time series served as drought indices for the analyses.

2.3 | Grassland habitat types

We used habitat probability maps based on the EUNIS (European Nature Information System) Habitat Classification as a proxy for the spatial distribution of grassland habitats in Germany. EUNIS provides a European-wide hierarchical classification system for terrestrial and marine habitats based on phytosociological vegetation types and additionally includes abiotic and geographic characteristics (Chytrý et al., 2020; Davies et al., 2004). EUNIS habitat probability maps were modelled based on vegetation plot data of the European Vegetation Archive using predictor variables capturing climate, soil, topography, and remotely sensed land cover and phenology (Hennekens, 2023). From all habitat probability layers, we selected habitat types occurring in Germany from the relevant grassland habitat groups R1, R2, R3, and R4 (habitat names and codes according to EUNIS2020, refer to Table S1 for habitat codes according to EUNIS 2020 and EUNIS2007; Chytrý et al., 2020). We excluded habitat types with very sparse vegetation cover which are unlikely to occur within the permanent grasslands we focused on. We finally retained 12 habitat probability layers (Table S1). From those, we selected the habitat type with the highest probability for every grassland pixel to obtain our final grassland habitat type map.

The four habitat groups were distributed spatially according to their environmental and biophysical conditions (Figure 1). Dry grasslands (R1) characterized by a low productivity and usually low management intensities (EEA, 2024) occur throughout eastern and Central Germany and to a smaller extent in western and southern regions. They are located in the most continental regions in eastern Germany and also in the central uplands in elevations up to 1000 m a.s.l. Most dry habitats were characterized by high average summer temperatures and VPD (Figure 1b). Mesic grasslands (R2) grow on more fertile soils compared to dry grasslands including mesotrophic to eutrophic areas (EEA, 2024). They are abundant on the lowland coastlines in northwestern Germany, partly growing on organic soils and characterized by an Atlantic climate (Figure 1b). Mesic grasslands also spread to higher elevations with higher levels of summer precipitation towards southern regions including low and medium altitude hay meadows, as well as mountain hay meadows (Figure 1b). Wet and seasonally wet grasslands (R3) include seasonally flooded or inundated grasslands that can be heavily modified and under intensive management (European Commission et al., 2016). These habitats are found in northern Germany along rivers and other water bodies, as well as along coastlines of the Baltic Sea, including areas with organic soils. The habitat group is also abundant in continental southeastern regions and in the Alpine foreland in higher elevations (Figure 1). Alpine and subalpine grasslands (R4) are mountainous grasslands covering only a small spatial extent in Germany (Figure 1a; Table S1). They occur on high elevations in the Alps with the highest precipitation sums (Figure 1b). These grasslands usually grow on shallow soils and are partly used as pastures (EEA, 2024).

2.4 | Sampling design

We based our drought sensitivity analysis on two large samples of Landsat/Sentinel-2 pixels from the grassland vitality maps. For the first sample, we randomly selected 10,000 pixels from all 30 m grassland pixels in Germany. We used this sample to analyze the relationship of grassland vitality to several drought indices. We created a second random sample stratified by habitat type to quantify drought sensitivities for different grassland habitat groups and types. For this sample, we randomly selected 500 pixels per habitat type, resulting in 6000 pixels overall. We introduced a minimum distance of 100 m between pixels to reduce spatial autocorrelation in both samples. For each pixel, we extracted seasonal grassland vitality and corresponding meteorological drought indices (i.e., anomalies of VPD, temperature, precipitation, CWB, and soil moisture). For the subsequent statistical analyses, we retained all samples with a maximum of 10 missing grassland vitality observations to reduce the potential influence of missing data.

2.5 | Statistical analyses

We investigated the effect of meteorological drought on grassland vitality by building mixed effects models predicting grassland vitality from each drought index, i.e., temperature, precipitation, soil

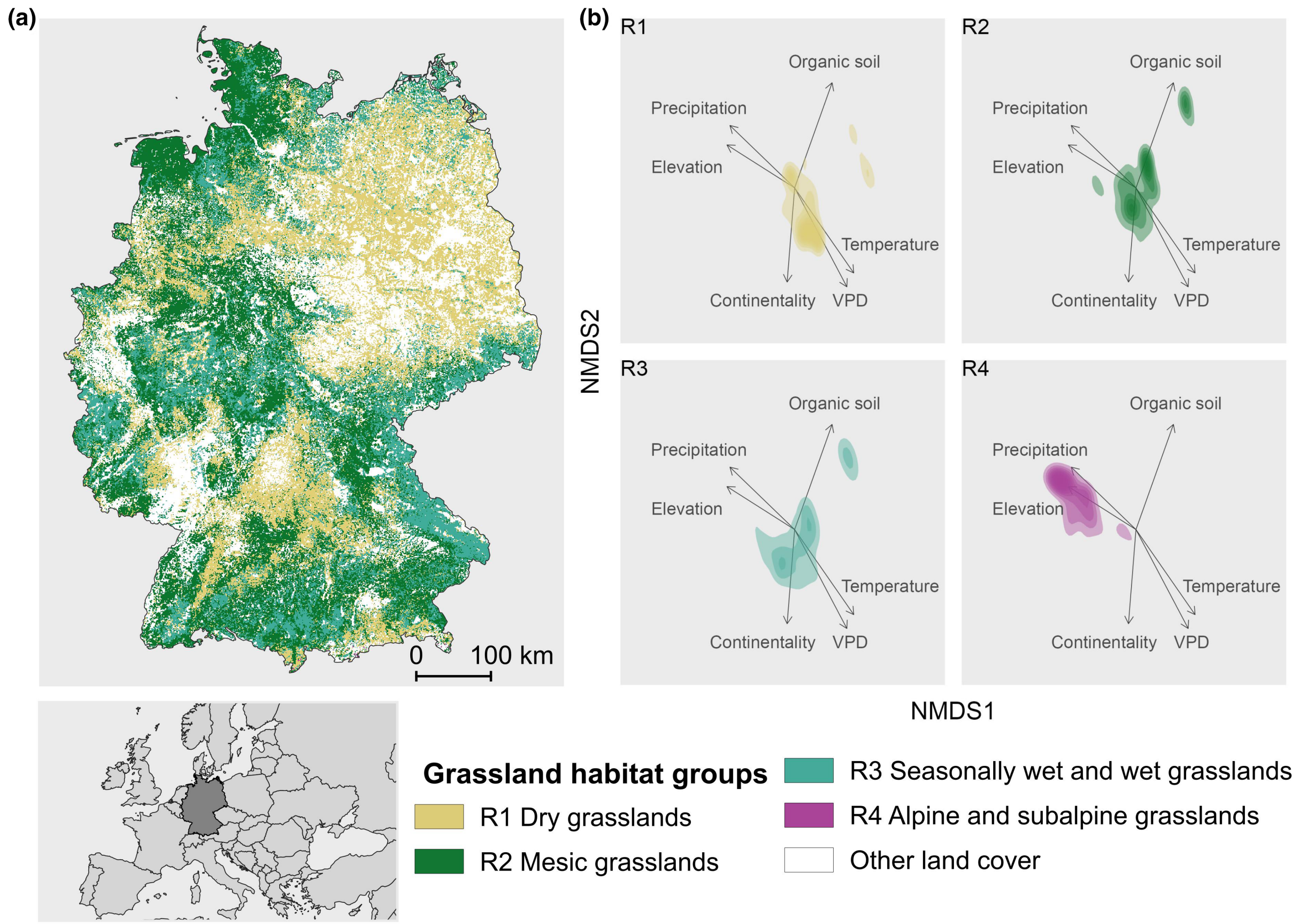

FIGURE 1 Distribution of grassland habitat groups for the study area of Germany (a; habitat probability data from Hennekens, 2023) and their position in a multivariate environmental space derived from non-metric multidimensional scaling (NMDS) ordination using an Euclidean distance matrix (b). The habitat map was aggregated to 1 km spatial resolution for visualization and thus represents the most likely habitat group for grasslands in the grid cell. Environmental variables used for NMDS comprise mean temperature, precipitation, and Vapor Pressure Deficit (VPD) for summer months (see Section 2.2), elevation (NASA JPL, 2013), continentality (calculated following Conrad, 1946), and presence of organic soil (Tegetmeyer et al., 2021). Map lines delineate study areas and do not necessarily depict accepted national boundaries.

moisture, CWB, and VPD (Figure 2). Based on the best performing index, we built a second mixed effects model to investigate how drought sensitivity varied for different grassland habitat groups and habitat types. Models were built using the *lme4* package in R (Bates et al., 2015; R Core Team, 2023). We included years and sample locations as random effects in our models to account for any temporal and spatial variability of grassland drought sensitivity. We kept a fixed intercept for the second random effect as grassland vitality measures the deviation from the samples average and is thus already standardized to the local conditions. We used marginal and conditional R^2 to assess the relation between grassland vitality and the five drought indices and to select the best performing index. We added habitat groups and habitat types as fixed effects to the model of the best performing index. We included interactions of the predictor with the drought index to test whether drought sensitivities are different between grassland habitat groups and between habitat types. To further investigate the temporal variation of drought sensitivity, we built simple linear models based on data subsets from 5-year moving windows using the best performing drought index as a predictor for grassland vitality (following a similar approach as Jiao et al., 2021; Li et al., 2024). We used the Theil-Sen estimator to derive a trend estimate of drought sensitivity. To evaluate the robustness of results obtained using 5-year time windows, we also tested 10 and 15 years as aggregation periods.

