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RESEARCH ARTICLE

Experimental drought reduces the productivity and stability of a calcareous grassland

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Abstract

1. Grasslands, which encompass 40% of terrestrial ecosystems, hold global significance for food production, carbon storage and other ecosystem services. However, grasslands across the biosphere are becoming increasingly exposed to both wet and dry precipitation extremes resulting from climate change.
2. Therefore, understanding how grasslands will respond to precipitation extremes is a pressing issue for managing changes to biodiversity and ecosystem service provision.
3. Here, we use experimental manipulations of precipitation (50% increase and 50% decrease in growing-season precipitation) over 6 years to investigate the stability and resistance of both productivity and community diversity in a calcareous grassland community.
4. We found that decreased growing-season precipitation led to reductions in mean productivity (25% decrease in peak above-ground biomass) and its temporal stability (54% increase in the coefficient of variation of biomass across years). Productivity losses were more pronounced for graminoids and legumes, but this was not reflected in species per cent cover. Community composition was resistant to the precipitation manipulations, with no clear differences in overall community compositional turnover, dissimilarity or biodiversity indices. There was also no detectible effect of increased precipitation on productivity or community composition, which may indicate a lack of efficacy of the irrigation treatment in increasing soil moisture. Finally, the precipitation manipulations had no effect on temporal trends of community change, with an overall increase in richness and shift in grassland community composition across the study period independent of treatment.
5. *Synthesis*. While the diversity and composition of this calcareous grassland was resistant to precipitation extremes (at least in the short term), sustained reductions in growing-season precipitation reduced productivity and its temporal stability, particularly for graminoids and legumes. Therefore, we highlight that different properties of grasslands can vary in their responses to changes in precipitation.

R. Salguero-Gómez and A. Hector—Shared authorship.

KEYWORDS
biodiversity change, climate change, community resilience, DroughtNet, field experiment, precipitation

1 | INTRODUCTION

As a dominant terrestrial biome important for ecosystem services and food security, understanding the response of grasslands to climate change, and in particular changing precipitation patterns, is critical (Fay et al., 2008; Franklin et al., 2016; Hopkins & Prado, 2007). Despite the threat of climate change, its effects on plant communities are not uniform, and complex responses highlight the need for targeted community-level experiments (Gupta et al., 2020; Harrison et al., 2015; Kardol et al., 2010; Parmesan & Hanley, 2015). Key components of climate change that are expected to influence plant communities are more changeable, and more extreme, precipitation patterns (Hopkins & Prado, 2007; Knapp et al., 2015). For grasslands, which occupy 40% of terrestrial ecosystems and provide many ecosystem services (Abberton et al., 2010; O'Mara, 2012; Petermann & Buzhdygan, 2021), declines in use and extent after agricultural intensification, conversion and grazing may be exacerbated by precipitation shifts (Meng et al., 2021; Peeters, 2009). Thus, studying how grassland communities will respond to precipitation change will aid in safeguarding these globally important habitats.

In grasslands, one way that community responses to precipitation change have been explored is through productivity. Productivity in grasslands is typically measured through biomass (Fahey & Knapp, 2007). Indeed, there have been wide efforts to understand how grassland biomass changes with precipitation (Grime et al., 2008; Knapp et al., 2017; Kröel-Dulay et al., 2022; Smith et al., 2024). Generally, drought conditions reduce primary productivity in grasslands (Herben et al., 1995; Kardol et al., 2010; Smith et al., 2024; Wang et al., 2007), which can impact ecosystem services such as pollination (Phillips et al., 2018). However, despite overall reductions in productivity, grassland biomes with different baseline climatic conditions react differently, where arid or xeric biomes are more susceptible to losses in productivity with drought than mesic biomes (Cleland et al., 2013; Huxman et al., 2004; Moran et al., 2014). Productivity may also recover quickly when drought conditions subside, even in semi-arid grasslands (Luo et al., 2023). Conversely, there are relatively fewer studies investigating increases in precipitation (or irrigation), but a global meta-analysis (although largely in North America) revealed that ecological experiments with supplemented watering alone did not change biomass (DeMalach et al., 2017). Overall, there are grassland productivity declines in drought conditions, but understanding temporal dynamics in productivity with respect to precipitation is crucial in a wider range of grassland habitat types.

Community composition differences driven by changing precipitation patterns are less clear in grasslands. Harrison et al. (2015) presented findings that reductions in midwinter precipitation over 14 years reduced biodiversity in Californian grasslands. Furthermore, a recent study found that after 11 drought years, grassland communities in a German semi-arid grassland shifted to favour dry-grassland specialists and ruderal species, and composition change was mediated by microclimatic conditions of site topology (Mazalla et al., 2022). However, another long-term study of experimental precipitation manipulation in an infertile UK grassland found that although communities in drought (but not irrigated) conditions differed from control plots, interannual variation in natural precipitation and broad shifts in the community through time were better explanations for community change (Grime et al., 2008). Several studies have found that grassland communities are resistant to both experimentally induced drought and natural variation in precipitation (Cleland et al., 2013; Craine et al., 2013; Grime et al., 2000; Sternberg et al., 1999). A key mechanism proposed for community resistance to precipitation extremes is buffering via increased species diversity, whereby more species create redundancy in functional composition that is better adapted to withstanding precipitation extremes (Craine et al., 2013; Craven et al., 2018; Griffin-Nolan et al., 2019; Wagg et al., 2017). Furthermore, perceived resistance may be observed due to the lifespan of perennial plant species in a community, with much greater community differences in the seed bank resulting in a delayed response (Basto et al., 2018). To fully elucidate the temporal dynamics of community composition as precipitation patterns change, we need further long-term monitoring of grassland systems.

A notable case study of a grassland that is vulnerable to climate change are the calcareous grasslands, which we focus on here. Calcareous grasslands are typified by alkaline soils, often occurring on limestone or chalk bedrock, supporting up to 700 vascular plant species in Europe, and providing a wide range of ecosystem services such as pollination, carbon sequestration and recreation (Gibson & Brown, 1991; Grêt-Regamey et al., 2014; Klaus et al., 2021; Willems, 1990). There have been declines in the extent of many European calcareous grasslands, following agricultural intensification, scrub encroachment and grazer management (Grêt-Regamey et al., 2014; Ridding et al., 2020), which may accentuate effects of climate change. To preserve high levels of species diversity, calcareous grasslands are listed as recovering ecosystems and part of wider conservation management schemes in countries such as the United Kingdom (Gibson, 1986; Gibson & Brown, 1991; Maddock, 2008; Poschlod et al., 1998).

Here, we use 6 years (2016–2021) of biodiversity data from an experimental manipulation (50% increase and 50% decrease) of precipitation in a calcareous grassland to examine productivity and community resistance to precipitation change, an important component of climate change. We extend previous work on calcareous grasslands (Grime et al., 2000, 2008) through an analysis of detailed temporal dynamics in community composition and productivity, using annually replicated data. Specifically, we answered three key questions: (i) whether changes in precipitation affect above-ground annual net primary productivity (above-ground ANPP) and its temporal stability across years, (ii) whether calcareous grassland communities have a high resistance to drought conditions, and which species are important for driving community differences, and (iii) whether the effect of precipitation manipulation change over time, and whether these temporal dynamics affected by natural precipitation patterns. We address these questions by quantifying the stability of productivity and resistance of community composition, which are useful conceptual terms to integrate community responses to climate change and tools to compare communities from different ecosystems (Allen et al., 2019; Donohue et al., 2013; Pimm, 1984; Van Meerbeek et al., 2021). For stability, we monitored shifts in the mean and variability of productivity through time with respect to precipitation treatments. Shifts in abundance or productivity serve as early warning signals of community shifts and indicate decreased stability in ecological communities (Clements & Ozgul, 2016; Pimm, 1984). Then, we use the definition of resistance for community composition from Van Meerbeek et al. (2021), where community resistance is the ability of community composition to resist changes in system variables in response to a perturbation, which here is drought or increase in precipitation through time.

