

RESEARCH ARTICLE

Differential responses of community-level functional traits to mid- and late-season experimental drought in a temperate grassland

E. Fenollosa¹  | P. Fernandes¹ | A. Hector¹  | H. King¹ | C. S. Lawson² | J. Jackson¹  | R. Salguero-Gómez¹ 

¹Department of Biology, University of Oxford, Oxford, UK

²School of Environment, Earth and Ecosystem Sciences, The Open University, Milton Keynes, UK

Correspondence

E. Fenollosa

Email: erola.fenollosa@gmail.com

R. Salguero-Gómez

Email: rob.salguero@biology.ox.ac.uk

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Abstract

1. Extreme precipitation events are becoming more intense and frequent due to climate change. This climatic shift is impacting the structure and dynamics of natural communities and the key ecosystem services they provide. Changes in species abundance under these conditions are thought to be mediated by functional traits, morpho-physiological characteristics of an organism that impact its fitness. Future environmental conditions may, therefore, favour different traits to those in present-day communities.
2. After 6 years of manipulated precipitation levels, including drought (−50% of ambient precipitation), irrigation (+50% of ambient precipitation), and control (ambient precipitation), we measured five key functional traits (plant height, leaf dry matter content [LDMC], leaf thickness, specific leaf area [SLA], and leaf phosphorus concentration) in 586 individual vascular plants to study the effects of precipitation changes on community-weighted functional traits. Additionally, we tested whether the precipitation change effects on the traits depend on the time of the growing season.
3. As expected, reduced precipitation impacted community composition only for the late-season timing, after the seasonal field mowing, but led to a significant change in all community-level plant traits between season timings. Under drought, communities shifted towards shorter individuals with thicker but small leaves and lower phosphorous content. Overall, a combination of community reassembly and intraspecific variation contributed to community-weighted differences between control and drought plots for plant height, SLA, and LDMC traits. Species turnover was the main driver of community-weighted means (CWMs) shifts in all traits in the late-season but SLA. Whereas all traits showed variations at the community level with drought, SLA and LDMC were the most responsive traits at the species level. Nevertheless, our results suggest underestimation of intraspecific

J. Jackson and R. Salguero-Gómez shared senior-author.

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variation due to sensitive species lower abundance under stress. No differences in CWMs of functional traits were observed between control and irrigated plots.

4. **Synthesis:** Our findings suggest that functional trait composition of grassland communities may shift under climate change-induced drought, depending on the growing season timings. Trait-based attempts to predict ecosystem functioning must account for such temporal variation in community trait values.

KEYWORDS

community-weighted means, drought, functional traits, intraspecific variability

1 | INTRODUCTION

Climate change is predicted to alter the structure and function of biological communities worldwide (Díaz & Cabido, 1997; IPCC, 2022). Along with increasing global temperatures, climate change may increase the intensity and frequency of extreme climatic events such as droughts and deluges in some regions globally (Fischer et al., 2013). Changes in precipitation, such as increased frequency of extreme droughts or deluges, will favour certain species over others (Lavorel et al., 2011; MacGillivray et al., 1995; Mueller et al., 2005; White et al., 2000). Plant functional traits, the organismal features that determine plants' fitness through their influence on survival, growth, and reproduction (Laughlin et al., 2020; Violle et al., 2007), can facilitate the quantification of effects of extreme precipitation on natural plant communities (Díaz et al., 2016). Species favoured under novel climate regimes may have different functional traits to those found under previous regimes (Lavorel et al., 2011; White et al., 2000). As such, changes in functional trait values are expected to scale from individuals to whole communities (Griffin-Nolan et al., 2019; Lavorel et al., 2011; Luo et al., 2023; McGill et al., 2006), and impact the ecosystem structures and functions (Suding et al., 2008; Woodward & Diament, 1991). The relationship between individuals' functional traits and ecosystem function makes trait-based approaches promising tools for predicting community responses to climate change (Brodribb, 2017; Lavorel & Garnier, 2002; Quétiér et al., 2007; Soudzilovskaia et al., 2013). Therefore, identifying plant functional traits that are highly sensitive to the environment is critical for predicting changes in ecosystem structure and function under climate change (Andrew et al., 2022; Funk et al., 2017; Green et al., 2022; Lavorel et al., 2011; Lavorel & Garnier, 2002; McGill et al., 2006; Violle et al., 2007).

There has been considerable effort examining how environmental change shapes functional traits of plant communities (Kambach et al., 2023; Kimball et al., 2016; Lavorel & Garnier, 2002; McGill et al., 2006; Wellstein et al., 2017). Observational studies on precipitation gradients have shown significant correlations of functional traits to precipitation level (Dwyer et al., 2014; Harrison et al., 2015; Wright et al., 2005). For example, a significant inverse correlation was found between specific leaf area (SLA) and aridity when contrasting more than 2500 species at the global scale (Wright et al., 2005). However, experimental approaches could be more important for explicit, mechanistic understanding of

functional traits in mediating community changes and in attributing trait changes to specific environmental drivers (Grime et al., 2000; Hoover et al., 2014; Jamieson et al., 1998; Kröel-Dulay et al., 2022; Luo et al., 2023; Wilcox et al., 2021). For example, a global meta-analysis DeMalach et al. (2017) revealed that an increase in precipitation increased community biomass and induced changes in the community composition. Similarly, experimental studies have shown that drought alters community composition and shifts community functional traits (Griffin-Nolan et al., 2019; Jackson et al., 2024; Luo et al., 2023). However, experimental studies with simultaneous manipulation of both precipitation increase and reduction are needed for the prediction of ecosystem responses to climate change via shifts in plant functional traits.

Whether environment-driven shifts in community functional traits are mainly driven by changes in community composition (i.e., interspecific variation), intraspecific variation, or both, throughout the growing season remains poorly understood in functional trait studies. Not explicitly accounting for intraspecific variation is a likely reason why trait-based approaches have not yet delivered on being the 'Holy Grail of Ecology' (Shipley et al., 2016; Suding & Goldstein, 2008; Yang et al., 2020). Functional traits may vary significantly within species (Moran et al., 2016; Siefert et al., 2015; Violle et al., 2012), and could shift mean community trait values, even if species composition remains unchanged perhaps due to stabilising effects (Bricca et al., 2022; Luo et al., 2023; Pichon et al., 2022). Similarly, the contribution of intraspecific trait variation to functional traits of plant communities may also change with plant ontogeny (i.e., different stages of plants development and growth) at different times of the growing season. For instance, young recovering communities (i.e. early-successional) are typically more sensitive to environmental shifts (Grime et al., 2000; Odum, 1969). Similarly, Lemoine et al. (2018) showed how drought timing played a crucial role in drought sensitivity in two short grasses, and Kimmel et al. (2019) revealed a gradual impact of increased precipitation on community structure across years. Yet, our understanding of how impacts of climate-driven, precipitation changes on plant functional traits depend on the time of the growing season remains limited (Tardella et al., 2021; Vitra et al., 2019).

