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RESEARCH ARTICLE

Long-term aridity shapes grassland drought resistance and modulates the roles of plant diversity and functional composition

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Abstract

1. Understanding the drivers of plant community stability is crucial for predicting ecosystem responses to extreme drought events. In grasslands, drought resistance supports the maintenance of key functions such as above-ground primary productivity, making the identification of resistance drivers essential to guide management under climate change. Proposed factors contributing to grassland stability include multiple diversity facets, functional traits and long-term climate, but most assessments focus on temporal invariability under historical disturbance regimes, leaving mechanisms of extreme drought resistance and their variation across climatic contexts relatively underexplored.
2. Here, we analysed data from 54 grassland sites of the International Drought Experiment to examine the resistance of above-ground net primary productivity to a short-term (i.e. 1 year) extreme drought. We investigated the relative

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importance and joint influence of functional composition (i.e. community-weighted means of leaf and root traits), plant diversity facets (taxonomic, functional and phylogenetic) and climate (aridity and rainfall variability) on drought resistance. We used structural equation models to disentangle direct, indirect, and moderating pathways linking these drivers to drought resistance.

3. Long-term aridity appeared as one of the most important drivers of grassland resistance to drought, with more arid sites showing lower resistance. Moreover, aridity impacted resistance through indirect effects by shaping functional composition and plant diversity, and by moderating the influence of plant diversity and functional composition.
4. Functional composition related to dehydration avoidance and dehydration tolerance was also positively associated with resistance, while diversity had a weaker relationship with resistance, mostly through functional and phylogenetic facets. Interannual rainfall variability also influenced resistance, with different effects in more arid versus humid and less arid sites.
5. *Synthesis*. Widely studied stability drivers such as plant diversity and functional composition have only partial explanatory power for short-term drought resistance of above-ground productivity in grasslands at a global scale. The abiotic context, particularly long-term aridity, is crucial for understanding ecosystem responses to rainfall variation and can improve predictive models for advancing the study of ecosystem resistance to drought. Along with management practices that target high species diversity or specific traits, restoration and conservation practices should support vulnerable sites experiencing high aridity

KEYWORDS
above-ground net primary productivity, aridity, dominant-species hypothesis, drought resistance, ecosystem functions and services, extreme climatic events, insurance hypothesis, International Drought Experiment, niche complementarity, phylogenetic and taxonomic diversity

1 | INTRODUCTION

Understanding the drivers of ecosystem stability is a central question in ecology that has become increasingly important with global change (van Meerbeek et al., 2021). Ecosystem stability is a complex and multifaceted concept (Donohue et al., 2013), with recent frameworks differentiating three stability components: *temporal invariability* of ecosystem functions, *resistance* to change during a perturbation and *recovery* to reference conditions after perturbations (de Bello et al., 2021; van Meerbeek et al., 2021). However, much research has focused on temporal invariability, while the drivers of resistance and recovery remain comparatively underexplored (Donohue et al., 2016; Eisenhauer et al., 2024; Jentsch & White, 2019). This gap is particularly pressing in global grasslands, which harbour great biodiversity and provide important ecosystem services such as food production and carbon storage (Habel et al., 2013; Zhao et al., 2020) but face growing threats from more frequent and intense droughts projected under climate change (IPCC, 2023). Resistance to these extreme events is thus critical to sustaining grassland functions and services. For example, the impacts of droughts on net primary productivity (Ohlert et al., 2025; Smith et al., 2024), a key function affecting carbon storage and food production, are well documented but highly variable globally, with underlying mechanisms still unclear (Knapp et al., 2024; Smith et al., 2024). Therefore, understanding the drivers of drought resistance is essential to help predict grassland response and guide natural resource management under climate change.

Biotic factors, especially biological diversity, have long been considered primary drivers of ecosystem stability and resistance to drought (Craven et al., 2018; Isbell et al., 2015; Tilman et al., 2006). While earlier research has shown that taxonomic diversity can increase grassland resistance to drought (e.g. Isbell et al., 2015; Tilman & Downing, 1994), mechanisms underpinning this relationship do not rely solely on taxonomic diversity but also on other facets of

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biodiversity such as functional and phylogenetic diversity (Craven et al., 2018; de Bello et al., 2021). First, the complementarity hypothesis proposes that taxonomically diverse communities are more functionally diverse, with greater differences in resource use (i.e. resource partitioning; de Bello et al., 2021). This mechanism reduces competition and maintains function under limited resources (Felton & Smith, 2017), such as during periods of low water availability. Second, the insurance hypothesis states that higher functional diversity will include species that respond differently to perturbations, thus maintaining overall ecosystem function (Loreau et al., 2021; Yachi & Loreau, 1999). Indeed, recent studies have shown that functionally diverse grasslands were better able to resist drought than functionally poor grasslands (Bazzichetto et al., 2024; Griffin-Nolan et al., 2019; Song et al., 2024). Finally, phylogenetic diversity can also drive resistance by capturing unmeasured functional diversity and evolutionary history, thus reducing the likelihood that all species will respond similarly to a given perturbation (Cadotte et al., 2012; Tucker et al., 2019).

An alternative biotic mechanism explaining ecosystem-level resistance focuses on the dominance of species with higher capacity to remain stable under disturbance and/or stress (i.e. 'dominant-species hypothesis', also known as the 'mass-ratio hypothesis'; Grime, 1998). Under this hypothesis, the functional composition of the community (i.e. the community-weighted means of traits) is a more important driver of ecosystem function and stability than biodiversity per se (de Bello et al., 2021). Hence, functional traits associated with plant strategies to cope with stress and drought can help link the dominant-species hypothesis to drought resistance. Plant species can achieve this by either dehydration tolerance (i.e. withstanding low levels of water content in tissues), dehydration avoidance (i.e. maximizing water uptake and minimizing water loss to avoid dehydration), or dehydration escape (i.e. growing and reproducing rapidly before exposure to drought, Volaire, 2018). Dehydration-tolerant species occupy the slow end of the plant economics spectrum, reflecting their conservative resource use (Díaz et al., 2016; Wright et al., 2004), which is associated with their ability to tolerate stress (Grime, 2006). As such, communities dominated by species with traits aligned with slow-growing, dehydration-tolerant strategies are generally thought to be better able to resist drought (de Bello et al., 2021; Wilcox et al., 2021). However, recent evidence complicates this picture, suggesting that grasslands dominated by dehydration avoiders and escapers can also show high drought resistance (Yan et al., 2025).

Because most studies focus on a subset of biotic drivers, there is still a lack of understanding of the relative role of diversity and functional composition on grassland resistance to drought (de Bello et al., 2021). Moreover, abiotic ecosystem factors such as climate and soil properties can also impact ecosystem stability and resistance (Bondaruk et al., 2025; Ren et al., 2023; Wilcox et al., 2017). For example, long-term climate can directly affect drought resistance by limiting resource availability (e.g. drier conditions in more arid sites), which increases stress and decreases the overall capacity of species to resist drought, also known as 'resource-limitation hypothesis' (Huxman et al., 2004; Knapp et al., 2015; Smith et al., 2024). Similarly, soil properties such as soil texture and nutrient availability can directly influence drought resistance by determining soil water-holding capacity and vegetation productivity during drought (Abel et al., 2024; Bharath et al., 2020). Additionally, climate can impact grassland drought resistance indirectly through changes in functional composition and diversity of plants (i.e. mediation). For example, the 'stress adaptation hypothesis' states that long-term dry conditions could result in communities dominated by species with traits allowing them to cope with drought stress (Knapp et al., 2024; Nunes et al., 2017), while increased interannual rainfall variability has been linked to increases in grassland functional diversity (Gherardi & Sala, 2015; Hallett et al., 2019), both of which can in turn impact drought resistance. Finally, climate can also change the effect of biotic drivers on resistance to extreme events (i.e. moderation). Functional diversity, for example, might be less beneficial in dryland environments, as it could cause a faster depletion of already-limited resources due to complementarity (e.g. Van Peer et al., 2004). However, most comprehensive assessments of biotic and abiotic pathways driving grassland stability have focused on temporal invariability (Craven et al., 2018; García-Palacios et al., 2018; Ren et al., 2023), while the impact of these pathways on resistance remains largely unknown.