3 | RESULTS

Grassland vitality varied between and within individual years in the period from 1985 to 2021 (Figure 3). Individual years with high vitality losses were observed in 2003 and 2006 and two multi-year periods of high vitality loss occurred from 1989 to 1992 and from 2018 to 2020 (Figure 3b). The years 2003 and 2018 stand out as the most severely affected years, translating into an average increase of +25.64% and +32.62% in soil and dry vegetation cover, respectively. In several other years, vitality losses were limited to certain

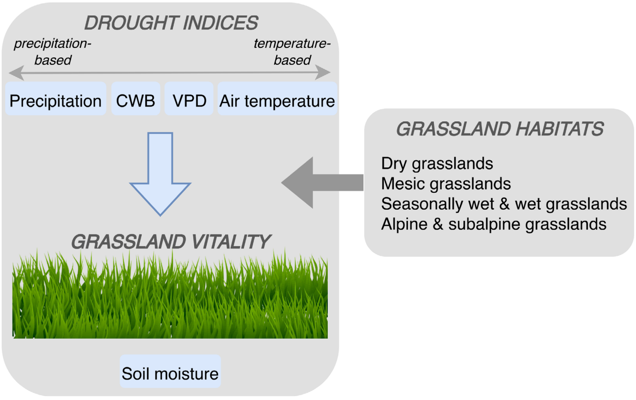

FIGURE 2 Drought indices tested for their effects on grassland vitality including anomalies of precipitation, air temperature, soil moisture, Climatic Water Balance (CWB, i.e., difference between precipitation and potential evapotranspiration), and Vapor Pressure Deficit (VPD, i.e., difference between actual and saturation water vapor pressure for specific air temperature). Grassland habitats characterized by different environmental conditions and grassland communities (right) potentially vary in their sensitivity to drought conditions.

regions (e.g., northern Germany in 2009, southern Germany in 2015, and northwestern Germany in 1995 and 1996) while the remaining grasslands showed close to average vitality or even vitality gains (Figure 3a).

We found robust positive relationships between grassland vitality and multiple drought indices, with marginal R^2 ranging from .09 to .22 (Table 1). Hence, a substantial share of grassland vitality and its variability in both space and time are explained by drought conditions. VPD showed the strongest relation to grassland vitality, accounting for 22% of the seasonal variability, and CWB, temperature, precipitation, and soil moisture anomalies explained considerably less variance (Table 1).

Grassland vitality had a positive relation to VPD and temperature, indicating a decreasing grassland vitality with positive anomalies in temperature and atmospheric water demand (Figure 4; Figure S1). CWB, soil moisture, and precipitation showed negative correlations with grassland vitality, indicating increasing dry vegetation cover with lower water availability (Figure S1). The relation between grassland vitality and VPD, as well as CWB, were linear across the value range, whereas soil moisture, temperature, and precipitation showed indication of non-linear relations to grassland vitality (Figure S1). Moreover, we observed that the most extreme drought years, i.e., 2003, 2018, and 2019 (calculated as the highest seasonal anomalies considering the mean of all drought indices) trigger the strongest vitality loss across all drought indices (Figure 4; Figure S1). Supporting this, lower marginal R^2 (i.e., considering only fixed effects) compared to conditional R^2 (i.e., considering both fixed and random effects) indicate a substantial temporal as well as spatial variability in the relation between grassland vitality and meteorological drought (Table 1). As VPD showed the most consistent relation to grassland vitality in terms of a linear response and in terms of explained variance, we used VPD to further evaluate the spatiotemporal variability of grassland drought sensitivity.

Drought sensitivity to VPD varied over time from 1985 to 2021 with a distinct increase beginning in the 2010s (Figure 5a). The highest sensitivities were reached in the last decade from 2012 to 2021. A positive trend of +0.003 (+0.002, +0.004) per year indicated that drought sensitivity increased over the past four decades. Moreover, higher drought sensitivities in 5-year time windows were linked consistently to the occurrence of high VPD anomalies in the same period (Figure 5b) indicating that the occurrence of extreme droughts (e.g., in 2018–2019) drive the increasing sensitivity of grasslands to VPD.

The positive effect of VPD on grassland vitality was persistent after controlling for different habitat groups and types covering varying environmental gradients and community compositions of grasslands. Yet, we found that the strength of sensitivity to VPD anomalies varied significantly (Figure 6). Drought sensitivity of grasslands increased from alpine to wet to mesic to dry grasslands, and thus along a moisture gradient. While dry, mesic, and (seasonally) wet grasslands were similar in their group-level sensitivity (effects of 0.13–0.15), alpine and subalpine grasslands were least sensitive to VPD anomalies (Figure 6). Drought sensitivity variation between habitat types revealed large differences within habitat groups, except for alpine and subalpine grasslands where effects were similar between the two habitat types.

4 | DISCUSSION AND CONCLUSIONS

We here mapped and quantified grassland vitality at national scale over the past four decades based on high-resolution remote sensing data. Our study revealed a high variability in grassland vitality in the years from 1985 to 2021, with grassland vitality fluctuating considerably between individual years (e.g., 2006–2007, 2017–2018). Years with low grassland vitality matched well with known drought events, e.g., in 1992, 2003, 2015, and 2018 (Dirmeyer et al., 2021; Zink et al., 2016), confirming the direct response of Central European grassland systems to summer droughts (Buras et al., 2020). The multi-year drought event from 2018 to 2020 stood out with the most severe and longest anomalies of grassland vitality among all years from 1985 to 2021. Similarly severe conditions of low grassland vitality were only detected in the single-year drought event in 2003. We observed low grassland vitality in another multi-year drought event from 1989 to 1992. Yet, grassland vitality was considerably closer to average in these years compared to the 2018–2020 event. Thus, our maps revealed that the drought event from 2018 to 2020 triggered an unprecedented decline of grassland vitality in the past four decades in terms of severity and duration.

Grassland vitality was consistently linked to meteorological anomalies over space and time. Among common drought indices, VPD explained variability in grassland vitality best. In line with this, we found that drought indices accounting for evaporative demand (i.e., VPD, temperature, and CWB) explained grassland vitality better than drought indices accounting for only water availability (i.e.,