Here, we experimentally manipulated precipitation for 6 years in a semi-natural calcareous grassland to examine precipitation variability effects on plant community composition, intraspecific trait

variability, and interspecific trait variability across the growing season. Specifically, we compared the functional trait composition between plots receiving a drought (−50% ambient precipitation) treatment, irrigation treatment (+50% ambient precipitation), and ambient precipitation (control plots) in mid (July 2021) versus late growing season (September 2021). We measured five functional traits (i.e., leaf dry matter content [LDMC], leaf thickness, SLA, leaf phosphorous concentration, plant height) indicating leaf economics spectrum and plant size of the most abundant species (Díaz et al., 2016), and calculated their community-weighted trait means considering variation at the species level (specific community-weighted mean [CWM]) and without it (fixed CWM), using the framework proposed by Lepš et al. (2011). We used the trait data to address the following hypotheses: H1: Regardless of the time of the season, community composition will differ among precipitation treatments because the relative abundance of plants exhibiting drought tolerance traits (e.g., higher leaf thickness; Pérez-Harguindeguy et al., 2013) would increase in drought plots, but not in irrigated plots. H2: CWM trait values (fixed CWM and specific CWM) of each of the assessed traits would differ among the precipitation treatments because plants are likely to differ in their water-use strategy under ambient versus drought versus irrigation treatments, regardless of growing season time. Specifically, we expect lower plant height and SLA, and higher LDMC and leaf thickness in drought plots, as most abundant species exhibit trait syndromes related to conservative water-use strategies that enhance their survival (and ultimately their abundance) under drought (Helsen et al., 2017; Kramp et al., 2022; Luo et al., 2023; Wright et al., 2004). On the other hand, we expect the contrasting effects on CWM traits in irrigated plots (Korell et al., 2021; Song et al., 2016). Leaf phosphorus concentration is also expected to be lower in drought plots than irrigated and ambient plots because of a positive correlation with SLA along the leaf economics spectrum and the limitation in resource acquisition (Luo et al., 2023; Wright et al., 2004). We also expect the patterns of CWMs responses to differ between mid-season versus late-season, as the annual mid-season mowing management may influence the traits responses to the precipitation treatments during the late-season. Regardless of the precipitation treatment, we expect the community composition change to be mainly driven by fixed CWM than specific CWM because of the post-mowing community reassembly. However, given the high sensitivity of early-successional plant communities to environmental change (Grime et al., 2000), we expect the role of fixed vs. specific CWM on community composition change to differ between the precipitation treatments (Kimmel et al., 2019; Lemoine et al., 2018).

2 | MATERIALS AND METHODS

2.1 | Study site

The experiment was conducted at the Upper Seeds field site (51°46′16.8″N 1°19′59.1″W, 155 m a.s.l.) in Wytham woods, Oxfordshire, UK. The study site is a calcareous temperate grassland characterised by a shallow soil depth (300–500 mm depth) alkaline

soils (Gibson & Brown, 1991), a daily average temperature ranging between −5 and 26°C, a mean annual temperature of 11.5°C (2016–2021), daily total precipitation of 0–40 mm (2016–2021) and an annual total precipitation of 686 mm (2016–2021) (Table S1). According to the Köppen-Geiger climate classification, the study site constitutes a maritime temperate climate (Cfb) (Peel et al., 2007). The site is currently managed for maintenance by mowing twice per year, a common practice across most European grasslands (Török et al., 2018). The first mowing takes place mid-growing season (late July), and the second at the end of the growing season (late September).

To test our hypotheses, we experimentally manipulated precipitation levels using the RainDrop (rainfall and drought platform) long-term ecological experiment for 6 years, and in July and September 2021 we determined species abundance and sampled the most abundant species using functional traits measurements. RainDrop is integrated in the DroughtNet global coordinated research network (<https://droughtnet.weebly.com/>). The RainDrop experiment has been running since 2016 and consists of twenty-five 5 m × 5 m permanent plots distributed across the study site in five randomised blocks (A:E) (Figure S1). Each block includes five plots that receive one of the following treatments during the growing season (March–September): drought (−50% ambient precipitation), irrigation (+50% ambient precipitation), two ambient control plots (no manipulation), and procedural control (inverted rain shelters). Rain shelters intercept 50% of precipitation for the drought plots. In each drought plot, precipitation is intercepted by gutters and collected in containers situated next to each rain shelter. Pipes connect these deposits to sprinklers that spray the water onto the adjacent irrigation plots. This design is based on the proposal of Yahdjian and Sala (2002) and Gherardi and Sala (2013), which has been applied across >100 nodes of the DroughtNet network worldwide for exploring climate change-induced drought and deluge effects on community composition (Fischer et al., 2013; Smith et al., 2024). Furthermore, specific to our study site, climatic projections forecast shifts in annual precipitation from −20% to +20% under the 8.5RCP for 2080–2099 compared to 1981–2000 (UKCP18 Project, Met Office). Hence, the plots that experienced no precipitation manipulation served as ambient precipitation treatment (control) plots. Additionally, to control for shelter effects, each block has one procedural control plot. These consisted of rain shelters with inverted gutters that allow 100% of precipitation to pass through.

Ongoing work at this field site has revealed no differences in community composition between the procedural and ambient controls (Jackson et al., 2024). Therefore, we did not measure traits from the procedural control plots, and instead sampled one additional ambient control plot per block. To minimise edge effects, we split the 5 m × 5 m plot into four quarters and marked out a 1 m × 1 m quadrat in the centre of the study quarter from which we took all trait and abundance measurements. Data were collected at two different times along the growing season: mid-growing season (July 2021) and late-growing season (September 2021), just before each seasonal mowing.