2 | METHODS

2.1 | Study site

The RainDrop (rainfall and drought platform) experiment is situated in a ~2-ha area ('five-acre field') in the Upper Seeds grasslands (51°46′16.8″ N 1°19′59.1″ W, 166 m a.s.l.) of the University of Oxford's Wytham Woods estate, Oxfordshire, UK (Figure 1). Upper Seeds is a recovering calcareous grassland, which was intermittently used for arable agriculture from the Second World War until the late 1970s, before the site was managed as a grassland beginning in 1978 (Gibson, 1986; Grime et al., 2000). Grazing by sheep has been excluded throughout the experiment but did occur before the experiment. Upper Seeds, as with other calcareous grasslands, has a high level of floral biodiversity, in which graminoids constitute ~60% of species by biomass. Management consists of mowing all above-ground vegetation in mid-July at the peak of the growing season, and again in early October, coinciding with the end of the growing season. Biomass is removed following mowing. The site has a shallow soil depth (300–500 mm), alkaline soils (Gibson & Brown, 1991), a daily average temperature range of −5°C to 26°C (2016–2020) and a daily total precipitation range of 0–40 mm (2016–2020) (Rennie et al., 2017).

2.2 | Experimental design

We explored grassland biodiversity responses to precipitation in the context of the global drought network (DroughtNet) international drought experiment. DroughtNet's international drought experiment is a coordinated distributed experiment with over 100 sites globally (https://droughtnet.weebly.com/) (Smith et al., 2024). The goal of the DroughtNet experimental network is to explore ecosystem sensitivity to precipitation extremes through experimental manipulations of precipitation (Knapp et al., 2017). Precipitation manipulation is carried out by modifying natural precipitation patterns in each plot with rainout shelters, acting as a press disturbance (continuous change in the environment) maintained across several years. The manipulation was implemented in RainDrop as a randomised, replicated block design in which four

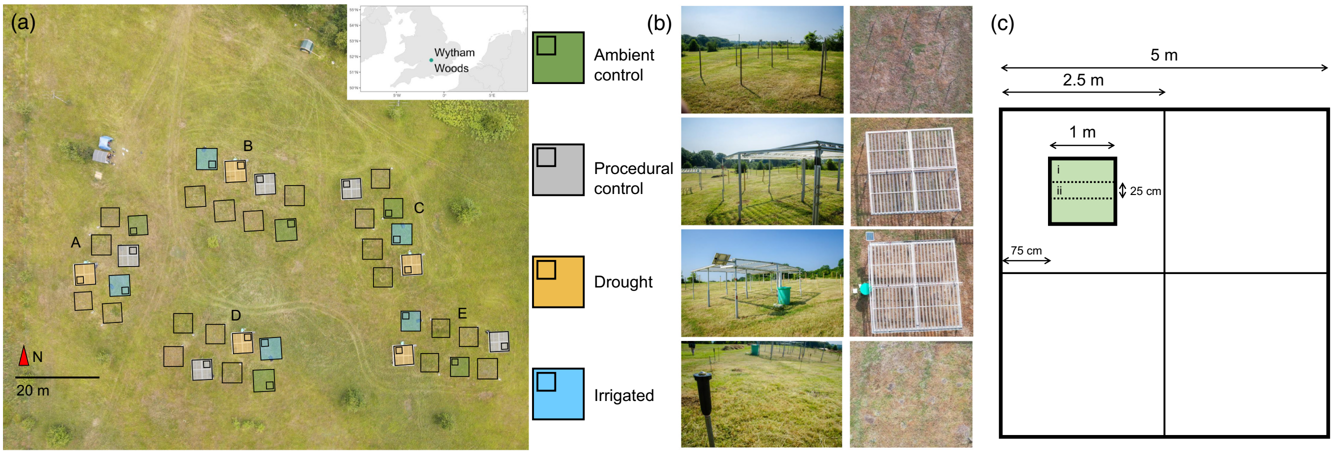

FIGURE 1 Experimental schematic of RainDrop on Upper Seeds, Wytham Woods with DroughtNet coordinated distributed experiment plots. (a) DroughtNet treatments are denoted by the colour of each 5 m × 5 m plot, and include Ambient control (green; no manipulation), Procedural control (grey; rainfall shelter but no change in rainfall), Drought (orange; −50% rainfall shelter) and Irrigated (blue; +50% rainfall with sprinklers). Letters indicate the five replicated and randomised experimental blocks A–E. Smaller squares indicate the biodiversity data collection area in each plot; the positions of which were randomised. (b) Photographs including ground-level (left) and aerial (right) views of each treatment type. (c) Experimental design schematic for each plot. Full 5 m × 5 m plot area, subdivided into quarters (2.5 m × 2.5 m), one of which contained the observation quadrat (green square—1 m × 1 m) used in this experiment. Species percentage cover (i) and biomass (ii) were collected from the observation quadrat. Each quadrat had a buffer of 75 cm.

treatments were repeated across five blocks ($n = 20$ experimental plots; Figure 1a, blocks A–E), in order to account for spatial variation and site topography, which varies by 5 m within the experimental area. Plots were therefore spatially nested within each block, which we accounted for with nested hierarchical random effects of plots within blocks in analyses.

Each replicated unit of 5 m × 5 m plots had one of four experimental treatments: ambient control plots (Ambient control), −50% precipitation rainout shelters to simulate drought (Drought), +50% irrigated plots with sprinklers to simulate increased precipitation (Irrigated) and procedural controls (Procedural control; precipitation shelter with no change to precipitation; Figure 1a). Biodiversity data collection occurs in the central 1 m × 1 m quadrat in one-quarter of each 5 m × 5 m plot, where the data collection quarter was randomised at the beginning of the experiment (Figure 1c). Therefore, each experimental quadrat has a buffer of 75 cm, which prevents wind-driven rain from entering the experimental quadrat (Figure 1c).

Rainout shelters consist of metal structures 1.5–2 m above the ground with transparent Perspex guttering. In the drought treatment, the rainout shelter gutters are approximately 10.4 cm wide and spaced such that 50% of the surface area of the plot is blocked by guttering. Irrigated treatment plots are supplied by water containers from the drought treatment, which collects precipitation with the transparent Perspex gutters, such that 50% additional precipitation is comprised of precipitation lost to the shelter (Gherardi & Sala, 2013). Procedural control plots were crucial to test the potential confounding effect of the drought treatment, in which similar structures and guttering are in place to simulate the microclimatic conditions of the shelter, but with guttering inverted to allow natural precipitation levels (Figure 1b). For example, although Perspex guttering was transparent to allow light to reach the plot, it reduced the light available to the grassland community to some degree. Thus, the procedural control enabled us to account for any such microclimatic effects. Precipitation manipulation percentages were selected through an assessment of long-term precipitation records, which found that extremes of annual precipitation differed from average years by ~40% (Knapp et al., 2015). At RainDrop, all drought treatments are removed between October and March of each year, when the Perspex gutters are inverted to restore natural precipitation levels, such that the experimental treatments are active during the growing season. However, rainout shelters and guttering remain throughout the year. To further test the validity of the experimental treatments at this site, we used preliminary data on soil moisture recorded from 13 of the 20 plots between August and September 2022. We found that simulated drought reduced median raw soil moisture by 37%, while there was only a modest soil moisture increase of 7% in the Irrigated treatment (Figure S1).