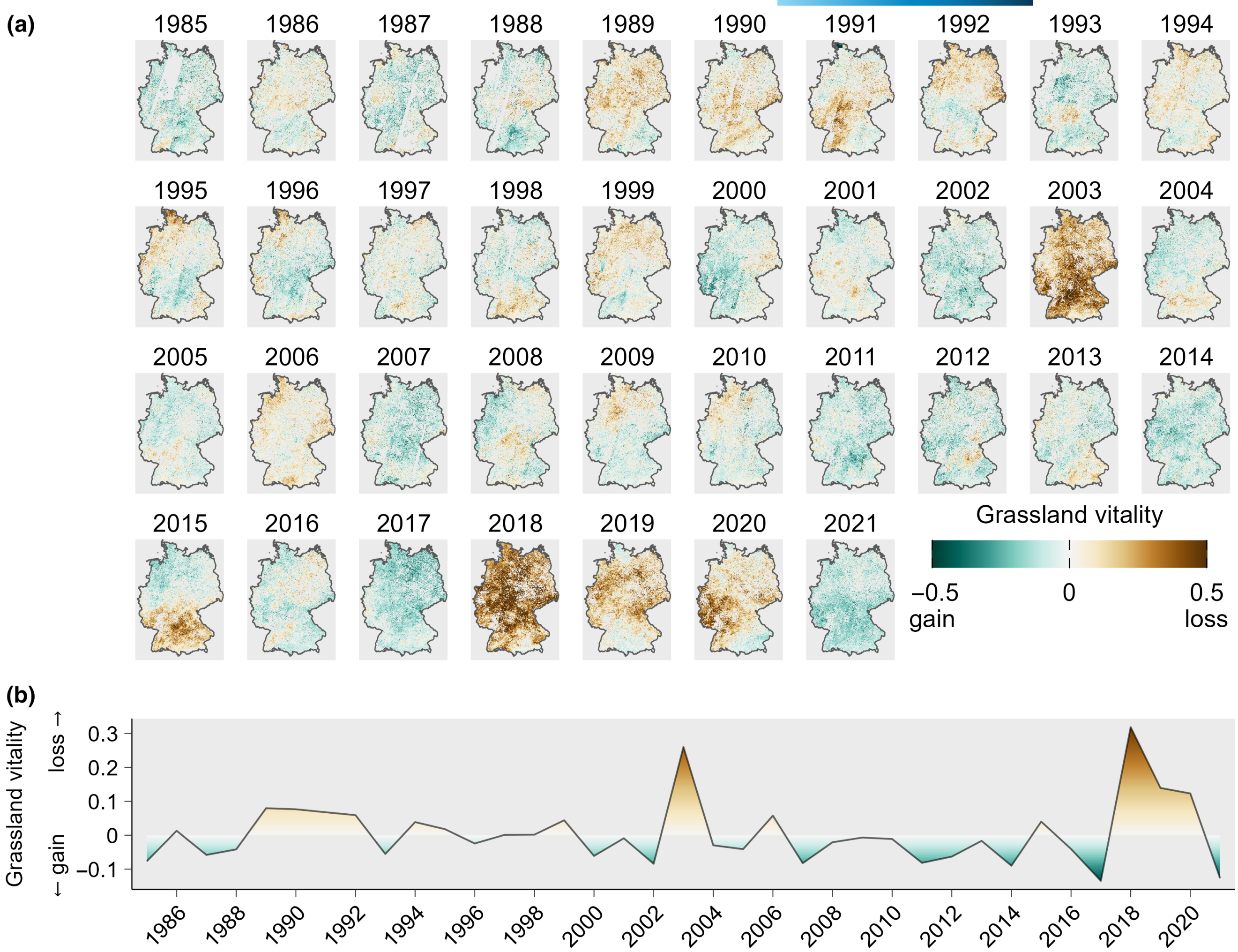

FIGURE 3 Maps (a) and time series (b) of seasonal vitality for grasslands from 1985 to 2021. Positive values indicate vitality loss with higher-than-average dry vegetation and soil cover whereas negative values indicate vitality gain with higher-than-average green vegetation. Maps were aggregated to 1 km spatial resolution for visualization. Map lines delineate study areas and do not necessarily depict accepted national boundaries.

TABLE 1 Marginal and conditional R^2 of mixed effects models for grassland vitality explained by different drought indices.

Drought index	Marginal R^2	Conditional R^2
Vapor pressure deficit	.22	.42
Temperature	.16	.69
Climatic water balance	.14	.29
Soil moisture	.10	.27
Precipitation	.09	.24

precipitation and soil moisture). Precipitation and soil moisture capture water availability, but do not explicitly account for interactions with atmospheric conditions relevant for vegetation response to drought (Grossiord et al., 2020). Our findings hence corroborated previous studies, indicating that not only lack of precipitation but compounding high temperatures are a critical factor to which grasslands in Central Europe respond most strongly during droughts (De Boeck et al., 2011, 2016; Reynaert et al., 2021). Almost a quarter of the variability in grassland vitality was explained by VPD anomalies in the same year, demonstrating that grasslands react to summer drought without a major time lag, as is found, e.g., in forest systems (Buras et al., 2020; Reichstein et al., 2007; Senf & Seidl, 2018; Stampfli et al., 2018). We integrated observations from June to September to assess the link between grassland vitality and summer drought, but the vegetation responses to drought may vary within the growing season (Jentsch et al., 2007; Jin et al., 2023) and may depend on previous drought exposure (Walter et al., 2011). Differentiating the drought response for different phases of the growing season could allow to additionally assess, e.g., the influence of spring droughts on shifts in grassland phenology and productivity (Wolf et al., 2013). Yet, summer droughts are expected to affect ecosystems most severely in the coming decades in Central Europe (Aalbers et al., 2023; Markonis et al., 2021). We here focused on the immediate effects of drought on grassland vitality, i.e., the resistance of grasslands in terms of vegetation growth during a drought period. Drought resilience, i.e., the capacity of a grassland to recover after a drought is another important factor which can affect long-term ecosystem functioning (Craine et al., 2013; Griffin-Nolan et al., 2019; Stampfli et al., 2018) and thus warrants further research. We here observed a linear relation of grassland vitality to VPD (Figure 4). Yet, different drought thresholds were observed for grasslands species (Ingrisch et al., 2023). For individual sites, these thresholds could thus lead to a non-linear response of grassland vitality to drought indices. While such an analysis was beyond the scope of this study, grassland vitality time series from recent years with increased observation frequency (i.e., >30 cloud-free observations per season; Okujeni et al., 2024) together with meteorological data would be well suited to uncover such thresholds.

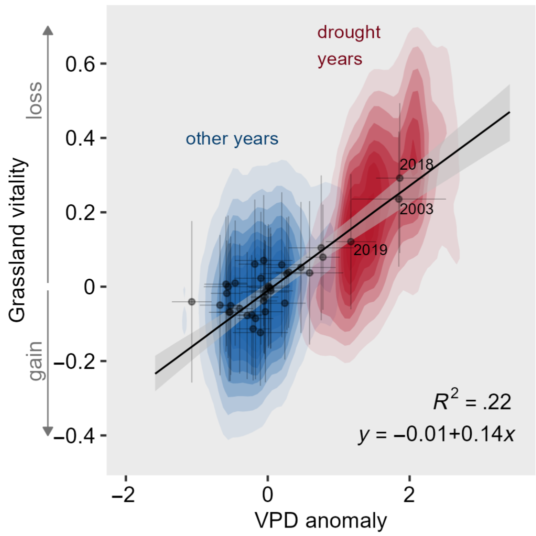

FIGURE 4 Linear relation and 95% confidence intervals for the relation of seasonal grassland vitality to anomalies of Vapor Pressure Deficit (VPD) from a mixed effects model. Underlying data are from the three most extreme drought years, i.e., 2003, 2018, and 2019 (red), and all other years (blue). Light to dark colors indicate increasing data density. Points represent average values of June, July, August, and September for each year from 1985 to 2021. The corresponding figure for other drought indices can be found in the supplementary material (Figure S1).

Our study confirmed findings from experimental studies indicating a generally high, but varying effect of atmospheric water demand on grassland vitality. Combining spatially explicit, large-scale satellite and meteorological data, we showed that these varying effects replicate under real-world conditions and relate to different grassland habitats. Grassland habitat types are characterized by distinct biotic and abiotic characteristics, which can influence the grassland drought response. First, grassland sensitivity decreased for habitats along a moisture gradient from dry, mesic, wet to subalpine and alpine habitat types. Similar relations between ecosystem productivity and mean annual precipitation have been previously established across ecosystems including grasslands (Huxman et al., 2004; Maurer et al., 2020; Sala et al., 2012), and also hold true for gradients within the semi-natural to agriculturally improved grasslands in Central Europe. Lowest sensitivities were found for grasslands in subalpine or alpine habitats, which are located at highest elevations and also have the highest precipitation (Figure 1). Given that drought indices measure extremes relative to the mean, our results indicate that even extreme meteorological anomalies are not yet a limiting factor for grassland vitality of subalpine and alpine grasslands due to the generally higher water availability (Zang et al., 2020). Secondly, edaphic factors modify the drought response of grasslands. Higher drought sensitivities were associated with habitat types characterized by

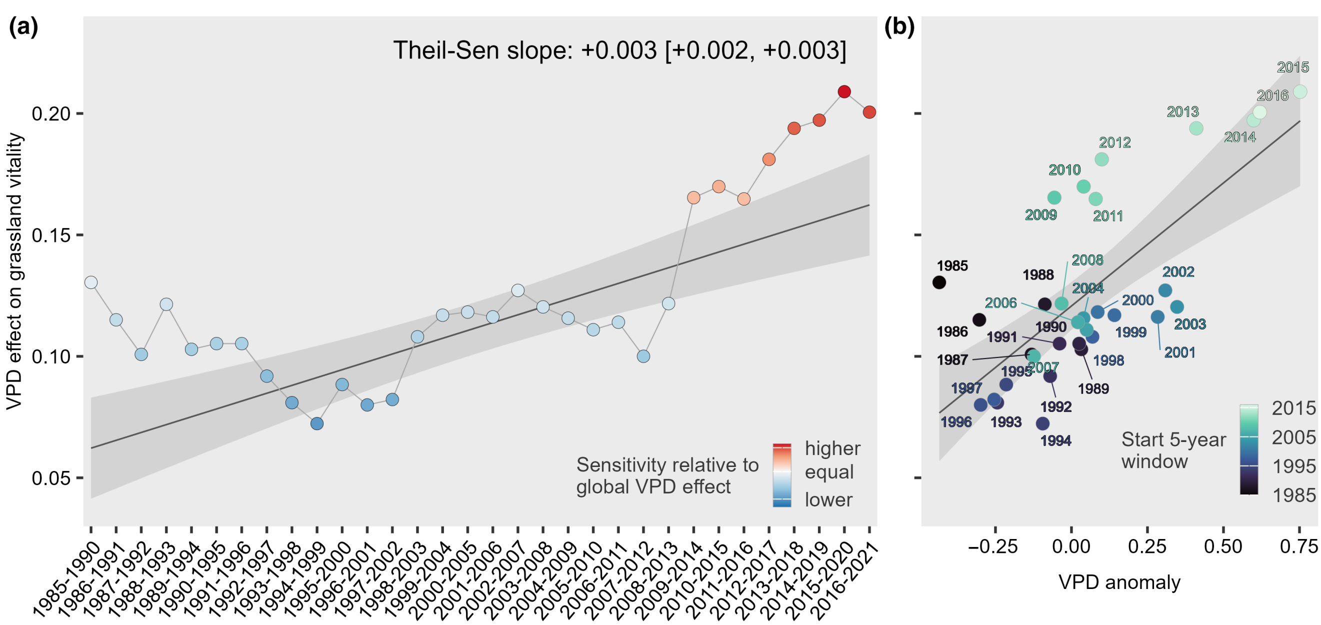

FIGURE 5 Changing sensitivity of grassland vitality to Vapor Pressure Deficit (VPD) from 1985 to 2021 (a) and relation of VPD sensitivity to VPD anomalies (b). Sensitivity for each 5-year time period was derived based on simple linear models. The trend from 1985 to 2021 (a) is based on the Theil-Sen estimator with 95% confidence intervals. Results for aggregation intervals of 10 and 15 years are given in Figure S2.