2.2 | Data and metrics

2.2.1 | Species abundance

We collected species abundance data to assess community composition dissimilarity between the precipitation treatments (H1) and possible differences in CWMs between treatments (H2). To do so, we quantified species percentage cover for all vascular plant species and bare soil percentage cover using a 1 m × 1 m quadrat (with 10 cm grid) at each examined permanent plot. We first estimated the percentage cover independently for every species in each quadrat (one per plot), and next transformed these estimates into relative abundances that sum to 100%. Because the mid-season mowing removed the inflorescence from all grasses, species identity was difficult to know for many graminoid species during the late-season, which may impact the observed community effects. In the late-season, only two of the graminoid species (*Brachypodium pinnatum* and *Brachypodium sylvaticum*) were identifiable at the species level because of their distinctive leaves. For these two *Brachypodium* species, we recorded percentage cover as described above. Separately, we recorded the pooled abundance of all other graminoid species. Although we identified graminoid species in the mid-season, to ensure sound comparisons between mid-season and late-season abundance data (non-metric multidimensional scaling [NMDS] analysis), we combined the mid-season abundance of non-*Brachypodium* graminoids in analyses to contrast CWMs among precipitation treatments at the different times.

2.2.2 | Trait measurement and CWM

We quantified key functional traits of the grassland community to test whether CWM trait values differ among precipitation treatments and whether the differences are driven by different factors (interspecific vs. intraspecific trait variation) at the two contrasted growing seasons timings (H2). Trait measurement was performed at the same time species abundance was measured (July and

September 2021). We measured height, SLA, leaf thickness, LDMC and leaf phosphorus on the most abundant species in each quadrat, totalling 586 individual plants. We measured traits using a standardised protocol (Pérez-Harguindeguy et al., 2013), briefly summarised in Table 1. For the selected species to be representative of the community, we focused on species that contributed to a cumulative abundance of at least 80% within each quadrat, following Garnier et al. (2004) and Pakeman and Queded (2007). Next, in each quadrat, we randomly selected three mature, healthy individuals per species for trait measurement. Leaf traits were measured on one young but fully developed leaf per individual with the exception of leaf phosphorus, which require pooling three leaves per species per plot to obtain the 50 mg of dry weight required for the analysis (Esslemont et al., 2000). After pooling, 69 samples (out of a total of 195 potential samples) reached the dry weight threshold and thus were eligible for analysis. Leaf phosphorus concentration was estimated using inductively coupled plasma mass spectrometry following Esslemont et al. (2000). Briefly, samples were digested with 1 mL of concentrated nitric acid and 0.7 mL of hydrogen peroxide at 50°C overnight and diluted 25 times with MilliQ water prior analysis.

Community-weighted means of each trait were calculated in each quadrat for all treatments. CWM are commonly used in trait-based ecology to quantify shifts in community mean trait values due to macro and micro-environmental selection (Bruehlheide et al., 2018; Garnier et al., 2004; Griffin-Nolan et al., 2019; Kambach et al., 2023). We calculated CWM of the five assessed traits using the framework proposed by Lepš et al. (2011), and the *trait.transform* and *trait.CWM* functions from Lepš et al. (2011) and Götzenberger et al. (2020), which are included in *cati* R package (Taudiere & Violle, 2016). This framework disentangles the effect of interspecific variability (species turnover) and the combination of species turnover and their intraspecific trait variability as fixed CWMs and specific CWMs, respectively. Briefly, to calculate the specific CWMs, we multiplied the mean trait value per dominant species in each treatment by each species' relative abundance in the quadrat. The resulting species products were summed, and their abundances rescaled following de Bello et al. (2021). Our

TABLE 1 Brief descriptions of functional traits measured in this study and measurement protocol.

Trait	Description
Height	Shortest distance between ground and the highest photosynthetic tissue (leaf) without manipulation (excluding inflorescences). Measured using tape measure
Leaf dry matter content (LDMC)	Dry mass of a leaf divided by its water-saturated mass. Dry mass obtained by drying leaf at 70°C for 72 h. Water-saturated mass measured within 5 h of sampling, with leaves being kept in vials containing water to prevent dehydration until measurement
Leaf thickness	Thickness of leaf lamina, excluding leaf midrib and significant secondary veins. Measured using digital callipers
Specific leaf area (SLA)	One-sided area of fresh leaf divided by its dry mass. Area measured in ImageJ (Schneider et al., 2012) after scanning each leaf alongside a ruler for calibration. Dry mass obtained by drying leaf at 70°C for 72 h
Leaf phosphorus concentration (P content)	Total amount of phosphorus per unit dry mass of leaf. Measured using ICP-MS (Esslemont et al., 2000).

Note: Descriptions summarised from Pérez-Harguindeguy et al. (2013).
Abbreviation: ICP-MS, inductively coupled plasma mass spectrometry.

target of sampling species with a cumulative abundance of 80% was achieved for all traits in all quadrats, with the only exception of leaf phosphorus, for which the threshold was achieved in 25% of quadrats only (Table S2). Because we observed that the measured traits did not vary significantly across the growing season for any of the studied species, we used the same trait values for both growing season timings, with the exception of plant height. Due to the graminoids identification difficulties at the late-season, and because all graminoids (*Agrostis capillaris*, *Arrhenatherum elatius*, *B. pinnatum*, *B. sylvaticum*, *Dactylis glomerata*, *Holcus lanatus*, and *Trisetum flavescens*) showed similar height in comparison to other functional groups in the mid-season, we used the height of *B. pinnatum*, the most abundant identifiable graminoid (ca. 34%, whereas the non-*Brachypodium* graminoids showed relative abundances <18% at the mid-season), as the height of late-season non-*Brachypodium* graminoids. To calculate fixed CWM, a single mean trait value for individual species was used for all quadrats. Whilst changes in fixed averages across treatments would reflect species turnover, changes in specific averages reflect both between and within-species variability in traits (Lepš et al., 2011).

When trying to test for differences at the species level (intra-specific variation), not all species presented a consistent number of samples, as their abundance might depend on the sensitivity to the treatment. We therefore restricted analysis of each species responses to different treatments (i.e., precipitation-driven intraspecific variation) to the species that had enough replication to do so, considering the recommended replicate number to account for natural trait variation ($n=30$ at each precipitation level, Pérez-Harguindeguy et al., 2013). These species consisted of three graminoids (*B. pinnatum*, *T. flavescens*, and *A. elatius*), three legumes (*Medicago lupulina*, *Trifolium repens*, and *Trifolium pratense*), and one non-leguminous forb (*Crepis capillaris*).

2.3 | Statistical analysis

2.3.1 | H1: Do precipitation treatments affect community composition?

We performed NMDS to contrast community composition between treatments (H1) using the *vegan* R package (Oksanen et al., 2020). NMDS is a form of dimension reduction that allows for differences in communities to be quantified. In its application to plant trait-based ecology, NMDS is based on the rank-order of species abundances and maximises the correlation between real-world distance and Bray Curtis distance in the ordination space. We assessed the significance of any differences in community composition using analysis of similarity (ANOSIM). To determine which species were responsible for any dissimilarities among treatments, we used similarity percentage (SIMPER). Differences between groups when performing multidimensional analysis (ANOSIM and SIMPER) were considered significant when the p -value was less than 0.05.