Here, we took advantage of the wide range of biotic and climatic contexts of a globally distributed drought experiment (International Drought Experiment; IDE) to tease apart the combined roles of plant diversity, functional composition and long-term climate of pre-drought communities in driving the resistance of grasslands to a one-year extreme drought (Figure 1). Short-term droughts lasting up to approximately 1 year are the most common droughts experienced by terrestrial ecosystems globally, and extreme short-term droughts (i.e. statistically rare in comparison to long-term climate history) are expected to increase in frequency with climate change (Naumann et al., 2018). Previous work from the IDE has shown that such short-term extreme droughts can severely reduce grassland above-ground productivity, which can have meaningful impacts on the global carbon cycle (Smith et al., 2024). We thus build on this work to investigate the drivers behind these responses. Although plant diversity and functional composition were not experimentally manipulated in the IDE, we used inherent variation in resistance and community characteristics both within and among sites to explore these relationships.

Specifically, we asked: (1) what are the relative roles of functional composition and plant diversity in driving the resistance of grassland above-ground productivity to extreme drought?; (2) how do different facets of plant diversity (functional, phylogenetic, taxonomic) influence resistance?; and (3) how do long-term climatic conditions related to water availability (aridity, rainfall variability) impact resistance and the roles of diversity and functional composition on resistance? We hypothesized that both functional composition (through the dominant-species effect) and diversity (through

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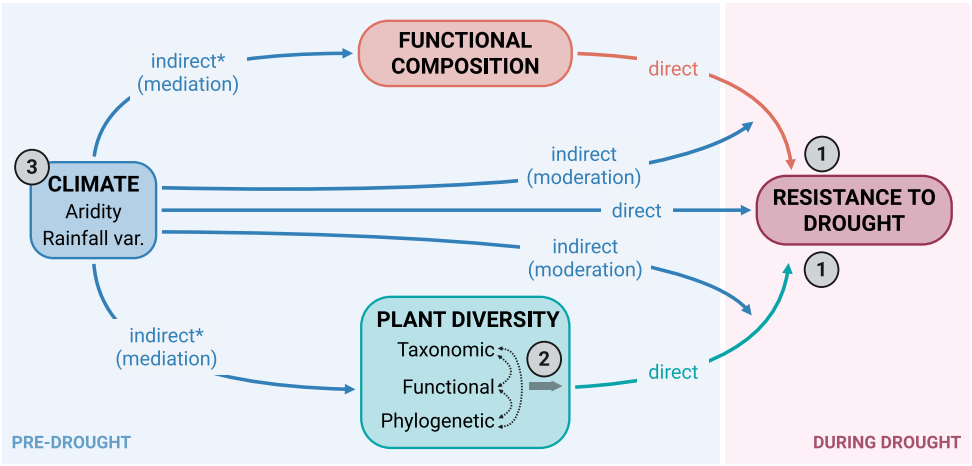


FIGURE 1 Conceptual model showing direct and indirect pathways through which functional composition (orange), plant diversity (green) and climate (blue) of pre-drought communities can impact resistance to short-term drought (red). Numbers correspond to study questions: (1) what are the relative roles of functional composition and plant diversity in driving the resistance of grassland above-ground productivity to extreme drought?; (2) how do different facets of plant diversity influence resistance?; and (3) how do long-term climatic conditions related to water availability impact resistance and the roles of diversity and functional composition on resistance? *Although these pathways are direct effects of climate on plant diversity and functional composition, they are labelled as indirect in reference to the indirect path through which climate can impact drought resistance. Var.: Variability. Created in BioRender. Bertuol-Garcia, D. (2025) https://BioRender.com/xynysbd.

complementarity, insurance and evolutionary history effects) would impact grassland resistance to drought and that the influence of taxonomic diversity would be mostly explained by an indirect path through functional and phylogenetic diversity. Moreover, we hypothesized that climate would impact resistance to drought both directly and indirectly through changes in and moderation of plant diversity and functional composition.

2 | MATERIALS AND METHODS

2.1 | Dataset

The Drought Network's International Drought Experiment (IDE; https://droughtnet.weebly.com) is a distributed experiment replicated in grassland and shrubland ecosystems across the world (Smith et al., 2024). At each site, at least three replicates of two treatments were applied to either maintain ambient-level precipitation (control treatment) or reduce precipitation to simulate a target extreme drought (drought treatment). To simulate drought, infrastructures composed of open-sided shelters with partial roofs made of strips of transparent acrylic or polycarbonate were deployed (Smith et al., 2024; Yahdjian & Sala, 2002). The percentage of roof coverage and thus of rainfall intercepted by rainout shelters was determined for each site to achieve a percent reduction in precipitation that simulated a 1-in-100-year drought under average ambient conditions (Lemoine et al., 2016; Smith et al., 2024). Each replicate contained one vegetation sampling plot of a minimum area of $2 \times 2\,m^2$. Within each vegetation plot, above-ground net primary productivity (ANPP) and plant cover were surveyed at least once a year. Species cover was visually estimated for each species rooted in $1 \times 1\,m^2$ permanent plots. ANPP was estimated from peak live biomass and current year's standing dead biomass, using methods appropriate for each ecosystem, following Fahey and Knapp (2007).

We filtered the IDE dataset to include sites that: (i) were in grassland habitats, (ii) had species cover data from drought treatments before the start of the experiment, and (iii) had ANPP data from both treatments in the first year following the start of experimental drought. The first year of drought was defined as the period at least 210 and less than 582 days since the start of the experiment, representing a full-growing season but less than 2 years. This resulted in 54 grassland sites on six continents, including a total of 257 vegetation plots (Figure 2, Appendix S1).

2.2 | Resistance to drought

We focused on the resistance of above-ground net primary productivity (ANPP) by calculating the log ratio of ANPP between drought and control plots in the first year after the experiment began (Smith et al., 2024). This metric measures the difference in order of magnitude of ANPP between treatments (Matos et al., 2020), with lower ANPP under drought when compared to controls indicating low resistance, and similar or higher ANPP indicating high resistance. This assumes control and drought plots start with similar ANPP, which was supported by their pre-treatment values showing no meaningful deviation from equality (Appendix S2).