2.3 | Data collection

The core experimental protocol consists of biodiversity and productivity monitoring within experimental plots, namely species diversity and abundance, and above-ground net biomass production. To explore how precipitation manipulation influences grassland dynamics and composition, we monitored three main features of biodiversity: total community above-ground ANPP, functional group-level above-ground biomass and species-level percentage cover of vascular plants, for each 1 m × 1 m quadrat in each year between 2016 and 2021. We define ANPP as the total above-ground biomass of vascular plants across the growing season in each year, which estimates the investment of energy into growth of plant structures. We collected biomass at the peak of the growing season, 20 June–14 July, and at the end of September, such that ANPP was estimated for the entire growing season. We estimated ANPP using a 'clip strip' of all vascular plant material in a 1 m × 0.25 m strip in the centre of each quadrat, collected after percentage cover data. The size of clip strips was chosen to efficiently measure biomass across all plots in sufficient time, and representativeness of the biomass samples was ensured through spatial replication in blocks. Clip strips were gathered using hand trimmers ~1 cm above the soil surface. Within 1 day of collection, we sorted clip strips into five functional groups: graminoids, legumes, non-leguminous forbs, woody species, and bryophytes and dried them at 70°C for 48 h, before weighing the dry biomass with an accuracy of ±0.1 g. Forbs are defined as any herbaceous flowering plant other than a graminoid. We used both functional group-level estimates of biomass and summed values of ANPP in analyses, which were scaled by a factor of four to the standardised measure of $\mathrm{g\,m^{-2}}$. Due to smaller biomasses estimated for woody (1.65% of total biomass) and bryophyte groups (1.20% of total biomass), we only included graminoids, legumes and forbs in subsequent ANPP analyses.

Percentage cover data collection occurred before the peak of the growing season in each year, in mid to late June. We estimated the percentage cover of all vascular plant species in each quadrat. Because species overlapped spatially, percentage cover estimates exceed 100%. Species names follow the International Plant Names Index (IPNI, 2022).

We added environmental context and explored how biodiversity changes are influenced by local weather patterns using weather data from the National Environment Research Council (NERC) Environmental Change Network (Rennie et al., 2017). A meteorological station was present in the five-acre field within 100 m of all experimental quadrats. Raw meteorological data consisted of 16 weather variables, which were gathered at hourly intervals between 2016 and 2020, but data were not available in 2021. We used the mean hourly precipitation and temperature in the spring (21 March–20 June) and summer (21 June–22 September; the growing season) for each year of study as weather variables of interest.

2.4 | General analysis

We analysed the experimental data with hierarchical Bayesian regression models using the *brms* package (Bürkner, 2017) in R version 4.1.3 (R Core Team, 2022). To perform model selection, we estimated the out-of-sample predictive performance of candidate models relative to base models that excluded predictor variables of interest. For each candidate model, we performed leave-one-out cross-validation with the *loo* criterion and the expected log-wise predictive density (*elpd*, where Δ *elpd* gives the change in *elpd* relative to another explanatory model; Vehtari et al., 2017). Therefore, *elpd* gives an estimate of predictive performance that is analogous to an information criterion. Where two candidate models were comparable in *elpd* (Δ *elpd* <2), we reported the model with fewer explanatory variables and explored the posterior coefficients of the model to make inference. Models were run across four Markov chain Monte Carlo chains for 4000 iterations with 2000 warm-up iterations, and the convergence of the model across chains was assessed by inspecting $\hat{R}$ values, which assess the degree of mixing between chains (Bürkner, 2017). Model priors were selected using prior predictive simulations, where ranges of coefficient values were assessed for plausibility relative to prior distribution parameters. For the full set of model priors, please refer to model code (https://doi.org/10.5281/zenodo.8135588). Following model selection, we performed a set of Bayesian hypothesis tests (Bürkner, 2017) to investigate whether there were consistent differences in biodiversity and biomass measures between procedural control and ambient control treatments, and the proportion of variance explained by the random effect of experimental block. Differences between control treatments were evaluated by comparing posterior distributions between ambient control and procedural control groups. We used the intraclass correlation coefficients (ICC) (Nakagawa & Schielzeth, 2010) to assess the proportion of variance explained by the random effect of block relative to the total population-level variance.

2.5 | Testing the effect of precipitation on grassland productivity and its temporal stability

To answer our first key question, we analysed how precipitation manipulation influences ANPP and its temporal stability. We examined responses at both the whole community level and at the functional group level, as well as the interannual temporal stability of above-ground ANPP. We define the temporal stability of productivity as the inverse of the interannual coefficient of variation (CV) of above-ground ANPP (He et al., 2022) for each quadrat. Where the response variable was the annual total and group-level ANPP, raw ANPP values were transformed using the natural logarithm, which were then modelled using a Gaussian distribution (although similar results were obtained using a Gamma distribution; Figure S3). In the ANPP models, the key predictors of interest were precipitation treatment and observation year. We used model selection to test the predictive performance for a set of candidate models including precipitation treatment (categorical variable, four levels), a linear effect of the observation year (continuous variable, *z*-scored), an autoregressive term for the observation year (order = 1), and two-way interactions between precipitation treatment and observation year (linear). We investigated linear effects of observation year to capture broad changes in the community through time, but with insufficient temporal sampling to ascertain non-linear dynamics. Additional annual fluctuations were tested with effects of local environmental variables, and random effects of observation year. We compared candidate models to base models that excluded predictor variables of precipitation treatment and observation year. ANPP models estimated at the level of functional group also included terms for functional group (categorical variable, three levels). The full set of candidate models for each ANPP response variable is detailed in Tables S1–S3. We also included a categorical predictor term for the month of harvest (middle or later part of growing season).

In all models, we included a nested (hierarchical), intercept-only random effect of the precipitation treatment (four levels) within block (five levels) to account for the experimental structure of RainDrop, and an intercept-only random effect of observation year (six levels) to capture additional interannual variability. Nested intercept-only random effects were appropriate for this study due to the static spatial organisation of plots (each with one replicate of each treatment) within blocks in the current experiment (Figure 1a), for which we aimed to account for additional variance from the treatments x block interaction. Models of the stability of ANPP do not include temporal effects, because the metric captured interannual variability in biomass for each quadrat resulting in a single value per plot. Thus, for temporal stability models we tested a candidate model with the precipitation treatment to the base model with no predictor variables (Table S3). When analysing temporal stability of ANPP, we validated the patterns in stability by testing the log-linear relationship between variance in ANPP and mean ANPP for each plot using Pearson's correlation, to test the role of Taylor's Power Law in driving these effects (Reckling et al., 2021; Figure S5). In ANPP models, we used weakly informed normal priors of $N(3.5, 0.5)$ for the global intercept term and $N(0, 1)$ for predictor variables. The intercept-only random effects were fitted using exponential priors with rates between 4 and 8.