2.3.2 | H2: How do precipitation manipulations alter CWM of traits in different periods of a season?

We fitted hierarchical linear mixed-effects models to test our expectations that both the specific and fixed CWM of each of the five assessed traits would differ between the three precipitation treatments in mid-season and late-season periods, but the pattern of the differences for each trait would differ between the two growing season timings (H2). We used the R package *lme4* to account for the blocked experimental design, where models were fit using maximum likelihood (Bates et al., 2015). Precipitation treatment (three levels: drought, control, irrigated) and timing in the growing season (two levels: mid- vs. late-season) were fixed effects, and block was considered as a random effect (five levels: A-E, where all treatments are represented). A significant interaction effect of precipitation treatment and seasonal timing indicated that the impact of the precipitation manipulation differed between the two timings. To meet the assumptions of gaussian distributions in our models, we log-transformed plant height, whilst other traits' data were not transformed. When interpreting the output of mixed-effects models, we focused on differences based on the 95% confidence intervals (CIs) overlap rather than relying on p -values following Flechner and Tseng (2011) and Bates et al. (2015), who discouraged the use of p -values in mixed-effect models.

Finally, to explore the link between trait and species abundance precipitation sensitivity, we contrasted the observed relative abundance decrease under the drought treatment (as we observed significant differences, see Section 3) with the position of all species along the two principal components of species traits variation using principal component analysis (PCA) from the *PCAtools* R package (Blighe & Lun, 2022). In addition, to further explore how specific CWM differ between treatments in each species, we fitted linear mixed-effects models, with only precipitation treatment as a fixed effect for individual species with enough replication across treatments.

All analyses were performed in R (R Core Team, 2021, v. 4.2.1).

3 | RESULTS

3.1 | Changes in community composition

When the community composition data of both growing seasons were pooled together, we found little difference between the species composition under the three precipitation treatments. This pattern is supported by the overlapping groups in the NMDS plot (Figure 1A). However, when growing season timings were considered separately, community composition in drought plots clustered separately from both control and irrigation treatments in the late-season ($p=0.001$), but not in the mid-season ($p>0.05$) (Figure 1B,C).

When we assessed how the community composition under the drought treatment differ from the other two treatments in the late-season, SIMPER analysis revealed that three species or groups

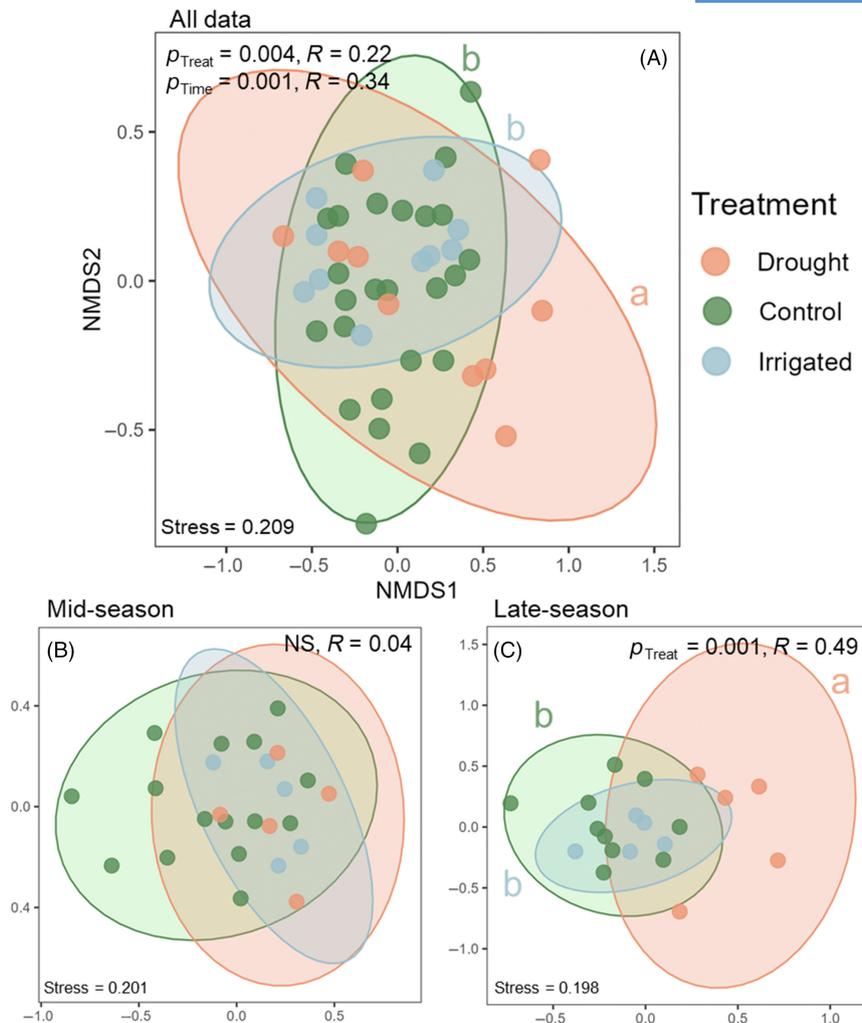


FIGURE 1 Community reassembly with precipitation treatments and growing season time. Non-metric multi-dimensional scaling (NMDS) plots showing differences in community composition between the treatments. Each point represents the community composition of a single quadrat, whilst its location in the plot represents its position in two-dimensional ordination space. Points that are closer together are expected to have similar community composition. Stress, a measure of goodness of fit that MDS tries to minimise, is estimated as the disagreement between observed distance and ordination distance that varies between 0 (total agreement) and 1 (total disagreement), is shown at bottom left of each plot. p -Values and R correspond to analysis of similarity (ANOSIM) results for the different grouping factors: Treatment and growing season time; and the R statistic: The degree of groups dissimilarity, where zero means groups are completely overlapped, and a positive value reflects how much bigger between groups variability is in contrast to within groups (up to one). Plots are drawn separately for (A) all community data across the summer of 2021, (B) the mid-season communities, and (C) the late-season communities. Ellipses depict 95% confidence levels and lowercase letters reflect significant differences between treatments (p -value).

were responsible for 70% of this difference (Table 2). For the comparison between control and drought treatments, these species were *B. pinnatum* (tor grass), non-*Brachypodium* graminoids, and the legume *Lotus corniculatus* (bird's-foot trefoil, Table 2). On other hand, tor grass, non-*Brachypodium* graminoids, and *T. repens* were responsible for 70% of the differences between irrigation and drought plots. In both comparisons, the graminoids (including *B. pinnatum*) and *T. repens* had lower relative abundances in drought plots compared to controls whilst *L. corniculatus* had higher relative abundances in drought plots (Table 2). However, only the difference in graminoids abundance (including *B. pinnatum*) had non-overlapping 95% CIs between control and drought treatments, with a significant decrease in relative abundance of

73% *B. pinnatum* and 65% of other non-*Brachypodium* graminoids (Table 2).