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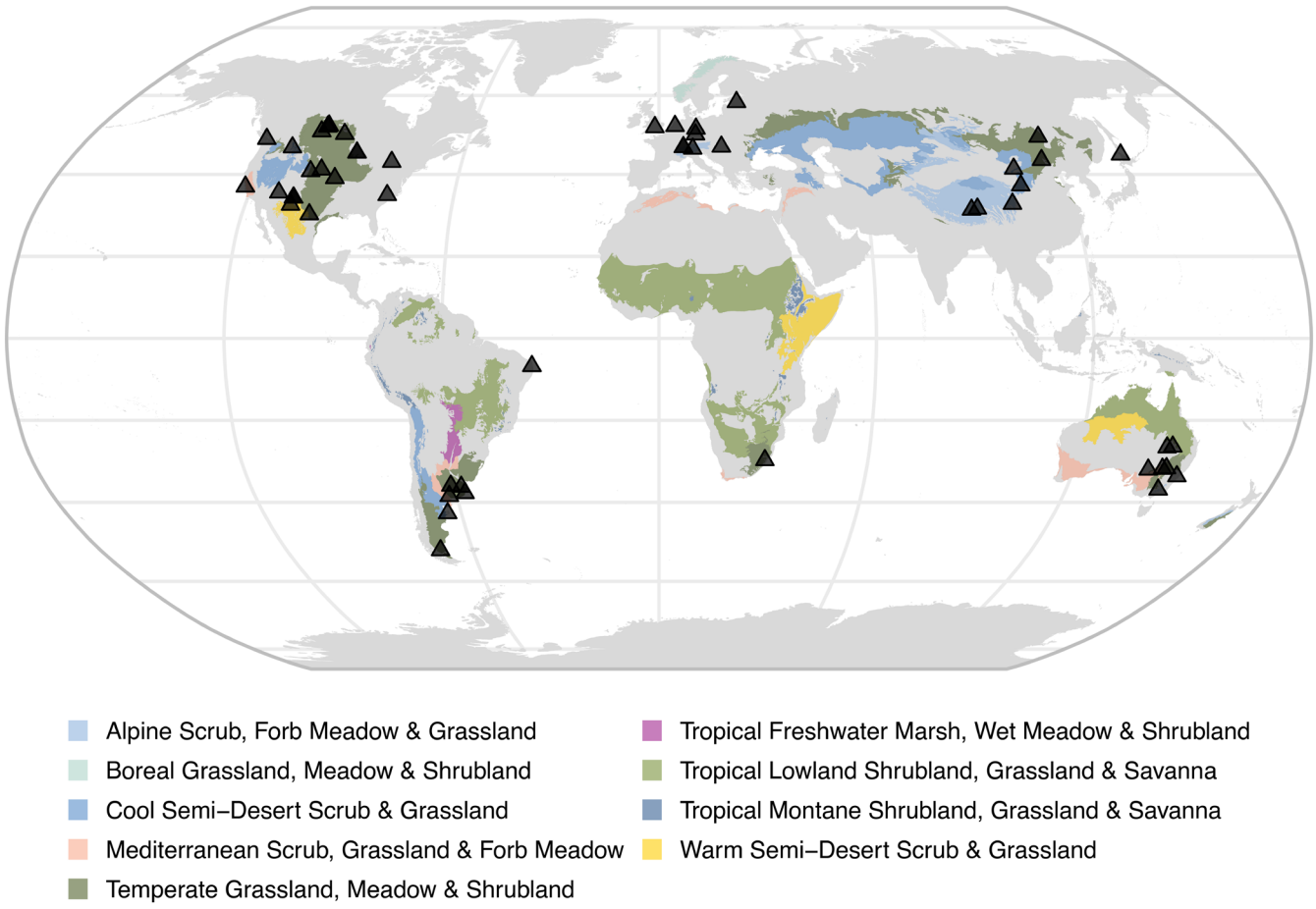


FIGURE 2 Locations of the 54 grassland sites of the International Drought Experiment used in this study. The background layer shows global grassland formation types according to Dixon et al. (2014), though some sites fall within grasslands at a finer spatial scale than depicted by this layer.

2.3 | Drivers of resistance

2.3.1 | Plant functional composition

We examined the functional composition of plant communities before the start of the experiment, focusing on traits related to dehydration avoidance and tolerance (i.e. leaf dry matter content, rooting depth, root dry matter content) (Garbowski et al., 2020; Volaire, 2018), the leaf and root resource economics spectrum (i.e. specific leaf area, leaf nitrogen concentration, root tissue density) (Weigelt et al., 2021; Wright et al., 2004), and important dimensions of plant form and function (i.e. plant height, seed mass) (Díaz et al., 2016; Westoby, 1998). Species scientific names were resolved using the World Checklist of Vascular Plants (Govaerts, 2023) and searched in global trait databases (Guerrero-Ramírez et al., 2021; Kattge et al., 2020; Society for Ecological Restoration et al., 2023; Tumber-Dávila et al., 2022; Weigelt et al., 2020, Appendix S3).

Due to limited availability of trait data at the species level, the trait query was implemented at the genus level (Appendix S4). To ensure this decision did not affect our results, we confirmed species- and genus-level trait values were correlated and verified that community functional composition and diversity metrics based on species- and genus-level traits were also significantly correlated (Pearson's $R = 0.67–0.99$, $p < 0.01$; Appendix S5). Six traits with sufficient coverage at the genus level were retained for subsequent analyses: specific leaf area (SLA), leaf dry matter content (LDMC), leaf nitrogen concentration, rooting depth, plant height, and seed mass. Overall, traits were available for 83.4% of the data in the genus-by-trait table. We imputed missing trait data based on a phylogenetic tree constructed at the genus level using the WCVP megatree and *U.Phylomaker* and *Rphylopars* in R (Goolsby et al., 2017; Jin & Qian, 2022, 2023; Smith & Brown, 2018; Zanne et al., 2014, Appendix S6).

We calculated community-weighted means (CWMs) of log-transformed traits for each treatment plot before drought using the mean imputed trait dataset and plant relative abundances from cover data. For consistency with trait data, species covers were summed for each genus in each plot. A principal component analysis with varimax rotation of the first two components was used to reduce the dimensionality of the CWM data (Appendix S7). The first rotated axis, which explained 35.8% of the variation, was positively associated with SLA and leaf nitrogen content, and negatively with LDMC (absolute loadings >0.5; Appendix S7). This axis captured a gradient from communities dominated by slow-growing, stress- and

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dehydration-tolerant species to those dominated by fast-growing, resource-acquisitive species (Appendix S7). The second rotated axis explained 30.2% of the variation and was positively associated with plant height, seed mass, and rooting depth (absolute loadings >0.5; Appendix S7), traits associated with both dehydration avoidance and tolerance in grasslands (Garbowski et al., 2020; Yan et al., 2025). These axes were used as indicators of the functional composition of each community, hereafter referred to as the 'slow-fast economic spectrum' (or '1st trait axis') and 'dehydration avoidance/tolerance' (or '2nd trait axis').

2.3.2 | Plant diversity

We considered the taxonomic, functional and phylogenetic facets of plant diversity in treatment plots before the start of the experiment as potential predictors of their resistance to drought during the experiment. For consistency with functional composition metrics, all diversity calculations were carried out at the genus-level using plant cover data for genera in each plot. We used three distinct metrics of plant diversity. Taxonomic richness (i.e. the number of genera in each plot) was used to measure taxonomic diversity. Functional diversity was calculated with the abundance-weighted functional dispersion metric (FDis) from the *FD* package (Laliberté & Legendre, 2010). For the phylogenetic facet, we use the phylogenetic tree constructed for trait imputation to calculate the abundance-weighted mean pairwise phylogenetic distance (MPD) between genera with the *picante* package (Kembel et al., 2010). These metrics capture the divergence dimension of functional and phylogenetic diversity, which influence competition for resources and community response to disturbances by reflecting on average how functionally or phylogenetically distinct the plants in the community are (Mammola et al., 2021; Tucker et al., 2017). Below, when referring to specific metrics and their results, we use the terms taxonomic richness, functional divergence, and phylogenetic divergence, but use 'diversity' when referring to multiple diversity facets or interpreting results.