2.6 | Testing the resistance of grassland communities to precipitation treatments

We answered our second key question by investigating whether the grassland community was resistant to precipitation treatments in three ways: with broad diversity indices, using community composition and turnover, and exploring individual species contributions to community change. First, we explored how broad diversity indices at the quadrat level were influenced by the precipitation treatments using linear hierarchical mixed-effects model selection, in an identical procedure as described in Section 2.4. We calculated biodiversity indices using the relative proportions, *p*, of each species from percentage cover estimates. The three biodiversity indices included were vascular plant species richness, the Shannon–Weiner diversity index, $H = -\sum p \ln p$ (Shannon & Weaver, 1963), and the Simpson's diversity index, $D = \sum p^2$ (Simpson, 1949). For the Shannon–Weiner and Simpson's indices, response variables were z-scored (mean and variance centred on 0) for analyses and models were fitted using a Gaussian distribution. Models with species richness counts were fitted using a Poisson distribution and a log link. Shannon–Weiner and Simpson's models were fitted with regularising priors of $N(0, 0.5)$ for both intercept and predictor terms, and Richness models were fitted with a prior of $N(3, 0.25)$ for the intercept.

To assess how the grassland community composition varied between precipitation treatments, we tested community dissimilarity using non-metric multi-dimensional scaling (NMDS) implemented in the *vegan* package (Clarke, 1993; Oskanen et al., 2022). Community-level data consisted of species percentage cover data for each quadrat, which is a single treatment in a given plot each year. We fitted the NMDS using the Bray–Curtis dissimilarity index with a dimension of three, and up to 1000 random starts to reach convergence in stress values. Then, we compared the first two dominant NMDS axes between precipitation treatments. We used hierarchical linear mixed-effects models with a response variable of the NMDS axis scores, with model selection as described in Section 2.4. We fitted these models with regularising priors of $N(0,0.1)$ for both the global intercept and predictor variables. Then, in addition to the linear modelling framework, we explored statistical differences in Bray–Curtis similarities between precipitation treatments using analysis of similarities. Analysis of similarities tests differences in dissimilarity within sampling units compared with between sampling units (Oskanen et al., 2022). We also explored block-level community effects by testing the dissimilarity between experimental blocks by pooling data from the replicates within each block.

To further explore the drivers of community composition differences between sampling groups of precipitation treatments and observation years, we investigated which species were most important for community differences using Similarity Percentage analysis. Similarity Percentage is an extension of the Bray–Curtis dissimilarity measure for individual species within a community, for which the dissimilarity metric per species is averaged across pairs of sampling groups to give an overall contribution (standardised to sum to 1) of each species to differences for a set of sampling groups of interest (Clarke, 1993; Oskanen et al., 2022). We tested Similarity Percentage for the sampling groups of precipitation treatment, observation year and blocks. Then, following Similarity Percentage analysis, we explored variation in the relative abundance, p, of influential species between communities.

2.7 | Testing the temporal dynamics of the community and its drivers

We answered our third key question by exploring the temporal dynamics in the stability and resistance of the grassland community, and its potential climatic drivers. We estimated temporal trends in productivity, diversity indices and NMDS axes, as well as the similarities in floral communities between observation years. We extracted temporal trends from linear models of biodiversity specified in Section 2.5, which included linear or autoregressive effects of observation year, as well as two-way interactions between precipitation treatments and observation year. In addition to model selection, we also performed analysis of similarity tests for the NMDS communities between observation years and Similarity Percentage to identify influential species (Oskanen et al., 2022). Therefore, by assessing the temporal change in diversity indices and NMDS scores, we tested the temporal dynamics in this calcareous grassland. Furthermore, we explored which species had the largest changes in abundance over the study period, and thus which may have contributed most to temporal dynamics. For each species, we estimated the linear association between observation year and relative abundance, and explored which species had significant changes in relative abundance across plots.

Finally, to explore whether environmental drivers mediated temporal dynamics in the community, we tested how local weather variables influenced ANPP and biodiversity indices. Following the model selection framework in Section 2.4, we implemented linear models to investigate the impact of mean temperature and precipitation across the spring and summer-influenced biodiversity indices. In these models, linear terms for observation year were replaced with annual mean weather variables. We included both weather data for the current year and the previous year relative to biodiversity data collection, to test for current and lagged impacts of local weather on biodiversity differences.

3 | RESULTS

3.1 | Simulated drought reduces biomass production and its temporal stability

We found that simulated drought substantially reduced both above-ground ANPP and productivity's temporal stability (Figure 2). Across all observation years and experimental quadrats, there was a mean total ANPP of 303 ± 138 (S.D.) $\mathrm{g\,m^{-2}}$. Graminoids were the dominant functional group by biomass, with 63.6% of all biomass measured, compared with 20.4% for legumes and 16.0% for forbs. For total annual above-ground ANPP between 2016 and 2021, the model with the highest predictive performance, and fewest parameters, was the model including only the categorical effect precipitation treatment ($\Delta\,elpd = 5.03$ relative to the base model; Table S1). Total above-ground ANPP was substantially reduced in the drought treatment ($\beta = -0.77$ [−1.04; −0.49]; β coefficients give the posterior mean difference compared with the ambient control treatment on the log-scale, with the 95% credible intervals), with a mean total above-ground ANPP of 137 ± 156 (S.D.) $\mathrm{g\,m^{-2}}$ compared with 182 ± 137 (S.D.) $\mathrm{g\,m^{-2}}$ for the ambient control treatment (Figure 2a). Thus, compared with ambient conditions, the mean ANPP was reduced by 24.7% in the drought treatment. In contrast, irrigated plots did not have any substantial change in ANPP compared with the ambient control ($\beta = -0.10$ [−0.37; 0.18]; Figure 2a). We did not find evidence for either an overall linear temporal trend in