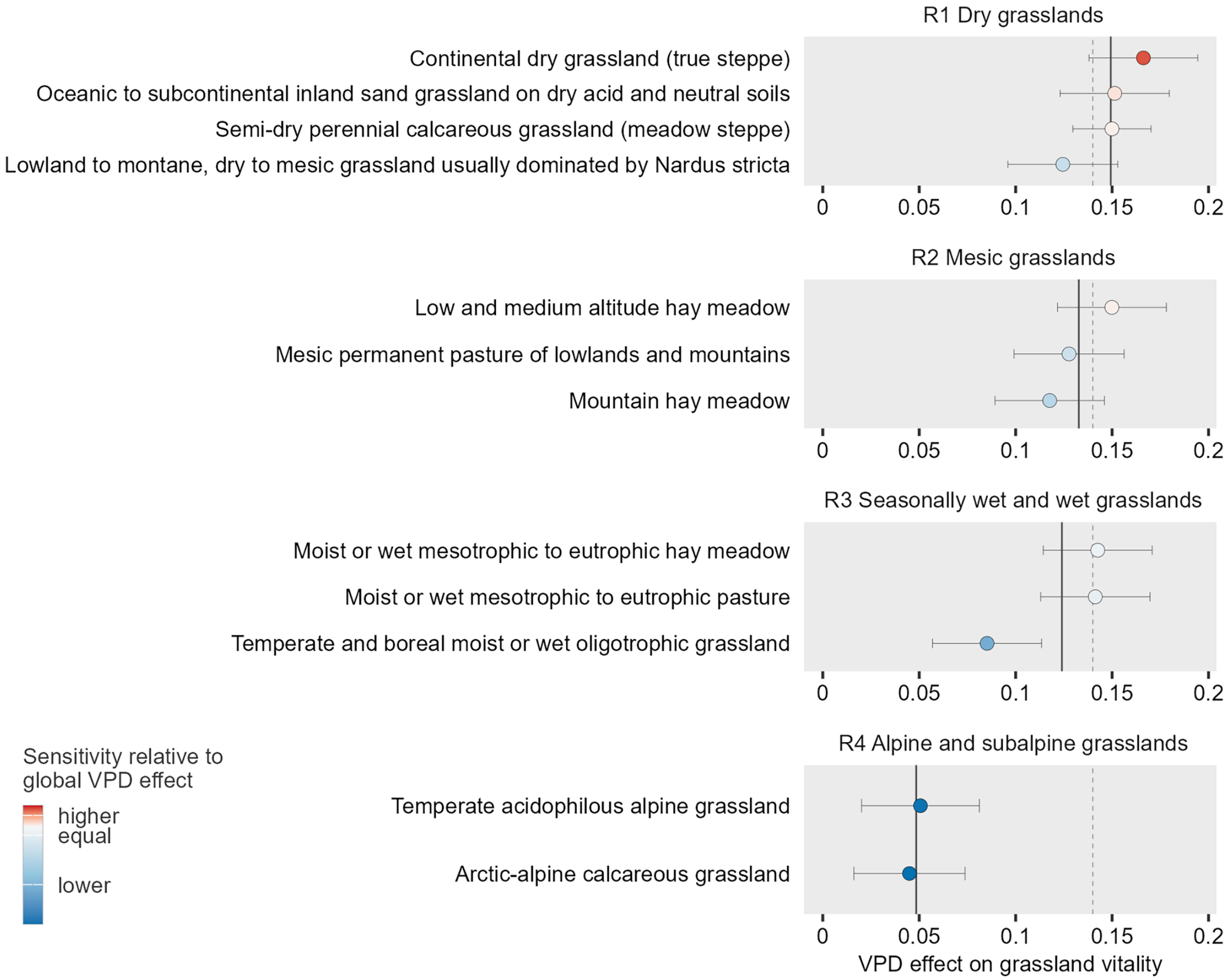

FIGURE 6 Effects of Vapor Pressure Deficit (VPD) on grassland vitality for 12 grassland habitat types. Solid vertical lines indicate group-wise effects (i.e., for habitat groups). Blue to red color gradient represents smaller to larger effects relative to the global estimate (dashed vertical line).

poor, sandy soils with low water holding capacities, such as *oceanic to subcontinental inland sand grassland on dry acid and neutral soils* (Schaminée et al., 2016), which are widespread in northern Germany. In contrast, lower drought sensitivities were found for habitats with more fertile, mesic soils, e.g., *mountain hay meadows* or *mesic permanent pastures of lowlands and mountains*. Moreover, inundated, nutrient-poor soil, or peat soils can buffer atmospheric drought effects by supplying sufficient water during drought periods, e.g., for *moist or wet mesotrophic to eutrophic pastures* and for *temperate and boreal moist or wet oligotrophic grasslands* (Schaminée et al., 2016), which had a low drought sensitivity. Lastly, drought sensitivity of habitat types might be further modified by their community composition. We here found that dry grassland habitat types like *continental dry grasslands* and semi-dry *perennial calcareous grasslands* were among the most drought-sensitive habitat types. Species typical for these habitats tend to be well adapted to drought periods and can have a high resilience (Grime et al., 2008; Schaminée et al., 2016). The productivity of dry grassland habitats is often still reduced during droughts (Jackson et al., 2024), which we observed here as well based on our vitality indicator. It is not possible to directly assess whether remotely sensed vitality loss, which is related to plant senescence and potential plant mortality, leads to shifts in species composition or long-term stability of a habitat. Yet, a recent study by Mazalla et al. (2022) showed that severe drought periods, as the one in 2018–2019, reduced character species of calcareous grasslands. The high drought sensitivity of these habitats found here underlines that such grasslands may be less resilient to future, potentially more severe droughts than previously assumed. In this study, we used probability information to derive habitat types as this was the only available, spatially continuous data source. To gain more detailed insights on drought sensitivity of individual habitats and potential shifts in community composition, remote sensing-based grassland vitality could be directly linked with in-situ data capturing the actual occurrence and cover of species. Similarly, additional nation-wide in-situ data on grassland management would be valuable to assess how grassland habitats respond to drought under different management intensities, a factor that has been shown to impact drought sensitivity of grasslands (Bütof et al., 2012; Luna et al., 2023). Nonetheless, we here provided, for the first time, a comprehensive overview on the drought sensitivity of the main grassland habitat types in Central Europe using fine-scale remote sensing time series.

Our results supported our a-priori expectation that grassland sensitivity to atmospheric water demand increased over time. We observed a consistently positive trend of VPD effects on grassland vitality suggesting that grassland vitality became more sensitive to drought in the past four decades. The trend was mainly caused by high sensitivities from 2010 to 2021. This was especially apparent for the multi-year drought in 2018–2019, which also triggered the strongest response in grassland vitality in the past four decades. The strong correlation to VPD anomalies further underlines that sensitivities increase with atmospheric water demand, which is predicted to increase further in the future due to rising temperatures and land-atmosphere coupling (Markonis et al., 2021; Seneviratne et al., 2006; Teuling, 2018). Moreover, a consistently higher sensitivity level from 2010 to 2021 indicates that regional to national scale spatial patterns of grassland vitality are increasingly driven by atmospheric water demand. Our findings for grasslands underpin recent studies observing an increasing coupling of ecosystem productivity and drought across different ecosystems in humid regions (Gampe et al., 2021; Jiao et al., 2021; Li et al., 2024).