2.3.3 | Climate

To examine long-term water availability and climatic fluctuations at the study sites, we focused on aridity and interannual rainfall variability, respectively. The aridity index is the ratio of mean annual precipitation to potential evapotranspiration (where lower values represent more arid conditions) and was retrieved as a measurement of the long-term water balance for each site from Zomer et al. (2022). Still, water availability can vary from year to year with certain locations experiencing higher fluctuations in rainfall over time. To capture this, we quantified interannual rainfall variability at the site level as the coefficient of variation in annual precipitation, using yearly precipitation values from 1979 to 2020 downloaded from the Multi-Source Weighted-Ensemble database (Beck et al., 2019).

2.4 | Controlling variables

While our primary focus was on functional composition, diversity and climate, we also considered soil characteristics and drought severity of each site to account for their potential influence on ecosystem responses to extreme drought. We extracted six globally available soil variables from the SoilGrids database, representing standard soil properties commonly used to describe and model soil characteristics: soil bulk density, cation exchange capacity, soil texture (proportions of clay, sand and silt), total nitrogen, soil organic carbon and soil pH (Hengl et al., 2017, Appendix S8). Soil properties were retrieved for each site, which were classified into six groupings of similar soil conditions via hierarchical clustering (Appendix S8). These soil groupings were then used as random effects in models predicting resistance, as sites with similar soil conditions are expected to respond similarly to drought. We also calculated drought severity from estimates of rainfall received by each treatment plot that consider both ambient rainfall and interception by rainout panels (see Smith et al., 2024 for details). The drought severity metric is the percent reduction from mean annual precipitation that drought plots experienced (Appendix S9) and was used as a covariate in models predicting resistance to account for its known effect on drought resistance (Smith et al., 2024).

2.5 | Data analysis

2.5.1 | SEM selection

To investigate direct and indirect paths between hypothesized drivers and ANPP resistance to drought, we fitted structural equation models (SEMs) using a model selection approach (Garrido et al., 2022). Here, we use standard SEM language to refer to modelled relationships as direct, indirect, and total effects, while acknowledging these do not imply experimental causation. Candidate SEMs were developed by combining different hypothesized pathways linking plant functional composition, plant diversity, site aridity and rainfall variability to drought resistance, all sharing a core structure linking functional composition, diversity and climate (Appendix S10). To investigate the roles of functional composition and plant diversity on resistance, models included either (i) the direct effect of a functional composition axis, (ii) the effect of diversity—via an indirect effect of taxonomic richness and direct effects of phylogenetic and functional divergence, or (iii) the combined effects of functional composition and diversity. Next, additional models were built by adding a direct effect of aridity, rainfall variability or both, on resistance. Finally, to test that taxonomic diversity is a weaker predictor of resistance compared to other diversity facets, we fitted an additional set of models where direct effects of functional and phylogenetic divergence were replaced by a direct effect of taxonomic richness. To avoid overfitting, each SEM included only one functional composition variable, with separate model selection rounds performed

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using each rotated PCA axis as the indicator variable for functional composition. All models included the direct effect of drought severity on resistance.

All SEMs were fitted using *piecewiseSEM* with linear mixed-effects models fitted using *glmmTMB* and maximum likelihood (Brooks et al., 2017; Lefcheck, 2016). We included random intercepts for sites in all component models and sites nested within soil groups for the model predicting resistance. Taxonomic richness was log-transformed to improve normality of residuals, and all models were fitted using a Gaussian distribution with an identity link function. We validated each component model of the full SEM by inspecting residuals using the *DHARMa* package (Hartig, 2021) and found that all models met the assumptions of normality and homoscedasticity without major violations (Appendix S11). Before model selection, we assessed the adequacy of the full SEM using directed separation tests and the Fisher's C statistic. The Fisher's C statistic gives the probability that the data were generated from the tested model, and therefore, a good model fit occurs when the probability is higher than a threshold (Lefcheck, 2016); we used $p > 0.05$ as our threshold to infer good model fit (Appendix S11). Candidate SEMs were then ranked by Akaike information criterion corrected for small sample size (AICc), and equally plausible models (ΔAICc <2) were refitted using the *lmer* function from the *lme4* package (Bates et al., 2015) with restricted maximum likelihood for more reliable coefficients. To compare direct, indirect and total effects of predictors on drought resistance, we calculated effects and associated standard errors for each refitted SEM through bootstrapping with the *SemEff* package (Murphy, 2024), averaged effects and standard errors across models following the equations in Johnson and Omland (2004), and visualized them using *tidyverse* (Wickham et al., 2019). Unless otherwise stated, SEM results are presented as standardized path coefficients with 85% confidence intervals (consistent with ΔAICc ≤2 criteria; Sutherland et al., 2023).

We examined the sensitivity of our results to using traits at the genus-level by running a species-level analysis using SLA as the indicator of plant functional composition and comparing results with the same analysis at the genus-level. We also assessed the impact of removing three phylogenetic divergence outliers (Appendix S12). Finally, to explore whether an alternative perspective on resistance would alter our findings, we calculated an additional resistance metric ('same-state resistance') that assigns equally low resistance to both positive and negative deviations from baseline (i.e. a symmetric metric; van Meerbeek et al., 2021) and inspected how results differed from those for the main metric of ANPP resistance.

2.5.2 | Multigroup SEM analysis

In the SEMs, only direct and mediating indirect effects were included, but our third question also involved understanding whether trait and diversity-based resistance drivers could be moderated by climate (Figure 1). We thus used multigroup analysis to identify SEM paths that differed between arid and non-arid sites, which would signal a moderating role of aridity. Following a recent analysis that indicated that diversity patterns change when crossing the aridity index threshold of 0.3 separating more arid from humid and less arid sites (Gross et al., 2024), we used this value as a breaking point to create the two categories. Because this analysis adds an interacting categorical variable to each path, we avoided fitting an overly complex model by using a simplified SEM with only taxonomic richness as the diversity variable. Multigroup SEMs were fitted with *glmmTMB* and *piecewiseSEM* (Brooks et al., 2017; Lefcheck, 2016), and differences in unstandardized path coefficients between groups were assessed using Wald's tests. Unstandardized path coefficients were used for inference only in the multigroup analysis because different variances between groups prevent the use of standardized coefficients for comparisons between groups.

3 | RESULTS

On average, ANPP resistance in drought plots was −0.5 (±0.79 SD), corresponding to a 39% reduction in ANPP (±56% SD, back-transformed from log ratios) relative to control plots. Resistance varied widely among plots, ranging from a 98% reduction to a 226% increase in ANPP compared to controls. This variation in ANPP resistance was partially explained by modelled drivers, with selected SEMs accounting for 11%–14% of variability through fixed effects (marginal R^2), and up to 49% when including random effects (conditional R^2; Figure 3; Appendix S13: Table S10). That is, 19%–21% of variance in ANPP resistance was explained by differences between soil property groupings, while 10%–19% was explained by differences between sites within soil groupings (Appendix S13: Table S10). All selected models showed adequate fit to the data (Fisher's *C* $p = 0.49–0.89$; $n = 257$; Figure 3).