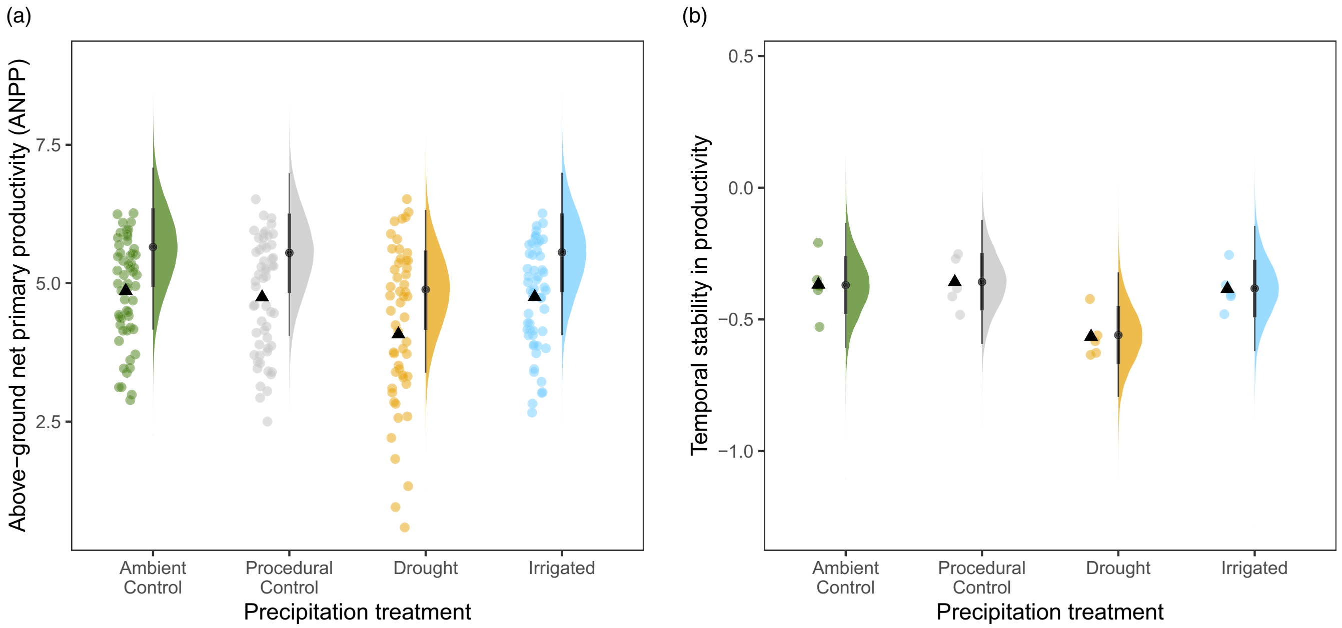

FIGURE 2 Drought reduces annual net primary productivity (ANPP) and its temporal stability. (a) Total above-ground ANPP with respect to precipitation treatments, where ANPP is the natural log-transformed above-ground biomass in g m^{-2}. (b) Temporal stability in productivity (inverse of interannual coefficient of variation in biomass) with respect to precipitation treatment. Coloured points give raw data across blocks and years and black triangles give the mean total ANPP. There is a negative skew in raw ANPP data, which leads to reductions in mean ANPP values relative to predictions, but this skew did not impact model convergence or influence our findings (Figure S3). Distributions are derived from 8000 draws of the full posterior distribution including random effects, with probability density function boxplots giving the posterior mean and uncertainty.

ANPP, or for an interaction between observation year and treatment (Table S1; Figure S2). The model with the highest predictive performance included the linear effect of observation year, but the *elpd* was not substantially increased relative to the simpler model including only the effect of treatment (Table S1), and the raw data showed no clear temporal pattern in ANPP (Figure S2). There was a weak negative skew in raw ANPP values, but skew did not impact model convergence (Figure S3). Furthermore, we re-ran model selection using a gamma distribution, which did not change the qualitative results (Figure S3b). We observed a similar pattern for temporal stability in productivity, with a Δ *elpd* of 3.15 for the model including precipitation treatment compared with the base model (Table S3). Temporal stability in productivity was substantially reduced in the drought treatment (β = −0.19 [−0.32; −0.06]), equating to a 53.5% increase in the coefficient of variation of biomass (CV = 0.56) relative to the ambient control treatment (CV = 0.37) (Figure 2b). There were no discernible differences in temporal stability in productivity for both ambient control and procedural control treatments or the irrigation treatment (Figure 2b). Furthermore, we did not find evidence for a log-linear relationship between variance in ANPP and mean ANPP for each plot (ρ = 0.42, p = 0.07), increasing our confidence in our observation of reduced stability (Figure S5).

The reductions in overall ANPP were driven primarily by decreases in the biomass of graminoids and legumes (Table S2; Figure S4). Forbs did not exhibit ANPP reductions in the drought treatment (β = −0.03 [−0.46; 0.39]), but reductions were accentuated in both graminoids (β = −1.00 [−1.41; −0.59]) and legumes (β = −0.87 [−1.29; −0.46]) (Figure S4). Therefore, we observed mean reductions in ANPP of 36.1% and 36.4% for graminoids and legumes, respectively. Both mean total ANPP and group-level ANPP were strongly overlapping between ambient control and procedural control treatments (β = 0.11 [−0.17; 0.38], β = 0.31 [−0.11; 0.72]; differences in posterior means between ambient control and procedural control). Furthermore, we did not find substantial variance in total biomass between blocks (ICC or σ_{block} = 0.01 [0.00; 0.05]) although the ability of the design to estimate this variance component is limited given the limited replication of five blocks.

3.2 | Community diversity and composition were resistant to drought and irrigation

We found evidence that species composition in these calcareous grassland communities is resistant to precipitation treatments, both in terms of broad diversity indices and community composition (Figure 3). For species richness, the Shannon–Weiner index and the Simpson's index, we did not observe differences in indices between precipitation treatments (Figure 3a–c). For all three indices, the Δ *elpd* compared with the base model was below 0.6, indicating no clear association between the indices and precipitation treatments, so we retained models excluding precipitation treatment