Our study confirmed and emphasized the high sensitivity of Central European grassland systems to the ongoing and anticipated increase of droughts in the light of global climate change (Spinoni et al., 2018). High atmospheric water demand amplifies drought stress on grasslands physiologically and through increased evaporation of soil moisture (Grossiord et al., 2020; Zhou et al., 2019). Such hotter droughts, characterized by low precipitation and concurrent high temperatures, are becoming the dominant drought type in Central Europe (Markonis et al., 2021). Given the expected increase of hot droughts in the next decades, drought effects on grasslands will likely rise as well. In our study period from 1985 to 2021, the years 2003 and 2018–2019 were the most prominent examples of compounding droughts and heatwaves, when we also observed the most severe decline in grassland vitality. While the consecutive drought from 2018 to 2019 was unprecedented in the last 250 years, similar 2-year events are expected to occur up to seven times more often until 2100, affecting between 30% and 60% of Central European grasslands (Hari et al., 2020). Considering the already increasing drought sensitivity of Central European grasslands, future droughts with similar characteristics as past severe droughts will have far reaching, negative effects on grassland productivity and other ecosystem services. Globally, dryland ecosystems, where water availability is already marginal, face the most severe challenges with varying precipitation patterns and extreme events under climate change (Cherwin & Knapp, 2012; IPCC, 2022; Zhang et al., 2022). We found here that even in (sub-)humid climate, grasslands become more sensitive to atmospheric water demand. While meteorological droughts span large geographic areas, the observed spatial variability of grassland sensitivity underscores the need to consider drought impacts on ecosystems on a regional scale. This ultimately helps to develop strategies for drought impact mitigation and adaptation focusing on drought-sensitive regions.

AUTHOR CONTRIBUTIONS

Katja Kowalski: Conceptualization; formal analysis; methodology; writing – original draft; writing – review and editing. **Cornelius Senf:** Conceptualization; formal analysis; methodology; writing – review and editing. **Akpona Okujeni:** Conceptualization; writing – review and editing. **Patrick Hostert:** Conceptualization; funding acquisition; writing – review and editing.

ACKNOWLEDGEMENTS

This research was funded within the frame of "GreenGrass" (Federal Ministry of Education and Research, Germany (BMBF), grant number: 031B0734I). Funding was received through the Einstein Research Unit "Climate and Water under Change" from the Einstein Foundation Berlin and Berlin University Alliance (ERU-2020-609). We thank three anonymous reviewers who helped to improve this work. Open Access funding enabled and organized by Projekt DEAL.

CONFLICT OF INTEREST STATEMENT

The authors declare that they have no conflict of interest.

DATA AVAILABILITY STATEMENT

The data and code that support the findings of this study are openly available at https://doi.org/10.5281/zenodo.11061320.

ORCID

Katja Kowalski https://orcid.org/0000-0002-3053-704X
Cornelius Senf https://orcid.org/0000-0002-2389-2158
Akpona Okujeni https://orcid.org/0000-0003-4558-5885
Patrick Hostert https://orcid.org/0000-0002-5730-5484

REFERENCES

Aalbers, E. E., van Meijgaard, E., Lenderink, G., de Vries, H., & van den Hurk, B. J. J. M. (2023). The 2018 west-central European drought projected in a warmer climate: How much drier can it get? *Natural Hazards and Earth System Sciences*, *23*(5), 1921–1946. https://doi.org/10.5194/nhess-23-1921-2023

Barkhordarian, A., Saatchi, S. S., Behrangi, A., Loikith, P. C., & Mechoso, C. R. (2019). A recent systematic increase in vapor pressure deficit over tropical South America. *Scientific Reports*, *9*(1), 15331. https://doi.org/10.1038/s41598-019-51857-8

Bastos, A., Orth, R., Reichstein, M., Ciais, P., Viovy, N., Zaehle, S., Anthoni, P., Arneth, A., Gentine, P., Joetzjer, E., Lienert, S., Loughran, T., McGuire, P. C., Sungmin, O., Pongratz, J., & Sitch, S. (2021). Vulnerability of European ecosystems to two compound dry and hot summers in 2018 and 2019. *Earth System Dynamics*, *12*(4), 1015–1035. https://doi.org/10.5194/esd-12-1015-2021

Bates, D., Mächler, M., Bolker, B., & Walker, S. (2015). Fitting linear mixed-effects models using lme4. *Journal of Statistical Software*, *67*(1). https://doi.org/10.18637/jss.v067.i01

Bengtsson, J., Bullock, J. M., Egoh, B., Everson, C., Everson, T., O'Connor, T., O'Farrell, P. J., Smith, H. G., & Lindborg, R. (2019). Grasslands—More important for ecosystem services than you might think. *Ecosphere*, *10*(2), e02582. https://doi.org/10.1002/ecs2.2582

Buras, A., Rammig, A., & Zang, C. S. (2020). Quantifying impacts of the 2018 drought on European ecosystems in comparison to 2003. *Biogeosciences*, *17*(6), 1655–1672. https://doi.org/10.5194/bg-17-1655-2020

Bütof, A., Von Riedmatten, L. R., Dormann, C. F., Scherer-Lorenzen, M., Welk, E., & Bruelheide, H. (2012). The responses of grassland plants to experimentally simulated climate change depend on land use and region. *Global Change Biology*, *18*(1), 127–137. https://doi.org/10.1111/j.1365-2486.2011.02539.x

Buttler, A., Mariotte, P., Meisser, M., Guillaume, T., Signarbieux, C., Vitra, A., Preux, S., Mercier, G., Quezada, J., Bragazza, L., & Gavazov, K. (2019). Drought-induced decline of productivity in the dominant grassland species *Lolium perenne* L. depends on soil type and prevailing climatic conditions. *Soil Biology and Biochemistry*, *132*, 47–57. https://doi.org/10.1016/j.soilbio.2019.01.026

Chang, J., Ciais, P., Viovy, N., Vuichard, N., Sultan, B., & Soussana, J.-F. (2015). The greenhouse gas balance of European grasslands. *Global Change Biology*, *21*(10), 3748–3761. https://doi.org/10.1111/gcb.12998

Chen, Q., Timmermans, J., Wen, W., & van Bodegom, P. M. (2022). A multi-metric assessment of drought vulnerability across different vegetation types using high resolution remote sensing. *Science of the Total Environment*, *832*, 154970. https://doi.org/10.1016/j.scitotenv.2022.154970

Chen, Q., Timmermans, J., Wen, W., & van Bodegom, P. M. (2023). Ecosystems threatened by intensified drought with divergent vulnerability. *Remote Sensing of Environment*, *289*, 113512. https://doi.org/10.1016/j.rse.2023.113512

Cherwin, K., & Knapp, A. (2012). Unexpected patterns of sensitivity to drought in three semi-arid grasslands. *Oecologia*, *169*(3), 845–852. https://doi.org/10.1007/s00442-011-2235-2

Chytrý, M., Tichý, L., Hennekens, S. M., Knollová, I., Janssen, J. A. M., Rodwell, J. S., Peterka, T., Marcenò, C., Landucci, F., Danihelka, J., Hájek, M., Dengler, J., Novák, P., Zukal, D., Jiménez-Alfaro, B., Mucina, L., Abdulhak, S., Aćić, S., Agrillo, E., … Schaminée, J. H. J. (2020). EUNIS habitat classification: Expert system, characteristic species combinations and distribution maps of European habitats. *Applied Vegetation Science*, *23*(4), 648–675. https://doi.org/10.1111/avsc.12519

Ciais, P., Reichstein, M., Viovy, N., Granier, A., Ogée, J., Allard, V., Aubinet, M., Buchmann, N., Bernhofer, C., Carrara, A., Chevallier, F., De Noblet, N., Friend, A. D., Friedlingstein, P., Grünwald, T., Heinesch, B., Keronen, P., Knohl, A., Krinner, G., … Valentini, R. (2005). Europe-wide reduction in primary productivity caused by the heat and drought in 2003. *Nature*, *437*(7058), 529–533. https://doi.org/10.1038/nature03972

Conrad, V. (1946). Usual formulas of continentality and their limits of validity. *Eos, Transactions American Geophysical Union*, *27*(5), 663–664. https://doi.org/10.1029/TR027i005p00663

Craine, J. M., Ocheltree, T. W., Nippert, J. B., Towne, E. G., Skibbe, A. M., Kembel, S. W., & Fargione, J. E. (2013). Global diversity of drought tolerance and grassland climate-change resilience. *Nature Climate Change*, *3*(1), 63–67. https://doi.org/10.1038/nclimate1634

Dangal, S. R. S., Tian, H., Pan, S., Zhang, L., & Xu, R. (2020). Greenhouse gas balance in global pasturelands and rangelands. *Environmental Research Letters*, *15*(10), 104006. https://doi.org/10.1088/1748-9326/abaa79

Davies, C., Moss, D., & Hill, M. O. (2004). EUNIS habitat classification revised 2004. https://inpn.mnhn.fr/docs/ref_habitats/Davies_&_Moss_2004_EUNIS_habitat_classification.pdf

De Boeck, H. J., Bassin, S., Verlinden, M., Zeiter, M., & Hiltbrunner, E. (2016). Simulated heat waves affected alpine grassland only in combination with drought. *New Phytologist*, *209*(2), 531–541. https://doi.org/10.1111/nph.13601