Across all selected models, the direct effect of functional composition related to dehydration avoidance and dehydration tolerance (second trait axis) on ANPP resistance was stronger than that of plant diversity (Appendix S13: Table S10). That is, communities dominated by taller species with deeper roots and larger seeds showed, on average, higher ANPP resistance to drought (standardized path coefficient 0.14; 85% CI 0.04–0.24; Figure 3). In contrast, there was no evidence for a direct effect of plant functional composition when using the first trait axis in SEM selection, reflecting a weak relationship between dominance of traits related to the leaf economics spectrum (i.e. SLA, leaf nitrogen content, and LDMC) and ANPP resistance (−0.01; −0.06–0.04; Appendix S13: Figure S14 and Table S12). There was also no evidence of a significant relationship between functional composition and ANPP resistance when using community-weighted means of SLA at the species- or genus-level as indicators (Appendix S14).

The direct effect of plant diversity on ANPP resistance was mostly driven by functional and phylogenetic divergence, while selected models did not support a direct effect of taxonomic

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(a) Model selection

M#	C	df	p	K	AICc	Δ	w_i	$\sum w_i$	Mar R^2	Cond R^2	FC	Div.			Cl.		
												PD	FD	TR	Ar	RV	DS
6	12.79	20	0.89	30	3910.35	0.00	0.20	0.20	0.14	0.45	✓	✓	✓		✓		✓
4	23.59	24	0.49	28	3911.61	1.26	0.11	0.30	0.11	0.44	✓				✓		✓
9	15.58	20	0.74	30	3912.09	1.74	0.08	0.39	0.11	0.49	✓	✓	✓			✓	✓
12	11.91	18	0.85	31	3912.31	1.96	0.07	0.46	0.14	0.46	✓	✓	✓		✓	✓	✓
16	20.66	22	0.54	29	3912.37	2.02	0.07	0.53	0.12	0.44	✓			✓	✓		✓
7	22.73	24	0.54	28	3912.42	2.07	0.07	0.61	0.09	0.51	✓					✓	✓
10	21.08	22	0.52	29	3912.98	2.63	0.05	0.66	0.11	0.47	✓				✓	✓	✓
5	20.09	22	0.58	29	3913.00	2.65	0.05	0.71	0.13	0.42		✓	✓		✓		✓
3	24.93	22	0.30	29	3913.17	2.82	0.05	0.76	0.09	0.45	✓	✓	✓				✓
18	23.38	22	0.38	29	3913.62	3.27	0.04	0.80	0.10	0.50	✓			✓		✓	✓
20	18.72	20	0.54	30	3914.08	3.73	0.03	0.83	0.12	0.46	✓			✓	✓	✓	✓
8	22.15	22	0.45	29	3914.23	3.88	0.03	0.86	0.10	0.44		✓	✓			✓	✓
21	11.04	16	0.81	32	3914.28	3.93	0.03	0.89	0.14	0.46	✓	✓	✓	✓	✓	✓	✓

(b) Average model

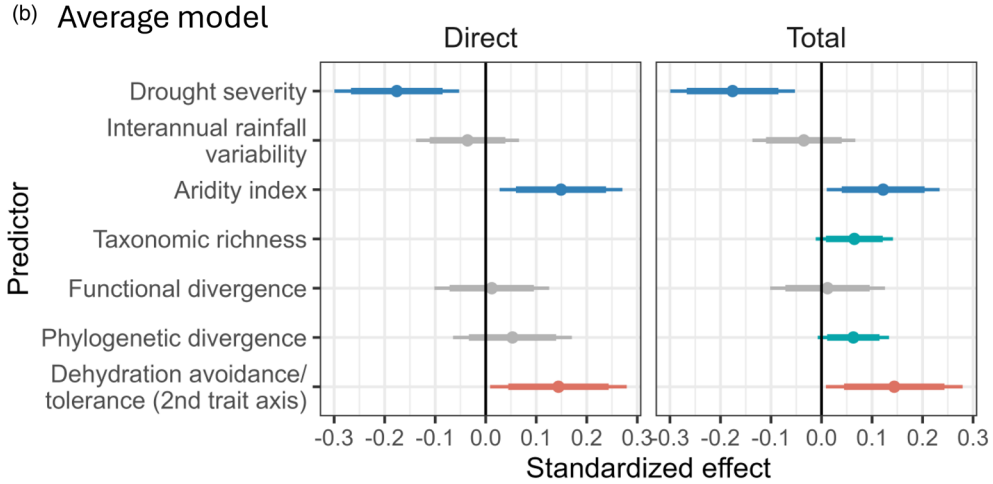


FIGURE 3 Aridity and functional composition related to dehydration avoidance and tolerance were strongly associated with above-ground net primary production (ANPP) resistance to drought, while plant diversity had a weak relationship, mostly through phylogenetic and functional facets. (a) Best-ranked models in model selection using the second trait axis as the indicator for functional composition. This axis was considered an indicator of dehydration avoidance/tolerance in grassland communities by being positively associated with rooting depth, plant height, and seed mass (Appendix S7). The table shows models summing up to 0.90 in cumulative Akaike weights (see Table S10 for full table). Selected models (ΔAICc ≤2) are highlighted in white, while other models are shown in grey. The right side shows direct effects on resistance that were included in models. Only links between variables that differed between candidate models are shown. (b) Direct and total effects on resistance for each predictor variable of the average SEM, calculated by averaging the selected models shown in (a). Total effects are the sum of direct and indirect effects throughout the entire SEM and therefore can include variables that only have an indirect effect on resistance (see Figure 4 for model paths). Thinner lines show 95% confidence interval, and thicker lines show 85% intervals. Significant relationships at $p \leq 0.157$ (consistent with ΔAICc ≤2 criteria; Sutherland et al., 2023) are shown in colour (blue: Climate variables; green: Diversity variables; orange: Functional composition variable), and non-significant relationships are shown in grey. M#: Model number; *C*: Fisher's *C*, df: Fisher's *C* degrees of freedom, *p*: Fisher's *C* *p*-value, K: Model degrees of freedom; AICc: Akaike Information Criterion corrected for small sample sizes; Δ: Delta AICc, w_i: Akaike weights; $\sum w_i$: Cumulative Akaike weights, Mar: Marginal R^2 of resistance; Cond R^2: Conditional R^2 of resistance; FC: Functional composition; Div.: Diversity; PD: Phylogenetic divergence; FD: Functional divergence; TR: Taxonomic richness; Cl.: Climate; Ar: Aridity; RV: Interannual rainfall variability; DS: Drought severity.

richness on ANPP resistance (Figures 3 and 4). Still, taxonomic richness showed a positive relationship with ANPP resistance when considering its indirect effect through increases in functional and phylogenetic divergence (0.07; 0.01–0.12; Figure 3). Individually, phylogenetic and functional divergence were estimated to have weak and non-significant direct effects (0.05; −0.03–0.14, and 0.01; −0.07–0.10, respectively), but their combined effect on ANPP resistance was positive (albeit small) and significant, as indicated by a significant total effect of phylogenetic divergence on ANPP resistance (0.06; 0.01–0.11; Figure 3).