3.2 | CWMs under precipitation treatments

Precipitation treatment, specifically the drought treatment, affected CWM trait values, but the effects were observed more strongly in the late-season (post-mowing) than in the mid-season (pre-mowing) (Figure 2). In the mid-season specific CWM of almost all the assessed traits (plant height, LDMC, SLA, and leaf phosphorus concentration) showed lower mean values in the drought plots compared to the control (Figure 2; non-overlapping

TABLE 2 Comparison of the species that cumulatively contribute to over 85% of the dissimilarity between the differences observed in Figure 1: The communities in the drought (D) vs. control (C) and irrigated (I) plots in the late-season.

Timing	Comparison	Species	Dissimilarity contribution (%)	Cumulative sum (%)	Mean RA (%)
Late-Season	Control-Drought	<i>Brachypodium pinnatum</i>	35.4	35.4	D: 10.1–C: 36.9 ^a
		Graminoids ^b	29.6	65	D: 11.0–C: 31.2 ^a
		<i>Lotus corniculatus</i>	12.6	77.6	D: 29.0–C: 10.9
		<i>Trifolium repens</i>	4.4	82	D: 2.1–C: 4.8
		<i>Galium verum</i>	3.1	85.1	D: 0.8–C: 2.9
	Irrigation-Drought	<i>Brachypodium pinnatum</i>	43.9	43.9	D: 10.1–I: 44.5
		Graminoids ^b	24.5	68.4	D: 11.0–I: 25.6
		<i>Trifolium repens</i>	11.6	80	D: 2.1–I: 11.6
		<i>Lotus corniculatus</i>	6.2	86.2	D: 29.0–I: 5.1

Note: Contributions to dissimilarities were calculated using SIMPER (similarity percentage) analysis. Mean relative abundances (RA) are species absolute abundance rescaled such that the abundances of all species in a quadrat sum to 100%.

^aIndicates non-overlapping 95% confidence intervals between relative abundances of different treatments.

^bExcludes *Brachypodium* species which were assessed separately.

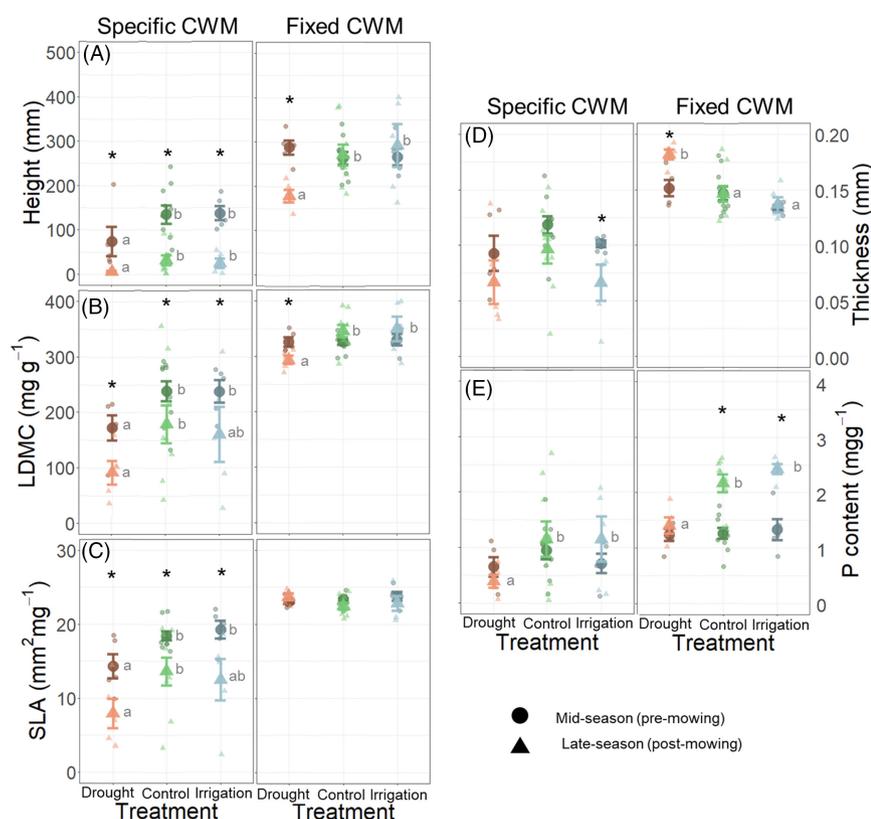


FIGURE 2 Community-weighted means (CWMs) of functional traits fixed (single mean trait used for each species, reflecting species turnover) and specific (different trait values for species in each quadrat were used, reflecting turnover and intraspecific variation) with treatment and growing season timing. Comparison of CWM values for each functional trait (A–E) between the three precipitation treatments: Control (green), drought (orange), and irrigation (blue). Each translucent small point represents the CWM of an individual quadrat, whilst bold points represent the mean for each timing (mid- vs. late-season) with 95% CI. Asterisks and different small letters symbolise non-overlapping 95% CI between mid- versus late-growing season within each treatment and between treatments within each timing respectively. LDMC, leaf dry matter content; SLA, specific leaf area.

95% CIs). No significant differences between fixed CWM of control and drought plots were detected in the mid-season for any trait. Both specific and fixed CWM for all measured traits were also similar between irrigated and control plots in the mid-season (Figure 2; overlapping 95% CIs).

In the late-season, reduced precipitation induced differences in all traits in either specific, fixed or both CWMs. As in the mid-season, overlapping 95% intervals were detected for all traits in fixed and specific CWM between irrigation and control plots. In drought plots, a significant reduction in plant height, LDMC, and

P content (in both specific and fixed CWM), an increase in leaf thickness (only in fixed CWM) and SLA (only in specific CWM) were observed (Figure 2). These differences were found mainly in the fixed CWM, where a single mean trait value is used, and therefore differences are associated with species turnover. As the specific CWM were calculated using a trait value per plot, it reflects not only species turnover but also reveals high intraspecific variability in plant height, LDMC and P content contributing to the differences between control and irrigation against the drought treatment.