De Boeck, H. J., Dreesen, F. E., Janssens, I. A., & Nijs, I. (2011). Whole-system responses of experimental plant communities to climate extremes imposed in different seasons. *New Phytologist*, *189*(3), 806–817. https://doi.org/10.1111/j.1469-8137.2010.03515.x

DESTATIS. (2022). Dauergrünland nach Art der Nutzung im Zeitvergleich. https://www.destatis.de/DE/Themen/Branchen-Unternehmen/Landwirtschaft-Forstwirtschaft-Fischerei/Feldfruechte-Gruenland/Tabellen/zeitreihe-dauergruenland-nach-nutzung.html

Dirmeyer, P. A., Balsamo, G., Blyth, E. M., Morrison, R., & Cooper, H. M. (2021). Land-atmosphere interactions exacerbated the drought and heatwave over northern Europe during summer 2018. *AGU Advances*, *2*(2). https://doi.org/10.1029/2020AV000283

EEA. (2024). EUNIS habitat type hierarchical view (marine version 2022 & terrestrial version 2021). https://eunis.eea.europa.eu/habitats-code-browser-revised.jsp

European Commission, Directorate-General for Environment, Tsiripidis, I., Piernik, A., Janssen, J., Tahvanainen, T., Molina, J., Giusso del Galdo, G., Gardfjell, H., Dimopoulos, P., Šumberová, K., Acosta, A., Biurrun, I., Poulin, B., Hájek, M., Bioret, F., Essl, F., Rodwell, J., García Criado, M., … Gigante, D. (2016). *European red list of habitats. Part 2, Terrestrial and freshwater habitats*. Publications Office. https://doi.org/10.2779/091372

Felton, A. J., & Goldsmith, G. R. (2023). Timing and magnitude of drought impacts on carbon uptake across a grassland biome. *Global Change Biology*, *29*(10), 2790–2803. https://doi.org/10.1111/gcb.16637

Fu, Z., Ciais, P., Bastos, A., Stoy, P. C., Yang, H., Green, J. K., Wang, B., Yu, K., Huang, Y., Knohl, A., Šigut, L., Gharun, M., Cuntz, M., Arriga, N., Roland, M., Peichl, M., Migliavacca, M., Cremonese, E., Varlagin, A., … Koebsch, F. (2020). Sensitivity of gross primary productivity to climatic drivers during the summer drought of 2018 in Europe. *Philosophical Transactions of the Royal Society, B: Biological Sciences*, *375*(1810), 20190747. https://doi.org/10.1098/rstb.2019.0747

Gampe, D., Zscheischler, J., Reichstein, M., O'Sullivan, M., Smith, W. K., Sitch, S., & Buermann, W. (2021). Increasing impact of warm droughts on northern ecosystem productivity over recent decades. *Nature Climate Change*, *11*(9), 772–779. https://doi.org/10.1038/s41558-021-01112-8

Gharun, M., Hörtnagl, L., Paul-Limoges, E., Ghiasi, S., Feigenwinter, I., Burri, S., Marquardt, K., Etzold, S., Zweifel, R., Eugster, W., & Buchmann, N. (2020). Physiological response of Swiss ecosystems to 2018 drought across plant types and elevation. *Philosophical Transactions of the Royal Society, B: Biological Sciences*, *375*(1810), 20190521. https://doi.org/10.1098/rstb.2019.0521

Gibson, D. J. (2009). *Grasses and grassland ecology*. Oxford University Press.

Gilgen, A. K., & Buchmann, N. (2009). Response of temperate grasslands at different altitudes to simulated summer drought differed but scaled with annual precipitation. *Biogeosciences*, *6*(11), 2525–2539. https://doi.org/10.5194/bg-6-2525-2009

Griffin-Nolan, R. J., Blumenthal, D. M., Collins, S. L., Farkas, T. E., Hoffman, A. M., Mueller, K. E., Ocheltree, T. W., Smith, M. D., Whitney, K. D., & Knapp, A. K. (2019). Shifts in plant functional composition following long-term drought in grasslands. *Journal of Ecology*, *107*(5), 2133–2148. https://doi.org/10.1111/1365-2745.13252

Grime, J. P., Fridley, J. D., Askew, A. P., Thompson, K., Hodgson, J. G., & Bennett, C. R. (2008). Long-term resistance to simulated climate change in an infertile grassland. *Proceedings of the National Academy of Sciences of the United States of America*, *105*(29), 10028–10032. https://doi.org/10.1073/pnas.0711567105

Grossiord, C., Buckley, T. N., Cernusak, L. A., Novick, K. A., Poulter, B., Siegwolf, R. T. W., Sperry, J. S., & McDowell, N. G. (2020). Plant responses to rising vapor pressure deficit. *New Phytologist*, *226*(6), 1550–1566. https://doi.org/10.1111/nph.16485

Guerschman, J. P., Hill, M. J., Leys, J., & Heidenreich, S. (2020). Vegetation cover dependence on accumulated antecedent precipitation in Australia: Relationships with photosynthetic and non-photosynthetic vegetation fractions. *Remote Sensing of Environment*, *240*, 111670. https://doi.org/10.1016/j.rse.2020.111670

Habel, J. C., Dengler, J., Janišová, M., Török, P., Wellstein, C., & Wiezik, M. (2013). European grassland ecosystems: Threatened hotspots of biodiversity. *Biodiversity and Conservation*, *22*(10), 2131–2138. https://doi.org/10.1007/s10531-013-0537-x

Hari, V., Rakovec, O., Markonis, Y., Hanel, M., & Kumar, R. (2020). Increased future occurrences of the exceptional 2018–2019 central European drought under global warming. *Scientific Reports*, *10*(1), 12207. https://doi.org/10.1038/s41598-020-68872-9

Henebry, G. M. (2019). Methodology II: Remote sensing of change in grasslands. In D. J. Gibson & J. A. Newman (Eds.), *Grasslands and climate change* (pp. 40–64). Cambridge University Press. https://www.cambridge.org/core/books/grasslands-and-climate-change/methodology-ii-remote-sensing-of-change-in-grasslands/03D29FED9ED8E62B2DD2A1D0573BB962

Hennekens, S. M. (2023). Predicted suitability for EUNIS habitat types (100m resolution) for EU27 countries (Initial version) [dataset]. https://portal.geobon.org/ebv-detail?id=15

Hovenden, M. J., Newton, P. C. D., & Porter, M. (2017). Elevated CO_2 and warming effects on grassland plant mortality are determined by the timing of rainfall. *Annals of Botany*, *119*(7), 1225–1233. https://doi.org/10.1093/aob/mcx006

Huete, A., Didan, K., Miura, T., Rodriguez, E. P., Gao, X., & Ferreira, L. G. (2002). Overview of the radiometric and biophysical performance of the MODIS vegetation indices. *Remote Sensing of Environment*, *83*(1), 195–213. https://doi.org/10.1016/S0034-4257(02)00096-2

Huxman, T. E., Smith, M. D., Fay, P. A., Knapp, A. K., Shaw, M. R., Loik, M. E., Smith, S. D., Tissue, D. T., Zak, J. C., Weltzin, J. F., Pockman, W. T., Sala, O. E., Haddad, B. M., Harte, J., Koch, G. W., Schwinning, S., Small, E. E., & Williams, D. G. (2004). Convergence across biomes to a common rain-use efficiency. *Nature*, *429*(6992), 651–654. https://doi.org/10.1038/nature02561

Huyghe, C., De Vliegher, A., Van Gils, B., & Peeters, A. (2014). *Grasslands and herbivore production in europe and effects of common policies*. éditions Quae. https://www.quae-open.com/produit/72/9782759221585/grasslands-and-herbivore-production-in-europe-and-effects-of-common-policies

Ingrisch, J., Umlauf, N., & Bahn, M. (2023). Functional thresholds alter the relationship of plant resistance and recovery to drought. *Ecology*, *104*(2), e3907. https://doi.org/10.1002/ecy.3907

IPCC. (2022). *Climate change 2022: Impacts, adaptation and vulnerability. Contribution of Working Group II to the Sixth Assessment Report of the Intergovernmental Panel on Climate Change* (H.-O. Pörtner, D. C. Roberts, M. Tignor, E. S. Poloczanska, K. Mintenbeck, A. Alegría, M. Craig, S. Langsdorf, S. Löschke, V. Möller, A. Okem, & B. Rama, Eds.). Cambridge University Press.