Aridity and drought severity were also strongly associated with ANPP resistance. Drought severity had a direct, negative effect on resistance to drought (−0.18; −0.27 to −0.09; Figure 3), while aridity impacted resistance through multiple pathways (Figure 4).

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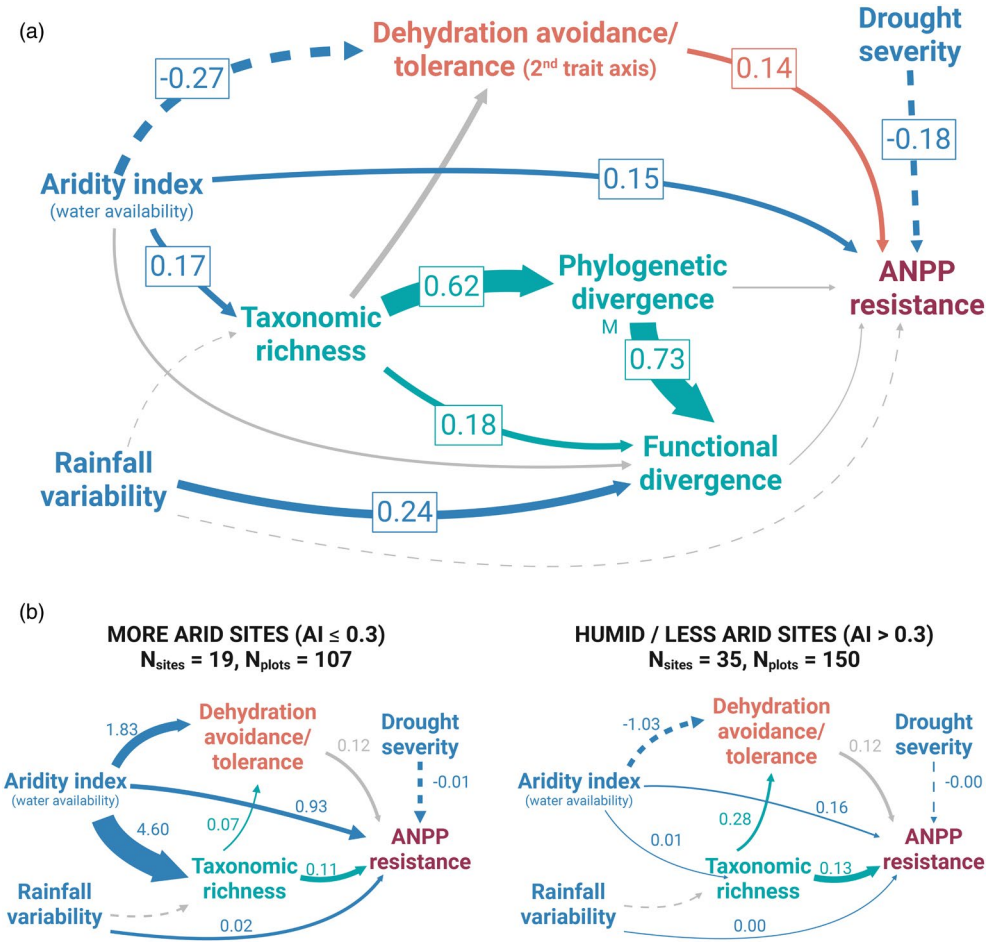


FIGURE 4 Aridity impacted above-ground net primary production (ANPP) resistance through direct and indirect pathways and moderated the association with other drivers. (a) Average structural equation model (SEM) produced by averaging selected models. Estimated marginal and conditional R^2 of ANPP resistance in this model, calculated by the weighted mean across selected models, were 12.8% and 45.7%, respectively. Solid lines indicate positive relationships, while dashed lines show negative relationships. Line width is proportional to the absolute standardized path coefficient, shown in squares for significant paths ($p \leq 0.157$, consistent with ΔAICc ≤2; Sutherland et al., 2023). Non-significant paths are shown in grey (see Figure S13 for all path coefficients and confidence intervals of the average SEM). The aridity index represents the long-term water availability of a site, where higher values represent less arid conditions. (b) Moderating effect of aridity as shown by the multigroup analysis comparing more arid (aridity index ≤0.30) and humid and less arid (aridity index >0.3) sites (full results in Table S11). For each path, line width is proportional to the difference in magnitude of unstandardized path coefficients (shown next to lines) between the two groups. Unstandardized effects sizes should only be used to compare effect sizes of the same paths between groups, and not to compare effect size of different paths within groups. Coloured arrows indicate path coefficients that were significantly different between groups ($p \leq 0.05$, test statistics in Table S11), grey arrows indicate no significant difference. ANPP: Above-ground net primary productivity; AI: Aridity index. Created in BioRender. Bertuol-Garcia, D. (2026) https://BioRender.com/x8wiaqo.

More arid sites (with lower aridity index) were, on average, dominated by taller species with deeper roots and larger seeds (−0.27; −0.45 to −0.09), which indirectly increased resistance to drought (Figure 4). However, more arid sites also had lower taxonomic richness (0.17; 0.04–0.30; Figure 4). This decrease in taxonomic richness resulted in a negative indirect effect of aridity on resistance through decreases in functional and phylogenetic divergence, as evidenced by the presence of the pathway going through phylogenetic and functional divergence in the top-ranked models (Figure 3). Nonetheless, the indirect effect of aridity on resistance, which accounts for its impacts through changes in both diversity and functional composition, was estimated to be weak and non-significant in the average SEM (−0.03; −0.06 to 0.01; Figure S13). The largest effect of aridity was a direct effect of decreased resistance in more arid sites (i.e. positive effect of the aridity index; 0.15; 0.06–0.24), resulting in a negative total effect of aridity on ANPP resistance (0.12; 0.04–0.20; Figures 3 and 4).

Aridity also moderated the effect of resistance drivers: the direct effect of diversity on resistance was weaker in more arid sites compared to humid and less arid sites (unstandardized path coefficients 0.11 and 0.12, respectively; SS = 0.4, df = 1; $p = 0.01$), while aridity (0.93 vs. 0.16; SS = 0.4, df = 1, $p = 0.02$), rainfall variability (0.02 vs. 0.00; SS = 0.4, df = 1, $p < 0.01$), and drought severity (−0.01 vs. 0.00; SS = 0.4, df = 1, $p < 0.01$) had stronger effects in more arid sites

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(Figure 4). The direct effect of traits related to dehydration avoidance and tolerance (second trait axis) was the same regardless of the level of aridity (0.12 vs. 0.12; SS = 0.4, df = 1, $p = 0.16$; Figure 4), but the direct effect of traits related to the slow-fast economics spectrum (first trait axis) was positive in more arid sites (0.14) and negative (−0.15) in humid and less arid sites (SS = 0.4, df = 1, $p = 0.01$; Appendix S13: Table S13). All trends were qualitatively similar when the three outlier plots with high phylogenetic divergence were removed.

Results based on the same-state resistance metric were broadly consistent with those of the main ANPP resistance metric, but SEMs explained less variance overall (Appendix S15). Key differences included weaker direct effects of both functional composition axes, the inclusion of a direct effect of all diversity facets (rather than just functional or phylogenetic) among selected models, and a stronger role of rainfall variability for same-state resistance (Appendix S15).