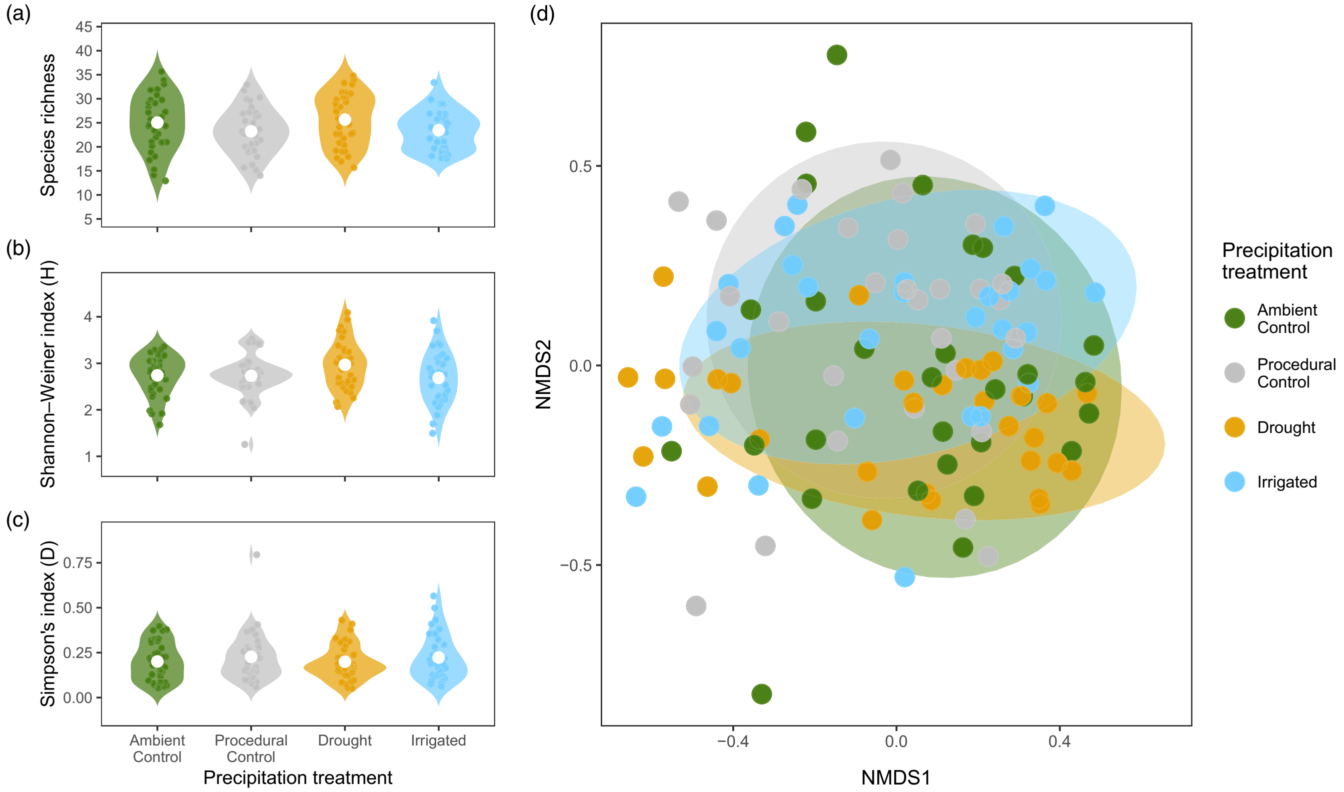

FIGURE 3 Calcareous grassland community diversity is resistant to precipitation manipulations. (a–c) Raw data distributions for species richness (a), Shannon–Weiner index (b) and Simpson's index (c) with respect to precipitation treatment. Coloured points indicate raw data, and violins give an estimate of data density across each index. White points indicate mean biodiversity index values. (d) Non-metric multi-dimensional scaling (NMDS) results for community composition, where the first two axes (NMDS1 and NMDS2) are displayed with respect to precipitation treatments. Ellipses are the 80% two-dimensional quantiles of the NMDS axes.

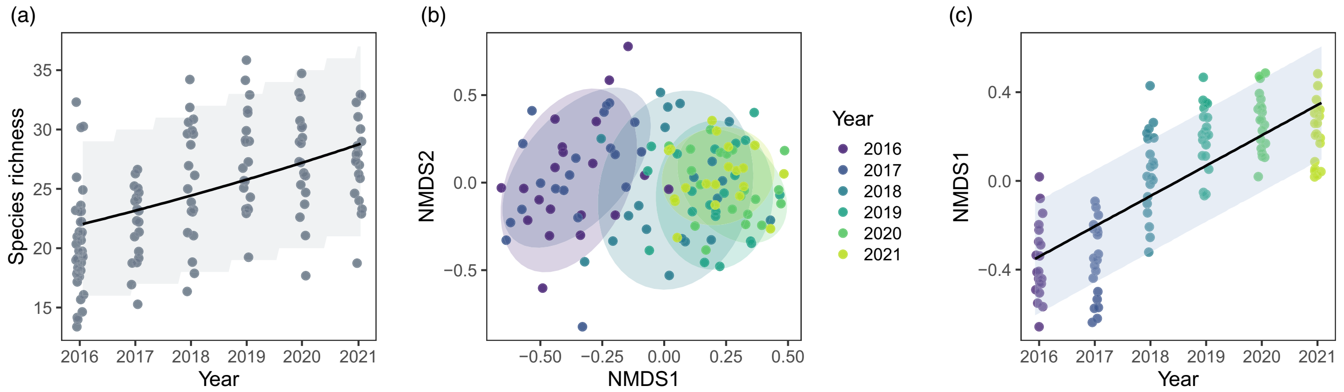

FIGURE 4 Changes in the grassland diversity and community composition 2016–2021. (a) Increases in species richness between 2016 and 2021. Grey points give raw observations of species richness for each quadrat in each treatment. Solid line indicates the posterior mean prediction with 90% credible intervals, which include random effects. (b) Non-metric multi-dimensional scaling (NMDS) results for community composition, where the first two axes (NMDS1 & NMDS2) are displayed with respect to observation year. Ellipses are the 80% two-dimensional quantiles of the NMDS axes. (c) Increases in NMDS1 over the observation period. Points give observed NMDS1 scores for each quadrat for a given treatment and block across the study period. Solid black line indicates the posterior mean, with 90% credible interval.

(Tables S4–S6). Similarly to ANPP, there were no clear differences in ambient control and procedural control treatments for richness, Shannon–Weiner index or Simpson's index. Furthermore, the mean posterior block-level variance (ICC or σ_{block}) was below 0.03 for all indices.

Community composition was also not clearly associated with the precipitation treatments. There was no clear association between NMDS axes one and two (NMDS1 and NMDS2) and precipitation treatment (Figure 3d; Figure S8), or between precipitation treatments and NMDS3 (Figure S8). A lack of community composition differences between treatments was further supported by the analysis of similarities, for which within-sample dissimilarity was broadly comparable to dissimilarity between samples (Figure S9; marginally significant relationship).

3.3 | Shifts in community composition and richness increase across the study period

Instead of an effect of precipitation treatment, we found evidence for overall temporal changes in the calcareous grassland communities, with increases in species richness and changes in community composition (Figure 4). However, these changes were not affected by the precipitation treatments. We recorded a total of 109 vascular plant species between 2016 and 2021 across all plots. Across all plots the annual total number of species recorded did not change substantially, ranging between 54 (2017) and 64 (2019). At the quadrat level, species richness ranged between 13 and 36 species m^{-2} with a mean of 24.4 ± 5.14 (S.D.) species. We found a positive association between species richness and observation year, such that there were increases in richness over the study period (Figure 4a; $\beta = 0.10$ [0.04; 0.16]). Overall, between 2016 and 2021, there was an increase in mean richness at the plot level from 20.3 to 27.4 species (Figure 4a). Furthermore, we found a strong association between community composition and observation year (Figure 4b). The analysis of similarities indicated a large difference in within-year community differences compared with between-year community differences (Figure S9). Furthermore, we observed a strong positive association between NMDS1 and observation year, which was a substantially better predictive model compared with the base model ($\Delta\, elpd = 58.4$). There was a consistent increase in NMDS1 over the study period ($\beta = 0.23$ [0.20; 0.27]), indicating a shift in community composition (Figure 4c).

In spite of observed temporal trends, we did not observe an association between productivity and average interannual weather conditions. Average spring and summer weather conditions were not strongly associated with any of the biodiversity indices or ANPP (Figures S6 and S7). Finally, we explored which species had the largest impact on community change across the years. Four species had significant positive temporal trends in abundance across plots (*Bromus commutatus*, *Medicago lupulina*, *Trisetum flavescens* and *Viola hirta*; Figure S10), but generally species richness increases at the plot level were not repeatedly associated with a specific group of species. We then used similarity percentages across species to investigate the species that were most influential in driving differences in community dissimilarity between years. Ten species had mean percentage contributions to dissimilarity above 2% (with *Potentilla reptans* lying on the boundary), of which four were graminoids, four were legumes and one was a forb (Figure 5a). Of these species however, *Arrhenatherum elatius* (graminoid), *Brachypodium pinnatum* (graminoid) and *Lotus corniculatus* (legume) had mean contributions of over 5% (median >6.5%) to community dissimilarity across years (Figure 5a,b). These three species were common, and varied substantially across the study period, with large interannual shifts, but displayed no clear pattern in relative abundance through time or with treatments (Figure 5b). In particular *Arrhenatherum elatius*, which is a common and dominant species, varied between an average abundance of 13.3% (relative abundance = 0.133) across all quadrats in 2018 to 2.3% in 2021 (Figure 5b).