Ivits, E., Horion, S., Fensholt, R., & Cherlet, M. (2014). Drought footprint on European ecosystems between 1999 and 2010 assessed by remotely sensed vegetation phenology and productivity. *Global Change Biology*, *20*(2), 581–593. https://doi.org/10.1111/gcb.12393

Jackson, J., Middleton, S. L., Lawson, C. S., Jardine, E., Hawes, N., Maseyk, K., Salguero-Gómez, R., & Hector, A. (2024). Experimental drought reduces the productivity and stability of a calcareous grassland. *Journal of Ecology*, *112*(4), 917–931. https://doi.org/10.1111/1365-2745.14282

Jackson, R. B., Canadell, J., Ehleringer, J. R., Mooney, H. A., Sala, O. E., & Schulze, E. D. (1996). A global analysis of root distributions for terrestrial biomes. *Oecologia*, *108*(3), 389–411. https://doi.org/10.1007/BF00333714

Jentsch, A., Kreyling, J., & Beierkuhnlein, C. (2007). A new generation of climate-change experiments: Events, not trends. *Frontiers in Ecology and the Environment*, *5*(7), 365–374. https://doi.org/10.1890/1540-9295(2007)5[365:ANGOCE]2.0.CO;2

Jiao, W., Wang, L., Smith, W. K., Chang, Q., Wang, H., & D'Odorico, P. (2021). Observed increasing water constraint on vegetation growth over the last three decades. *Nature Communications*, *12*(1), Article 1. https://doi.org/10.1038/s41467-021-24016-9

Jin, H., Vicente-Serrano, S. M., Tian, F., Cai, Z., Conradt, T., Boincean, B., Murphy, C., Farizo, B. A., Grainger, S., López-Moreno, J. I., & Eklundh, L. (2023). Higher vegetation sensitivity to meteorological drought in autumn than spring across European biomes. *Communications Earth & Environment*, *4*(1), Article 1. https://doi.org/10.1038/s43247-023-00960-w

Karlowsky, S., Augusti, A., Ingrisch, J., Hasibeder, R., Lange, M., Lavorel, S., Bahn, M., & Gleixner, G. (2018). Land use in mountain grasslands alters drought response and recovery of carbon allocation and plant-microbial interactions. *Journal of Ecology*, *106*(3), 1230–1243. https://doi.org/10.1111/1365-2745.12910

Knapp, A. K., Carroll, C. J. W., Griffin-Nolan, R. J., Slette, I. J., Chaves, F. A., Baur, L. E., Felton, A. J., Gray, J. E., Hoffman, A. M., Lemoine, N. P., Mao, W., Post, A. K., & Smith, M. D. (2018). A reality check for climate change experiments: Do they reflect the real world? *Ecology*, *99*(10), 2145–2151. https://doi.org/10.1002/ecy.2474

Kowalski, K., Okujeni, A., Brell, M., & Hostert, P. (2022). Quantifying drought effects in Central European grasslands through regression-based unmixing of intra-annual Sentinel-2 time series. *Remote Sensing of Environment*, *268*, 112781. https://doi.org/10.1016/j.rse.2021.112781

Kowalski, K., Okujeni, A., & Hostert, P. (2023). A generalized framework for drought monitoring across central European grassland gradients with Sentinel-2 time series. *Remote Sensing of Environment*, *286*, 113449. https://doi.org/10.1016/j.rse.2022.113449

Kröel-Dulay, G., Mojzes, A., Szitár, K., Bahn, M., Batáry, P., Beier, C., Bilton, M., De Boeck, H. J., Dukes, J. S., Estiarte, M., Holub, P., Jentsch, A., Schmidt, I. K., Kreyling, J., Reinsch, S., Larsen, K. S., Sternberg, M., Tielbörger, K., Tietema, A., … Peñuelas, J. (2022). Field experiments underestimate aboveground biomass response to drought. *Nature Ecology & Evolution*, *6*(5), 540–545. https://doi.org/10.1038/s41559-022-01685-3

Lewińska, K. E., Buchner, J., Bleyhl, B., Hostert, P., Yin, H., Kuemmerle, T., & Radeloff, V. C. (2021). Changes in the grasslands of the Caucasus based on Cumulative Endmember Fractions from the full 1987–2019 Landsat record. *Science of Remote Sensing*, *4*, 100035. https://doi.org/10.1016/j.srs.2021.100035

Lewińska, K. E., Hostert, P., Buchner, J., Bleyhl, B., & Radeloff, V. C. (2020). Short-term vegetation loss versus decadal degradation of grasslands in the Caucasus based on Cumulative Endmember Fractions. *Remote Sensing of Environment*, *248*, 111969. https://doi.org/10.1016/j.rse.2020.111969

Li, D., An, L., Zhong, S., Shen, L., & Wu, S. (2024). Declining coupling between vegetation and drought over the past three decades. *Global Change Biology*, *30*(1), e17141. https://doi.org/10.1111/gcb.17141

Luna, D. A., Pottier, J., & Picon-Cochard, C. (2023). Variability and drivers of grassland sensitivity to drought at different timescales using satellite image time series. *Agricultural and Forest Meteorology*, *331*, 109325. https://doi.org/10.1016/j.agrformet.2023.109325

Mackie, K. A., Zeiter, M., Bloor, J. M. G., & Stampfli, A. (2019). Plant functional groups mediate drought resistance and recovery in a multisite grassland experiment. *Journal of Ecology*, *107*(2), 937–949. https://doi.org/10.1111/1365-2745.13102

Markonis, Y., Kumar, R., Hanel, M., Rakovec, O., Máca, P., & AghaKouchak, A. (2021). The rise of compound warm-season droughts in Europe. *Science Advances*, *7*(6), eabb9668. https://doi.org/10.1126/sciadv.abb9668

Maurer, G. E., Hallmark, A. J., Brown, R. F., Sala, O. E., & Collins, S. L. (2020). Sensitivity of primary production to precipitation across the United States. *Ecology Letters*, *23*(3), 527–536. https://doi.org/10.1111/ele.13455

Mazalla, L., Diekmann, M., & Duprè, C. (2022). Microclimate shapes vegetation response to drought in calcareous grasslands. *Applied Vegetation Science*, *25*(3). https://doi.org/10.1111/avsc.12672

Miralles, D. G., Teuling, A. J., van Heerwaarden, C. C., & Vilà-Guerau de Arellano, J. (2014). Mega-heatwave temperatures due to combined