Differences in CWM between growing season timings were observed in all measured traits (Figure 2). The most notable effects were in plant height, LDMC and SLA, which were reduced in the late-season. Drought-treated plots showed higher differentiation between season timings than irrigated and control plots. Significant differences between mid- and late-season timings in drought plots were observed in plant height, and leaf thickness fixed CWM and for both specific and fixed CWM in LDMC.

Considering that community composition differed between drought and control plots only in the late-season, we explored the association between certain trait values and the abundance reduction/increase that the species exhibited in the late-season. For this reason, we used PCA with the four traits with highest representation among all species found in the grassland plots (SLA, height, LDMC and thickness) (Figure 3a). The main axis of variation (PC1) was positively associated with LDMC and height and negatively associated with SLA, whereas thickness was the main driver of PC2. When including the community composition change that we observed in the late-season (See previous section, Figure 1) in this bidimensional space, species with higher relative abundance differences between control and drought plots in the late-season had higher values of PC1 and PC2 (i.e. at the 2D PCA plot, top right of plot). This

association reveals that species with decreased relative abundance in drought plots in contrast to the control plots in the late growing season (drought-sensitive species) had higher height and LDMC, and smaller leaf thickness and SLA.

Both specific CWM and the association of some trait syndromes with abundance increase under drought suggest that intraspecific variation has an important role explaining CWM shifts. However, when trying to acknowledge the contribution of intraspecific variation in CWM drought shifts, not all species were abundant enough to test if they presented significantly different trait values under different precipitation regimes. Interestingly, the species with enough replication to assess intraspecific variation effects are the ones that contributed strongly to differences between treatments in terms of community composition as they explained a high percentage of the treatment's differentiation in SIMPER analysis (Table 2). Those species are three graminoids (*B. pinnatum*, *T. flavescens*, and *A. elatius*), three legumes (*M. lupulina*, *Trifolium repens*, and *T. pratense*), and one non-leguminous forb (*C. capillaris*) (Figure 3b). Of the five functional traits we measured, only height showed significant intraspecific variation among the precipitation treatments in two of the seven species with sufficient intraspecific replication (Figure 3b). We observed this variation only in the late-season, with two species (*M. lupulina* and

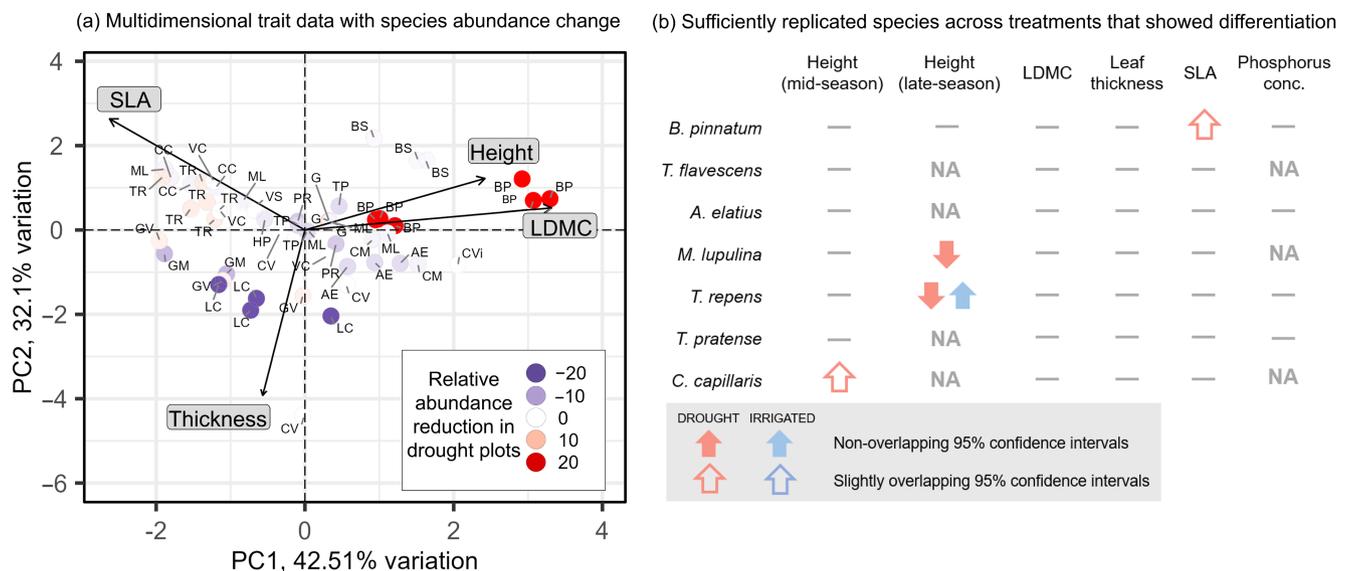


FIGURE 3 (a) Functional traits variation plays a role on species relative abundance between precipitation treatments: Functional traits principal component analysis (PCA). Axis percentages represent the explained variance proportion from each component. The colours represent the species relative abundance difference between drought and control treatments at the late-season (i.e., when higher differences in community composition were observed, Figure 1). For each species relative abundance difference has been calculated as mean relative abundance in control plots – mean in drought plots. Species with higher relative abundance difference values are those that have reduced their relative abundance at drought plots. P leaf content is not included here, as only 34% of observations had all five measures, whereas considering the other four traits, 68% of the data were complete, from a total of 18 species. Each dot includes the mean value from the different plots at each treatment and growing season time. Species codes are: AG, *Agrimonia eupatoria*; BP, *Brachypodium pinnatum*; BS, *B. sylvaticum*; CC, *Crepis capillaris*; CM, *Crataegus monogyna*; CV, *Clinopodium vulgare*; CVi, *Clematis vitalba*; G, non-*Brachypodium* graminoids; GM, *Galium mollugo*; GV, *Galium verum*; HP, *Hypericum perforatum*; LC, *Lotus corniculatus*; ML, *Medicago lupulina*; PR, *Potentilla reptans*; TP, *Trifolium pratense*; TR, *T. repens*; VC, *Veronica chamaedrys*; VS, *Vicia sativa*. (b) Intraspecific trait variation among precipitation treatments. Summary of significant (non-overlapping or slightly overlapping 95% CI) intraspecific trait variation for the seven most dominant plant species in our experiment. Direction of arrows indicate change, whilst dashes represent no change in trait values. Cells marked “NA” indicate instances where no sufficient trait data were available to measure intraspecific variation. Complete data is summarised in Table S3. LDMC, leaf dry matter content; SLA, specific leaf area.