4 | DISCUSSION

From our 6-year study of precipitation manipulation in a calcareous grassland, we show that simulated drought reduced productivity and its temporal stability, but that species diversity and composition were generally resistant. These results add to global findings of decreased grassland productivity with drought (Kröel-Dulay et al., 2022; Smith et al., 2024), but we add a key perspective that the reductions in productivity are coupled with reduced temporal stability, and an accentuated pattern in graminoids and legumes. Despite accentuated productivity loss in graminoids and legumes, we find that overall community composition in this calcareous grassland was resistant to 6 years of drought conditions, a finding consistent with other studies on calcareous grasslands (Craine et al., 2013; Grime et al., 2000, 2008). Increases in precipitation were not associated with any change in productivity or community composition, which may indicate a lack of efficacy in the irrigation treatment. Our study emphasises the need to explore detailed temporal dynamics in grassland communities alongside changing precipitation patterns, to understand how climate change will impact these vital ecosystems and the services they provide.

In the present study, experimental drought reduced the productivity of the calcareous grassland habitat and its interannual temporal stability, with 25% reductions in above-ground ANPP, and a 54% increase in productivity's coefficient of variation. Furthermore, despite a strong overall effect, reductions in productivity were driven primarily by losses in graminoid and legume biomass, but forb biomass did not change substantially. Productivity losses are concerning given calcareous grasslands are important ecosystems that are already vulnerable to other human impacts (Maddock, 2008). Reductions in primary productivity and biomass in response to drought have been widely reported in plant communities globally (Haddad et al., 2002; Kröel-Dulay et al., 2022; Smith et al., 2024). Reduction in productivity may be driven by water limitation, altered patterns of nutrient cycling following precipitation extremes (Haddad et al., 2002), or a diversion in the allocation of resources from survival to reproduction (Weißhuhn et al., 2011). A lack of biomass reduction in the forbs may be a result of deeper rooting depth in forbs relative to graminoids and legumes increasing access to water (Sydes & Grime, 1984), or increased water limitation relative to nitrogen limitation in legumes. Kröel-Dulay et al. (2022) found that experimental manipulations of precipitation often underestimate the impact of drought on biomass, failing to capture other abiotic processes that are associated with drought in real-world settings, including the interaction between drought timing and plant growth

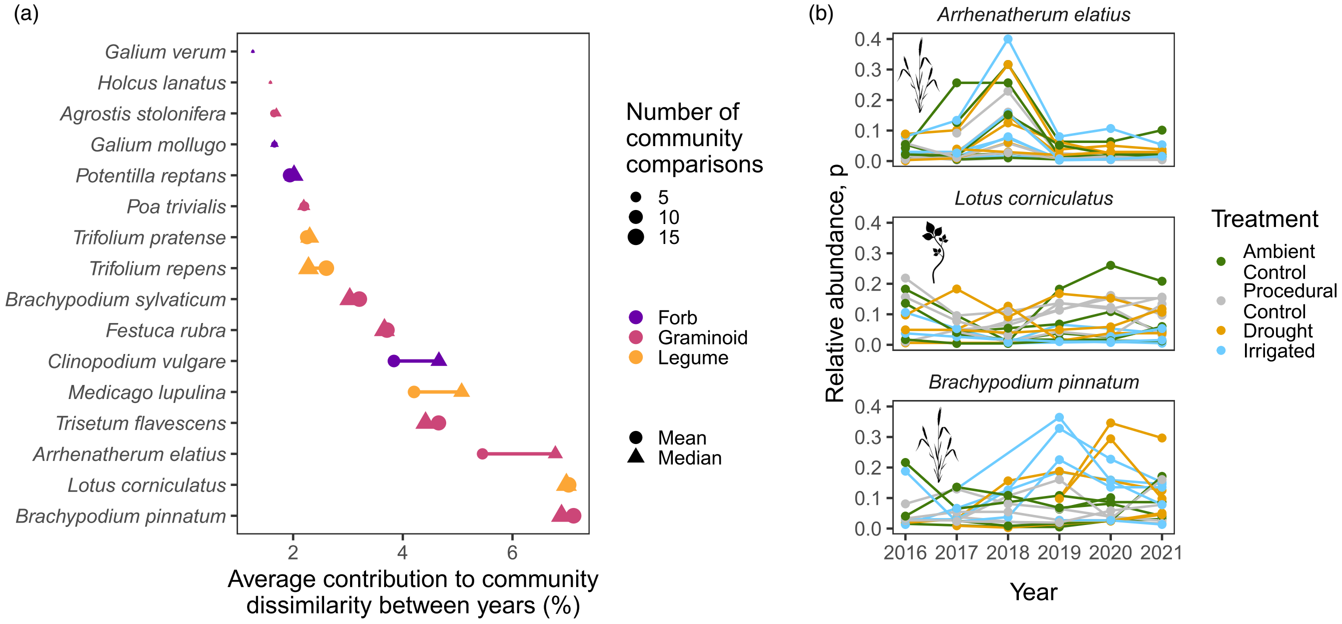

FIGURE 5 Commonly occurring graminoid and legume species drive community dissimilarity. (a) Similarity percentage results for species driving community dissimilarity across years. Only 16 species (of 109) with the highest contributions are shown. Circles give mean per cent contribution, and triangles mean per cent contribution, with the size of the point indicating the number of community comparisons and the colour denoting the functional group. (b) Change in relative abundance across years for three species with high contribution to dissimilarity across years. Points and lines give raw estimates of relative abundance in each quadrat for each species, indicating high variability in the relative abundance of the three most influential species across the study.

(Felton & Goldsmith, 2023). Furthermore, this calcareous grassland is a mesic system with moderate levels of annual precipitation, and productivity losses are likely to be amplified in more arid environments (Huxman et al., 2004; Moran et al., 2014). Ultimately, reduced precipitation threatens grassland productivity world-wide, and thus many ecosystem services that grasslands provide.

In addition to changes in mean productivity, drought also decreased the temporal stability by increasing the variance of productivity. Measures of stability in abundance (here biomass) can provide comparable metrics that forecast broader community-level changes as early warning signals (Clements & Ozgul, 2016; Wu et al., 2020). While previous studies have explored stability metrics in grasslands over short timescales (He et al., 2022), we add an important longer-term perspective to the narrative of grassland stability with changing precipitation patterns. Reduced stability could be the result of resource limitation (drought) increasing dependence on natural variation in precipitation, where productivity mediated through survival and reproduction is more reactive to limited precipitation levels (Grime et al., 2008; Weißhuhn et al., 2011). Worryingly, the early warning signal of reduced stability in productivity is supported by below-ground data from the calcareous grassland in Buxton, UK, where the seedbanks are highly altered by drought conditions, which may forecast rapid future community change (Basto et al., 2018). Further studies explicitly exploring metrics of community stability with respect to climate change in plant communities will provide valuable forecasts of the changing state of our ecosystems.

Importantly, over 6 years the diversity and composition of communities in this calcareous grassland were largely resistant to drought, despite the group-specific declines in the productivity of grasses and legumes. It is currently unclear why the composition metrics were largely unaffected by the productivity declines in grasses and legumes. Key findings from other long-term studies on calcareous grasslands support the composition resistance findings (Craine et al., 2013; Grime et al., 2000, 2008), but we add further temporal dynamics and investigation at the species level. We hypothesise that the grassland resistance could be the result of two main processes: (i) the maintenance of drought resistance through increased species and functional diversity over time, and (ii) insufficient time for precipitation change to influence the community, that is, lagged effects. There are clear global ecological signals that higher species diversity in linked to high stability (Craven et al., 2018; Hector et al., 2010). Importantly, resistance to climate extremes can also be compromised by reduced species diversity (Isbell et al., 2015). At the individual level, plant resistance is linked to functional traits such as leaf economic traits and root thickness (Anderegg et al., 2016; Tucker et al., 2011). At the community level, increased functional diversity, which is linked to species diversity, can stabilise grasslands after drought (Griffin-Nolan et al., 2019). Therefore, we hypothesise that the relatively high biodiversity of calcareous grasslands (Isbell et al., 2015), creates functional redundancy and therefore buffers the community to environmental change. These patterns may also be linked with wider climatic conditions, where arid grasslands have slower functional recovery from drought compared with mesic grasslands (Moran et al., 2014). Diversity in species and functional traits coupled with climatic variability across habitats may therefore explain why some grassland communities have responses to precipitation extremes (Harrison et al., 2015), and others do not (Grime et al., 2008). Long-term studies investigating coupled functional and community responses to precipitation extremes will be crucial in teasing apart these patterns.