4 | DISCUSSION

Here, we assessed the joint influence of biotic and abiotic factors on drought resistance of global grasslands using data from the International Drought Experiment. Functional composition of traits related to dehydration avoidance and dehydration tolerance showed stronger relationships with ANPP resistance than plant diversity, while pathways from plant diversity to resistance occurred through functional and phylogenetic facets. Surprisingly, long-term climate was more strongly associated with ANPP resistance to drought than widely studied biotic drivers. Aridity showed a direct negative relationship with resistance and, to a lesser extent, an indirect relationship through its associations with plant diversity and functional composition. Finally, aridity also played a key role by moderating the influence of other resistance drivers, resulting in differential effects of rainfall variability, diversity and functional composition on ANPP resistance to drought between more arid and humid or less arid sites.

4.1 | Functional composition and diversity facets

We found that plant functional composition was more strongly associated with ANPP resistance than plant diversity, mostly through traits related to dehydration avoidance and tolerance. That is, results revealed that grassland communities dominated by taller plants with deeper roots and larger seeds were more drought resistant, consistent with studies associating taller, larger-seeded herbaceous species with dehydration tolerance (Yan et al., 2025) and with greater resistance and temporal invariability in the face of drought (Luo et al., 2023). Although some studies report that low stature benefits plants under drought by reducing evapotranspiration (Volaire et al., 2023), the high resistance of communities dominated by taller species may relate to the association of taller size with deeper roots in our study. In our study, individual deep-rooted species had recorded rooting depths of up to 5 m, whereas deep-rooted communities had a weighted average rooting depth of 1.7 m. Such deep roots allow access to water stored deep in the soil profile during dry periods, thus supporting a strategy of dehydration avoidance (Künzi et al., 2025). These results also align with other studies showing that grasslands composed mainly of plants with stress-tolerance traits have low sensitivity to drought (Song et al., 2024; Wilcox et al., 2021).

Surprisingly, we found no evidence for an overall direct effect on resistance of traits associated with the plant resource economics spectrum (i.e. SLA, leaf nitrogen content and LDMC). This may partially be explained by extreme drought favouring a dehydration escape strategy (Griffin-Nolan et al., 2019; Knapp et al., 2024), which can mask relationships with resource economics traits, as dehydration tolerance and dehydration escape often have opposing values in some of the traits (e.g. SLA, leaf nitrogen content; Künzi et al., 2025; Yan et al., 2025). Our usage of genus-level trait data due to limited species-level coverage also likely reduced trait resolution and may have weakened our ability to detect relationships. However, a species-level analysis using SLA, a key plant economics spectrum trait with sufficient species-level data, similarly showed no evidence for association between functional composition and ANPP resistance (Appendix S14), suggesting this pattern holds across taxonomic levels. Finally, the lack of evidence for an overall direct effect of traits associated with the resource economics spectrum might also reflect contrasting relationships in more arid versus humid and less arid sites. Specifically, dominance of fast-growing, acquisitive and dehydration-escaping trait values in plant communities (higher values on the first trait axis) was associated with higher drought resistance in more arid sites (aridity index ≤0.3), while dominance of slow-growing, stress-tolerant trait values (lower values on the first trait axis) was associated with resistance in humid and less arid sites (aridity index >0.3). Despite these differences, our results generally support the dominant-species hypothesis, although the specific traits driving drought resistance might depend on context.

In selected models, the estimated direct effects of diversity on resistance were absent (i.e. for taxonomic richness) or weak and non-significant (i.e. for functional and phylogenetic divergence). However, their combined influence resulted in a significant, positive (albeit small) relationship with drought resistance, as evidenced by the total effect of taxonomic richness and phylogenetic divergence on ANPP resistance. Nonetheless, these effects were small compared to the direct effect of functional composition or aridity. This contrasts with the emphasis on biodiversity as a key driver of ecosystem stability and resistance (e.g. Isbell et al., 2015; Tilman & Downing, 1994; Yachi & Loreau, 1999), which could in part be due to the primary focus of this literature on the direct effect of biodiversity and its role on temporal invariability. Our results suggest that, when the broader context is considered and pathways from climate to resistance are included in models, the explanatory power of biodiversity might become weaker. That is, while resistance is higher in more diverse communities (Isbell et al., 2015; Smith et al., 2024), for regional and global studies such as ours, this likely reflects higher community diversity in less arid sites (but see Fraser et al., 2015),

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where lower aridity itself is directly linked to higher resistance (Figure 4). Indeed, other recent studies have also reported weak biodiversity-mediated pathways on grassland stability when climate is incorporated (Ren et al., 2023).

Still, in line with expectations, the relationship between plant diversity and resistance was mostly driven by functional and phylogenetic facets, with taxonomic diversity contributing only indirectly through its association with other facets. This supports the niche complementarity and insurance hypothesis (Loreau et al., 2021) and aligns with studies showing that functional diversity increases resistance or decreases sensitivity to drought (Bazzichetto et al., 2024; Griffin-Nolan et al., 2019; Song et al., 2024). While taxonomic diversity may be key for temporal invariability via the portfolio effect (Doak et al., 1998; Gross et al., 2014; Tilman et al., 1998), for resistance to a single extreme event, the stability-generating mechanisms of biodiversity seem to be weaker and mainly related to niche complementarity and insurance. Moreover, few studies have looked at the impact of phylogenetic diversity on drought resistance, and we extend the knowledge that it can help explain temporal invariability (Craven et al., 2018) to the resistance component of stability.

4.2 | Climate

Overall, climate was one of the most important explanatory factors for ANPP drought resistance, with more arid sites generally showing lower resistance. We cannot completely exclude the possibility that treatments were less effective in mesic areas due to challenges such as lateral water flow through the soil and difficulty of creating effectively dry conditions (Hoover et al., 2018), but our findings are in accordance with a growing body of literature reporting higher sensitivity to drought in arid sites (Knapp et al., 2015; Smith et al., 2024; Stuart-Haëntjens et al., 2018), although exceptions exist (e.g. Tielbörger et al., 2014).

The above relationship between aridity and drought resistance was evident via multiple pathways in the average SEM. First, there was a direct negative effect of aridity. Part of this effect may also involve indirect pathways through soil properties that co-vary with aridity. For instance, wetter sites tend to have lower pH due to increased soil leaching (Slessarev et al., 2016), which can influence nutrient availability, above-ground productivity, and thus drought resistance. However, to account for such effects, we included groupings of sites that shared similar soil characteristics such as pH and soil texture as random effects in models (Appendix S8). These soil groupings explained up to 21% of the variance in resistance, highlighting the importance of soil properties to understand drought responses, even though our usage of soil property data from a rough 250-m grid may have weakened our ability to detect relationships. Soil texture and bulk density, for example, influence vegetation resistance both through their effects on soil water and nutrient holding capacity and their impact on plant communities, with higher productivity maintained for deep-rooted dehydration-tolerant species on coarse soils in arid regions (Abel et al., 2024; Munson et al., 2015). Our results therefore suggest that soil properties, in addition to aridity, are key abiotic determinants of drought resistance, which has also been confirmed elsewhere by direct soil-based measurements on sites (Stampfli et al., 2018).