T. repens) being shorter under drought (*M. lupulina* control: 3.83 log [mm], 95% CI 3.66–3.99; drought: 2.75 log [mm], CI 2.29–3.22; *T. repens* control: 4.3 log [mm], CI 4.08–4.51; drought: 3.74 log [mm], CI 3.41–4.08). *T. repens* was also taller in the late-season irrigation treatment (irrigation: 4.85 log [mm], CI 4.57–5.13). We observed a marginally significant increase in height for *C. capillaris* in the mid-season drought plots (control: 5.9, CI 5.77–6.03; drought: 6.14, CI 6.01–6.27). Other than plant height, the only other trait that varied was SLA, which was marginally higher in the drought plots for *B. pinnatum* (control: 18.9 mm² mg⁻¹, CI 17.9–19.7; drought: 21.8 mm² mg⁻¹, CI 19.6–23.8). Model output with complete means and CIs for each of these seven species is summarised in Table S3.

4 | DISCUSSION

Climate change is altering biological communities globally, favouring some species based on their trait syndromes over others partly due to changes in the precipitation regime. Understanding the drivers of community-level functional traits is crucial to predict community responses to altered precipitation in natural plant communities. In this study, we investigated how traits respond to experimentally manipulated levels of precipitation, not only considering the community and the species, but also the individuals, which provide a better understanding of community variation. We report evidence for shifting CWM trait values in response to drought but not with increased precipitation.

4.1 | Precipitation-induced community reassembly mostly contributes to community-weighted functional traits shifts in the late-season

As hypothesised (H1), we found differences in community composition among precipitation treatments in the late-season. When exploring which effect this community composition change had into CWM, we found that it was an important contributor to height, LDMC, P content and leaf thickness CWM shifts under drought in the late-season as fixed CWM differences (7% decrease in height, 15% LDMC, 35% P content and 24% increase in leaf thickness). LDMC was the only trait that showed a drought-induced reduction in specific CWM in contrast with fixed CWM (48% vs. 15% respectively), indicating a higher relative importance of intraspecific variation in addition to species turnover in comparison with the other traits. The absence of this effect in the mid-season may be related to the high sensitivity of early-successional communities to environmental changes (Grime et al., 2000; Odum, 1969). Previous short-term (1–3 years) studies have reported absence or small effects of precipitation changes on community reassembly (Batbaatar et al., 2022; Vitra et al., 2019). Vitra et al. (2019) observed that drought altered community-weighted functional traits in early and late-season, but did not observe abundance-driven species turnover and community composition change, which would occur over longer drought

perturbations (Smith et al., 2009). After 6 years of manipulated precipitation at our study site, we observed community composition changes with an important decrease of graminoid abundance under drought. The lower abundance of grasses in drought plots agrees with other experimental studies in calcareous grasslands (Morecroft et al., 2004; Sternberg et al., 1999). Interestingly, similar effects were observed under short-term manipulated and observed precipitation gradients with both species turnover and intraspecific variations contributing to community-weighted functional trait responses to precipitation changes in a grassland community (Zuo et al., 2021).

4.2 | Community functional traits shift under drought but not irrigation

A 50% precipitation reduction in our temperate grassland community induced important shifts in CWMs of all examined functional traits. These shifts supported our hypothesis regarding how plant height, leaf thickness, SLA, and leaf phosphorous content should change with drought, but provided opposing support for our predictions regarding changes in LDMC (H2). Contrary to our expectation of increased LDMC under drought (H2) in both mid- and late-seasons, we observed a drought-induced 28% decrease in LDMC specific CWM in the mid-season (with no decrease in fixed CWM) and an almost 50% reduction in specific CWM in the late-season (15% reduction in fixed CWM), reflecting the importance of species intraspecific variation in this trait, especially in the late-season. The hypothesised change in LDMC was based on previous findings of observational studies (Dwyer et al., 2014; Harrison et al., 2015; Wright et al., 2005). However, a decrease in LDMC can also occur due to the geometric relationship with leaf thickness: $LDMC = 1/(SLA \times \text{Leaf thickness})$ (Vile et al., 2005). In addition, Wilcox et al. (2021) reported a negative relationship in a semiarid shortgrass prairie between leaf thickness and LDMC, which could explain the decrease in LDMC because of leaf thickness increase.

The observed drought-induced changes in the CWM of plant height, leaf thickness, SLA, and leaf P content aligned with our expectations as well as with findings from previous observational (Fonseca et al., 2000; Moles et al., 2009) and experimental studies (Luo et al., 2023; Zuo et al., 2021). However, the CWM of all our examined traits remained unchanged under the irrigation treatment compared to the control. This pattern may be due to the high levels of evapotranspiration reported at this field site, suggesting that this system is not water-limited (Jamieson et al., 1998). The estimated precipitation supplied by the irrigation treatment would have been around 1000 mm year⁻¹ (+50% of the ambient precipitation), which falls near the maximum annual precipitation at the climate type Cfb (maritime temperate climate) that the study site belongs to (Peel et al., 2007). Whilst manipulative experiments offer the unique opportunity to isolate environmental variables to test their effects on the community, they might fall short in perfectly simulating natural conditions, as key attributes as precipitation variability are challenging to replicate, and precipitation percentage reduction might have

differential effects in different biomes (Hoover et al., 2018; Knapp et al., 2015; Slette et al., 2019). An alternative explanation of a lack of effect in the irrigation treatment is that not enough time has passed yet. This is supported by the results from Kimmel et al. (2019) that observed gradual impacts of water addition over 10 years, whereas our study was conducted at the sixth year of treatment.

4.3 | Species adjustments to precipitation seem to differ between growing season timings despite the complexity of studying intraspecific variation across stress gradients

Contrary to our hypothesis of the ability of species to adjust functional traits under different precipitation levels (H2) (Pichon et al., 2022; Shipley et al., 2016; Violle et al., 2012), we report limited evidence of intraspecific variation in trait responses to drought when contrasting mean trait values for those species with sufficient replication. Only plant height, out of the five examined traits, varied significantly among precipitation treatments at the individual level in two of the seven species that had enough replication across treatments. This finding aligned with differences in height between treatments for both specific and fixed CWM analyses. However, concluding that intraspecific variation plays only a small role in CWM drought-induced shifts would be a biased result. Plant species abundance strongly depend on their distance to the optimal climatic conditions (Thuiller et al., 2004). In other words, species that need to adjust their metabolism to non-optimal conditions are also likely to decrease their abundance, due to the increased costs of stress responses (Baruch, 2011; Hutchinson, 1957; Lynn et al., 2023). Thus, the full spectrum of species intraspecific variance might not be observed with enough replication if the magnitude of the stress or the time scale is high. In our study, we did observe the role of intraspecific variability in the difference between CWM fixed and specific, though this evidence was not supported when testing individual species intraspecific variation with the few species that showed enough replication across treatments. Our results highlight the complexity of studying intraspecific variation across stress gradients, and in accordance with recent literature, highlight that the role of intraspecific variability in community shifts might be underestimated, and it might depend on the stress magnitude and temporal scale (Girard-Tercieux et al., 2023; Yang et al., 2020).