Our observations of resistance may also be explained by temporal factors. Interestingly, despite group-specific reductions in biomass for graminoids and forbs, these changes were not mirrored in community composition from percentage cover. However, the group-specific results for biomass may indicate that there will be shifts in community composition in the future, especially when there is mortality and turnover in perennial species. Understanding links between productivity and community composition, either through functional redundancy or species turnover and mortality, is a vital next step in this system. Furthermore, compared with some other grassland habitats, these calcareous grasslands have many perennial species that survive for several years. From 14 years of data from a calcareous grassland in the north of England, there was temporal drift in the community but overall resistance, which may also have been linked to longer-living species surviving but reacting in growth to interannual variation in the climate (Grime et al., 2008). A delayed turnover is also supported by the seed bank, which had strong responses to drought conditions in the same system, suggesting that subsequent generations in the community will have lasting impacts of drought (Basto et al., 2018). Therefore, our findings do not rule out long-term impacts from climate change on grassland communities, which may occur abruptly when tolerance limits are reached (Trisos et al., 2020), or in synergy with other drivers such as habitat fragmentation (Brook et al., 2008; Klaus et al., 2021).

In addition to community resistance to drought, we found that neither productivity or community composition responded to irrigation in this calcareous grassland. Given that soil moisture content at the end of the growing season was not substantially increased in the irrigation treatment, the resistance of the community to irrigation could indicate failure in the irrigation treatment to successfully increase soil moisture levels on the freely draining soil and underlying bedrock. Although failure of the irrigation treatment is a likely explanation, the readings of soil moisture were taken during the late summer when precipitation is typically lower, and so further study of the irrigation treatment's efficacy is needed. Furthermore, community resistance to irrigation is a finding that has been replicated across several grassland irrigation experiments globally (DeMalach et al., 2017). Nevertheless, in other systems precipitation increases have been associated with community and functional changes, also in conjunction with warming (Collins et al., 2022; Kimmel et al., 2019). Therefore, resistance to precipitation could also reflect an insufficiency in the extremity of the precipitation addition (Smith et al., 2024), and further study of the efficacy of precipitation manipulation is needed.

Our final key finding was a general (treatment-independent) temporal change in the community, where richness increased by over 7 species m^{-2} between 2016 and 2021 and a shift in community composition. The addition of the temporal dynamics in the community was one key advantage of the current study, and future work should focus on long-term temporal patterns in community change in response to precipitation extremes. The most likely explanation is that temporal changes indicate ongoing secondary succession following the cessation of agriculture in ~1980 and sheep grazing before the experiment, with both long-term recovery and community change following grazing. An earlier climate change experiment that compared responses of a calcareous grassland at Harpur Hill in Buxton with those of the Wytham Upper Seeds found grassland diversity and composition was more stable in the established pasture at Buxton compared with the larger changes seen in Upper Seeds that the authors attribute to its secondary successional state (Grime et al., 2000, 2008).

4.1 | Caveats

There are several factors that we did not control in the current experiment that have the potential to impact community responses to precipitation extremes. First, while it is unlikely that the temporal dynamics observed are purely successional change after agriculture, grazing at the site occurring up to the start of the experiment, and other experiments at the site may have impacted the current community (Gibson & Brown, 1991; Grime et al., 2000). A switch from grazing to mowing at the start of the experiment may be responsible for the current temporal shift in the community and increase in species richness. Second, is the role of spatial dynamics and immigration from other grasslands in the area, or meta-community dynamics, which we did not control in the current study (Furey et al., 2022). Immigration can maintain high levels of local species diversity in plant communities (Loreau & Mouquet, 1999), and while out of the scope of the current study, immigration may also have an impact, particularly on temporal dynamics. However, Upper Seeds is relatively isolated from other nearby areas of calcareous grassland. Third, the role of microclimate on community change, which has been demonstrated as an important mediator in grassland drought responses (Mazalla et al., 2022). The drought treatment shelters in particular may have influenced light availability, and created irregular patterns of rainfall (when combined with wind) that influenced the community. However, we controlled for these structural effects using a procedural control, which is rarely available in precipitation manipulation experiments, and a replicated block design, and found no detectible differences between procedural control and ambient control plots.

5 | CONCLUSION

The long-term monitoring of calcareous grassland communities with respect to experimentally controlled precipitation change can reveal detailed community responses, which are not available from snapshots of the community. Measuring and predicting the impact of climate change on plant communities can be facilitated by the approach taken here that combines long-term data on community composition and productivity. Future work should combine community and productivity data with information on functional traits and the corresponding below-ground responses.

AUTHOR CONTRIBUTIONS

This study was established by Kadmiel Maseyk and Andrew Hector. PI support and resources were provided by Andrew Hector, Roberto Salguero-Gómez, Kadmiel Maseyk, Nick Hawes and Clare S. Lawson. Data were collected primarily by Clare S. Lawson and Andrew Hector, with contributions to data collection from all authors. John Jackson performed data analysis and exploration, with support from Sara L. Middleton, Andrew Hector and Roberto Salguero-Gómez. John Jackson wrote the initial draft with support from Sara L. Middleton, Andrew Hector and Roberto Salguero-Gómez. Critical manuscript feedback and approval were provided by all authors.

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CONFLICT OF INTEREST STATEMENT

Andrew Hector is an editor of the *Journal of Ecology*, but took no part in the peer review and decision-making processes for this paper.

PEER REVIEW

The peer review history for this article is available at https://www.webofscience.com/api/gateway/wos/peer-review/10.1111/1365-2745.14282.

DATA AVAILABILITY STATEMENT

All code, output and data used in the current study are archived using the Zenodo repository: https://doi.org/10.5281/zenodo.8135588 (Jackson et al., 2023), which were created from the following GitHub repository: https://github.com/jjackson-eco/raindrop_biodiversity_analysis.

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SUPPORTING INFORMATION

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

Figure S1: Preliminary results of soil moisture differences.

Figure S2: No temporal trend in ANPP.

Figure S3: Exploring skew in ANPP.

Figure S4: Primary productivity separated by functional group.
Figure S5: The log-linear relationship between temporal stability in ANPP and mean ANPP.
Table S1: Model selection for ANPP.
Table S2: Model selection for group-level ANPP.
Table S3: Model selection for temporal stability of productivity.
Table S4: Model selection for the Shannon-Weiner index.
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Figure S7: Weather effects on biodiversity.
Figure S8: NMDS precipitation treatment effects.
Figure S9: Analysis of community similarities.
Figure S10: Significant temporal trends in relative abundance for four species.

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