soil desiccation and atmospheric heat accumulation. *Nature Geoscience*, *7*(5), 345–349. https://doi.org/10.1038/ngeo2141
Mittermeier, R. A., Turner, W. R., Larsen, F. W., Brooks, T. M., & Gascon, C. (2011). Global biodiversity conservation: The critical role of hotspots. In F. E. Zachos & J. C. Habel (Eds.), *Biodiversity hotspots: Distribution and protection of conservation priority areas* (pp. 3–22). Springer. https://doi.org/10.1007/978-3-642-20992-5_1
Montandon, L. M., & Small, E. E. (2008). The impact of soil reflectance on the quantification of the green vegetation fraction from NDVI. *Remote Sensing of Environment*, *112*(4), 1835–1845. https://doi.org/10.1016/j.rse.2007.09.007
Muñoz Sabater, J. (2019). *ERA5-land monthly averaged data from 1981 to present*. Copernicus Climate Change Service (C3S) Climate Data Store (CDS).
NASA JPL. (2013). *NASA shuttle radar topography Mission global 1 arc second* [dataset]. NASA EOSDIS Land Processes Distributed Active Archive Center. https://doi.org/10.5067/MEASURES/SRTM/SRTMGL1.003
Okujeni, A., Kowalski, K., Lewińska, K. E., Schneidereit, S., & Hostert, P. (2024). Multidecadal grassland fractional cover time series retrieval for Germany from the Landsat and Sentinel-2 archives. *Remote Sensing of Environment*, *302*, 113980. https://doi.org/10.1016/j.rse.2023.113980
O'Mara, F. P. (2012). The role of grasslands in food security and climate change. *Annals of Botany*, *110*(6), 1263–1270. https://doi.org/10.1093/aob/mcs209
Pellaton, R., Lellei-Kovács, E., & Báldi, A. (2022). Cultural ecosystem services in European grasslands: A systematic review of threats. *Ambio*, *51*(12), 2462–2477. https://doi.org/10.1007/s13280-022-01755-7
R Core Team. (2023). *A language and environment for statistical computing* (4.2.2) [computer software]. R Foundation for Statistical Computing. https://www.R-project.org/
Rakovec, O., Samaniego, L., Hari, V., Markonis, Y., Moravec, V., Thober, S., Hanel, M., & Kumar, R. (2022). The 2018–2020 multi-year drought sets a new benchmark in Europe. *Earth's Future*, *10*(3), e2021EF002394. https://doi.org/10.1029/2021EF002394
Reichstein, M., Ciais, P., Papale, D., Valentini, R., Running, S., Viovy, N., Cramer, W., Granier, A., Ogée, J., Allard, V., Aubinet, M., Bernhofer, C., Buchmann, N., Carrara, A., Grünwald, T., Heimann, M., Heinesch, B., Knohl, A., Kutsch, W., … Zhao, M. (2007). Reduction of ecosystem productivity and respiration during the European summer 2003 climate anomaly: A joint flux tower, remote sensing and modelling analysis. *Global Change Biology*, *13*(3), 634–651. https://doi.org/10.1111/j.1365-2486.2006.01224.x
Reinermann, S., Asam, S., & Kuenzer, C. (2020). Remote sensing of grassland production and management—A review. *Remote Sensing*, *12*(12), 1949. https://doi.org/10.3390/rs12121949
Reinermann, S., Gessner, U., Asam, S., Kuenzer, C., & Dech, S. (2019). The effect of droughts on vegetation condition in Germany: An analysis based on two decades of satellite earth observation time series and crop yield statistics. *Remote Sensing*, *11*(15), 1783. https://doi.org/10.3390/rs11151783
Reynaert, S., De Boeck, H. J., Verbruggen, E., Verlinden, M., Flowers, N., & Nijs, I. (2021). Risk of short-term biodiversity loss under more persistent precipitation regimes. *Global Change Biology*, *27*(8), 1614–1626. https://doi.org/10.1111/gcb.15501
Sala, O. E., Gherardi, L. A., Reichmann, L., Jobbágy, E., & Peters, D. (2012). Legacies of precipitation fluctuations on primary production: Theory and data synthesis. *Philosophical Transactions of the Royal Society, B: Biological Sciences*, *367*(1606), 3135–3144. https://doi.org/10.1098/rstb.2011.0347
Samaniego, L., Thober, S., Kumar, R., Wanders, N., Rakovec, O., Pan, M., Zink, M., Sheffield, J., Wood, E. F., & Marx, A. (2018). Anthropogenic warming exacerbates European soil moisture droughts. *Nature Climate Change*, *8*(5), 421–426. https://doi.org/10.1038/s41558-018-0138-5
Schaminée, J. H. J., Chytrý, M., Dengler, J., Hennekens, S. M., Janssen, J. A. M., Jiménez-Alfaro, B., Knollová, I., Landucci, F., Marcenò, C., Rodwell, J. S., & Tichý, L. (2016). Development of distribution maps of grassland habitats of EUNIS habitat classification (Report EEA/NSS/16/005). https://www.sci.muni.cz/botany/chytry/Schaminee_etal2016b_EEA-Report-Grasslands.pdf
Schwieder, M., Leitão, P. J., da Cunha Bustamante, M. M., Ferreira, L. G., Rabe, A., & Hostert, P. (2016). Mapping Brazilian savanna vegetation gradients with Landsat time series. *International Journal of Applied Earth Observation and Geoinformation*, *52*, 361–370. https://doi.org/10.1016/j.jag.2016.06.019
Seneviratne, S. I., Lüthi, D., Litschi, M., & Schär, C. (2006). Land–atmosphere coupling and climate change in Europe. *Nature*, *443*(7108), 205–209. https://doi.org/10.1038/nature05095
Senf, C. (2022). Seeing the system from above: The use and potential of remote sensing for studying ecosystem dynamics. *Ecosystems*, *25*(8), 1719–1737. https://doi.org/10.1007/s10021-022-00777-2
Senf, C., & Seidl, R. (2018). Natural disturbances are spatially diverse but temporally synchronized across temperate forest landscapes in Europe. *Global Change Biology*, *24*(3), 1201–1211. https://doi.org/10.1111/gcb.13897
Sheffield, J., & Wood, E. F. (2011). *Drought: Past problems and future scenarios*. Earthscan.
Spinoni, J., Vogt, J. V., Naumann, G., Barbosa, P., & Dosio, A. (2018). Will drought events become more frequent and severe in Europe? *International Journal of Climatology*, *38*(4), 1718–1736. https://doi.org/10.1002/joc.5291
Stampfli, A., Bloor, J. M. G., Fischer, M., & Zeiter, M. (2018). High land-use intensity exacerbates shifts in grassland vegetation composition after severe experimental drought. *Global Change Biology*, *24*(5), 2021–2034. https://doi.org/10.1111/gcb.14046
Tegetmeyer, C., Barthelmes, K.-D., Busse, S., & Barthelmes, A. (2021). Aggregierte Karte der organischen Böden Deutschlands. 2., überarbeitete Fassung. (01/2021; Greifswald Moor Centrum-Schriftenreihe).
Teuling, A. J. (2018). A hot future for European droughts. *Nature Climate Change*, *8*(5), 364–365. https://doi.org/10.1038/s41558-018-0154-5
Teuling, A. J., Seneviratne, S. I., Stöckli, R., Reichstein, M., Moors, E., Ciais, P., Luyssaert, S., van den Hurk, B., Ammann, C., Bernhofer, C., Dellwik, E., Gianelle, D., Gielen, B., Grünwald, T., Klumpp, K., Montagnani, L., Moureaux, C., Sottocornola, M., & Wohlfahrt, G. (2010). Contrasting response of European forest and grassland energy exchange to heatwaves. *Nature Geoscience*, *3*(10), 722–727. https://doi.org/10.1038/ngeo950
Vogel, A., Scherer-Lorenzen, M., & Weigelt, A. (2012). Grassland resistance and resilience after drought depends on management intensity and species richness. *PLoS One*, *7*(5), e36992. https://doi.org/10.1371/journal.pone.0036992
Volaire, F. (2018). A unified framework of plant adaptive strategies to drought: Crossing scales and disciplines. *Global Change Biology*, *24*(7), 2929–2938. https://doi.org/10.1111/gcb.14062
Walter, J., Nagy, L., Hein, R., Rascher, U., Beierkuhnlein, C., Willner, E., & Jentsch, A. (2011). Do plants remember drought? Hints towards a drought-memory in grasses. *Environmental and Experimental Botany*, *71*(1), 34–40. https://doi.org/10.1016/j.envexpbot.2010.10.020
Wellstein, C., Poschlod, P., Gohlke, A., Chelli, S., Campetella, G., Rosbakh, S., Canullo, R., Kreyling, J., Jentsch, A., & Beierkuhnlein, C. (2017). Effects of extreme drought on specific leaf area of grassland species: A meta-analysis of experimental studies in temperate and sub-Mediterranean systems. *Global Change Biology*, *23*(6), 2473–2481. https://doi.org/10.1111/gcb.13662
West, H., Quinn, N., & Horswell, M. (2019). Remote sensing for drought monitoring & impact assessment: Progress, past challenges and future opportunities. *Remote Sensing of Environment*, *232*, 111291. https://doi.org/10.1016/j.rse.2019.111291

Wilsey, B. J. (2018). *The biology of grasslands* (Vol. 1). Oxford University Press. https://academic.oup.com/book/26762/chapter/195661796

Wilson, J. B., Peet, R. K., Dengler, J., & Pärtel, M. (2012). Plant species richness: The world records. *Journal of Vegetation Science*, *23*(4), 796–802. https://doi.org/10.1111/j.1654-1103.2012.01400.x

Wolf, S., Eugster, W., Ammann, C., Häni, M., Zielis, S., Hiller, R., Stieger, J., Imer, D., Merbold, L., & Buchmann, N. (2013). Contrasting response of grassland versus forest carbon and water fluxes to spring drought in Switzerland. *Environmental Research Letters*, *8*(3), 035007. https://doi.org/10.1088/1748-9326/8/3/035007

Yin, J., Gentine, P., Slater, L., Gu, L., Pokhrel, Y., Hanasaki, N., Guo, S., Xiong, L., & Schlenker, W. (2023). Future socio-ecosystem productivity threatened by compound drought–heatwave events. *Nature Sustainability*, *6*, 259–272. https://doi.org/10.1038/s41893-022-01024-1

Zang, C. S., Buras, A., Esquivel-Muelbert, A., Jump, A. S., Rigling, A., & Rammig, A. (2020). Standardized drought indices in ecological research: Why one size does not fit all. *Global Change Biology*, *26*(2), 322–324. https://doi.org/10.1111/gcb.14809

Zhang, Y., Gentine, P., Luo, X., Lian, X., Liu, Y., Zhou, S., Michalak, A. M., Sun, W., Fisher, J. B., Piao, S., & Keenan, T. F. (2022). Increasing sensitivity of dryland vegetation greenness to precipitation due to rising atmospheric CO_2. *Nature Communications*, *13*(1), 4875. https://doi.org/10.1038/s41467-022-32631-3

Zhou, S., Williams, A. P., Berg, A. M., Cook, B. I., Zhang, Y., Hagemann, S., Lorenz, R., Seneviratne, S. I., & Gentine, P. (2019). Land–atmosphere feedbacks exacerbate concurrent soil drought and atmospheric aridity. *Proceedings of the National Academy of Sciences of the United States of America*, *116*(38), 18848–18853. https://doi.org/10.1073/pnas.1904955116

Zink, M., Samaniego, L., Kumar, R., Thober, S., Mai, J., Schäfer, D., & Marx, A. (2016). The German drought monitor. *Environmental Research Letters*, *11*(7), 074002. https://doi.org/10.1088/1748-9326/11/7/074002

SUPPORTING INFORMATION

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

How to cite this article: Kowalski, K., Senf, C., Okujeni, A., & Hostert, P. (2024). Large-scale remote sensing analysis reveals an increasing coupling of grassland vitality to atmospheric water demand. *Global Change Biology*, *30*, e17315. https://doi.org/10.1111/gcb.17315