Drought-induced shifts in SLA and LDMC were driven by interspecific variability both at mid- and late-season timings as they showed none or lower differences in fixed CWMs between precipitation levels in contrast with specific CWMs. Species adjustment of SLA and LDMC determined community responses under drought rather than species turnover, suggesting the responsive role of those traits in grassland communities under drought (Lavorel & Garnier, 2002; Liu et al., 2021; Violle et al., 2007), perhaps due to their relationship with hydraulic resistance (Olson et al., 2018) and water-use efficiency (Wellstein et al., 2017). All traits, with the exception of SLA, differed in fixed CWMs between treatments at the late-season time, supporting the role of species turnover in

CWMs shifts in response to drought. The difference in community traits between the mid- and late-season timings may be linked to the mid-season mowing of the field site. Previous studies in steppe ecophysiology stressed the importance of drought timing in drought sensitivity in short grasses (Lemoine et al., 2018). Additionally, young recovering communities are more sensitive to environmental changes (Grime et al., 2000; Odum, 1969). This effect could explain our finding of stronger treatment impacts in fixed CWM trait values after the mowing than before it. Furthermore, stronger effects of drought on community-weighted functional traits were observed after the growing peak (late-season) in two permanent grassland experimental sites at the Swiss Jura Mountains, which coincide with the longer and warmer summer days (Vitra et al., 2019). In our study, increased temperature and lower humidity may contribute to enhanced drought effects at the late-season.

Certain trait syndromes were determinant in this temperate grassland to species drought resistance: shorter plants (both at the individual and species levels) with thick but small leaves. This strategy reduces evaporative surface and decreases hydraulic vulnerability (Farquhar et al., 2002; Olson et al., 2018). This result aligned with previous results from Kramp et al. (2022), with smaller leaf species being more resistant to drought in a temperate grassland in Germany. Our study also agrees with Kramp et al.'s emphasis of the importance of a multidimensional approach of variation in multiple traits when trying to understand grassland responses to drought. Grasses, taller plants with thinner leaves, strongly reduced their abundance under drought, thus suggesting drought might not favour fast growing species, as suggested by the meta-analysis by Wellstein et al. (2017). Our result agrees with the report of drought-induced community shift into slower growing and more-resistant species (Wilcox et al., 2021). However, Griffin-Nolan et al. (2019) found a shift from drought tolerance to drought avoidance strategies with drought intensity, with communities having higher SLA, nutrients content and leaf turgor loss point. Contrary to the last study, but in agreement with ours, Luo et al. (2023) reported community shifts to decrease leaf phosphorous content due to nutrient acquisition restriction under drought conditions. In the light of these mixed findings, we support the recent proposal by Anderegg (2023) regarding the importance of exploring the link between plant strategies and traits. This selective impact of drought on different functional plant groups explains the reduction in functional diversity observed in this study in drought plots (Figure S2) and supports the reduction in functional diversity found in grasslands in some observational studies due to drought acting as an environmental filter (Harrison et al., 2015, 2018; Miller et al., 2019, but not in Griffin-Nolan et al., 2019). Our results indicate that functional diversity is a consequence but not a driver of drought impacts on grasslands.

5 | CONCLUSIONS

We provide key insights into how grassland communities may respond to climate change. Overall, we found evidence that short,

thick-leaved plants may be favoured under drought conditions, whilst grasses may become less abundant, leading to community-level functional shifts. We observed some intraspecific trait plasticity in response to drought, but the most dramatic effects were changes in community composition. The temporal variation of our CWM trait values suggests that effects of traits on ecosystem functioning might not be consistent across time. Specifically, we demonstrated how the importance of species turnover and intraspecific variation depends not only on the trait in question but the timing along the growing season (mid- vs. late-season). Therefore, trait-based attempts to predict ecosystem functioning must account for such temporal variation in community trait values. This temporal variation of environmental drivers' impact may prove to be an important step towards the "Holy Grail" of predicting ecosystem functioning from changes in traits.

AUTHOR CONTRIBUTIONS

Roberto Salguero-Gómez developed the original idea to study functional traits between treatments and Phil Fernandes proposed the characterisation of those traits at the community level, evaluating the role of intraspecific variation and species turnover to shifts in community-wide functional traits. This idea was developed by Phil Fernandes under the supervision of Roberto Salguero-Gómez and John Jackson. Study design and data collection was performed by Phil Fernandes, John Jackson, Roberto Salguero-Gómez, Clare Lawson, Andy Hector and Hannah King. Phil Fernandes analysed the data and prepared an academic report under the supervision of Roberto Salguero-Gómez. Erola Fenollosa configured the first manuscript draft, recalculating CWM following reviewer's suggestions and including additional data analyses. Initial manuscript feedback was provided by Roberto Salguero-Gómez. Further manuscript feedback was provided by all authors, who approved the manuscript for publication.

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CONFLICT OF INTEREST STATEMENT

The authors have no conflicts of interest to declare. All co-authors have seen and agree with the contents of the manuscript and there

is no financial interest to report. We certify that the submission is original work and is not under review at any other publication. Andy Hector is a Senior Editor of Journal of Ecology but took no part in the peer review and decision-making processes for this paper.

PEER REVIEW

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DATA AVAILABILITY STATEMENT

Data available from the Dryad Digital Repository: <https://doi.org/10.5061/dryad.kh18932gb> (Fenollosa et al., 2024).

ORCID

E. Fenollosa  <https://orcid.org/0000-0002-6189-2124>

A. Hector  <https://orcid.org/0000-0002-1309-7716>

J. Jackson  <https://orcid.org/0000-0002-4563-2840>

R. Salguero-Gómez  <https://orcid.org/0000-0002-6085-4433>

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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. Experimental design.

Figure S2. Functional richness across treatments.

Table S1. Climatic data for the experimental period (2016–2021), including the year of the study, 2021.

Table S2. Cumulative abundance of sampled species.

Table S3. Intraspecific variation summary.

Table S4. Hierarchical linear mixed-effect models results for fixed and specific CWM for all measured functional traits.

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