Nonetheless, by including soil groupings as random effects, we controlled for their effect without explicitly modelling it in SEMs; thus, the remaining direct path between aridity and resistance likely reflects a separate mechanism. Proposed mechanisms for this relationship involve biogeochemical constraints related to limiting resources and vegetation constraints related to plant life history and functional traits (Huxman et al., 2004). The latter is captured in our SEM through the indirect functional-composition path (see next paragraph), whereas the former is more consistent with the observed direct effect. This direct mechanism aligns with the resource-limitation hypothesis, which posits that water limitation is the strongest factor controlling plant growth in arid sites (Knapp et al., 2024). Plant species in these ecosystems are likely functioning near their physiological limits and have low or no capacity to cope with additional water stress, and hence are more sensitive to water reductions, leading to lower drought resistance through increased stress and competition (Bondaruk et al., 2025; Huxman et al., 2004; Knapp et al., 2024). In contrast, wetter sites, including those with high values of the aridity index in our study, would be limited by other resources and thus less affected by changes in water availability (Huxman et al., 2004; Knapp et al., 2024).

Secondly, aridity was also indirectly related to ANPP resistance through a diversity-mediated pathway (i.e. decreasing all facets of plant diversity) and a functional composition-mediated pathway (i.e. increasing the dominance of dehydration tolerance and avoidance traits). However, evidence for the diversity-mediated pathway was mixed: while paths from functional and phylogenetic divergence to resistance appeared in top-ranked models, their estimated direct effects—and the indirect effect of climate on resistance through these facets—were small and non-significant in the average SEM (Figure S13). This suggests that diversity plays a role but is relatively weak compared to other paths. In contrast, the observed functional composition-mediated pathway suggests support for the vegetation constraint or stress-adaptation hypothesis, which states that arid sites would be less sensitive to drought due to the presence of species adapted to chronic water stress (Huxman et al., 2004; Knapp et al., 2024). An alternative trait-based mechanism could involve long-term aridity selecting for dehydration escape via an annual life cycle (Kooyers, 2015), which could confer low resistance to a full-growing season of drought. However, we found no evidence for this mechanism: the estimated effect of aridity on the 1st trait axis, which included traits such as SLA and leaf nitrogen content typically associated with dehydration escape strategies (Funk et al., 2021), was weak and non-significant, as was the effect of this axis on drought resistance (Figure S14). Therefore, our results are consistent with both resource limitation and stress-adaptation being important

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mechanisms of drought resistance (Knapp et al., 2024), although the evidence for the resource limitation hypothesis was stronger (i.e. the direct effect of aridity on resistance).

Finally, aridity also has a key role in shaping resistance through moderation of other drivers, which has been previously described for temporal invariability (García-Palacios et al., 2018). Aridity not only altered the relationship between resource economics spectrum traits and drought resistance, as described above, but also weakened the positive effect of taxonomic richness on resistance. This again supports the mechanisms of the stress-limitation hypothesis (Huxman et al., 2004; Knapp et al., 2024), as additional species could increase competition for water in water-limited environments and decrease overall resistance to drought. It is important to note, however, that we were unable to investigate how aridity changed pathways from functional and phylogenetic diversity to resistance. Recent studies have shown that arid sites can have surprisingly high levels of functional diversity, reflecting plants' contrasting life history strategies for coping with long-term aridity (Gross et al., 2024; Maestre et al., 2021). Therefore, while a higher number of species (i.e., higher taxonomic richness) in arid sites could decrease resistance to drought, increases in functional diversity might have the opposite effect. Either way, these results suggest that long-term aridity is a key driver of drought resistance through direct, indirect, and moderating pathways, and that ignoring long-term climatic factors such as site aridity might lead to incomplete or misleading generalizations about the effects of biotic drivers of drought resistance.

Interannual rainfall variability also played a role in shaping drought resistance, although to a lesser extent than other drivers. First, higher rainfall variability was associated with higher functional divergence, a pattern consistent with studies showing that variable climates promote the coexistence of diverse functional strategies (Gherardi & Sala, 2015; Hallett et al., 2019). However, the estimated indirect effect of rainfall variability on resistance through this diversity-mediated pathway was weak and non-significant in the average SEM (Figure S13). Secondly, while we found no evidence of a direct effect of interannual rainfall variability on resistance when all sites were grouped together, this effect was different between more arid and humid or less arid sites. Due to the structure of our model selection approach, the influence of rainfall variability appears as a direct effect, but precipitation history can only impact current response to drought through a legacy effect (e.g. Hoover et al., 2021; Walter et al., 2013). One possibility is that larger and less frequent precipitation events associated with higher rainfall variability influence subsoil moisture availability differently depending on background aridity (Feldman et al., 2024; Hou et al., 2021; Nielsen & Ball, 2015). In arid sites, these events enhance subsoil moisture and productivity, whereas in non-arid areas, they lead to increased runoff and reduced subsoil water, diminishing primary productivity (Feldman et al., 2024; Hou et al., 2021). Consequently, more arid sites with variable rainfall might exhibit greater drought resistance, while more variable humid and less arid sites would be less resistant, again highlighting the key role of contextualizing drought response within the long-term climatic context for a better understanding of grassland drought resistance.

4.3 | Concluding remarks

Despite the significant effects identified, a considerable portion of the variation in drought resistance remained unexplained. This suggests that, beyond the key biotic and abiotic drivers assessed, factors such as community dynamics, soil-mediated processes and rainfall distribution patterns—including timing, frequency and drought legacies—may substantially influence resistance. In particular, exploring past drought legacies on the plant–soil system (e.g. Müller & Bahn, 2022; Walter et al., 2013) may reveal explanations for the encountered differences between more arid and humid or less arid sites. Additionally, the alternative resistance metric investigated suggests that measures such as same-state resistance may be less predictable in dynamic systems such as grasslands, where community composition and productivity fluctuate substantially over time and space (Cleland et al., 2013; Kreyling et al., 2011). In these environments, reduced precipitation can favour opportunistic species such as dehydration escaper and avoidant species (Kooyers, 2015), boosting productivity without maintaining consistent ANPP, and thus potentially explaining why functional composition showed weaker effects for same-state resistance.

On a global scale, an abiotic factor (long-term aridity) was strongly associated with above-ground productivity responses to short-term (i.e. 1 year) extreme drought in grasslands. In contrast, biotic factors (functional composition and plant diversity) provided lower explanatory power for extreme drought resistance, although traits related to dehydration avoidance and tolerance were more influential. To increase our understanding of the drivers of ecosystem stability and resistance, we therefore recommend focusing on other, less well-known mechanisms, as our models showed mixed support for widely studied drivers such as traits of dominant species and niche complementarity. More importantly, we show that contextualizing predictive models with climate and recent climate history is an important consideration for advancing the science of ecosystem resistance to drought.

Finally, our study suggests that arid sites are particularly vulnerable to future climate change. Arid sites showed lower resistance to extreme drought compared with non-arid sites. This finding is consistent with other studies (Bondaruk et al., 2025; Knapp et al., 2024; Smith et al., 2024; Stuart-Haëntjens et al., 2018) and support efforts to conserve vulnerable arid sites projected to experience severe drought. Still, we did not measure recovery from drought events nor the impact of longer-term drought. While some studies suggest that grassland drought responses might only occur or intensify after multiple years of drought (e.g. Griffin-Nolan et al., 2019; Ohlert et al., 2025), others report that drought duration does not intensify impacts (e.g. Batbaatar et al., 2022), with much therefore still unknown about the long-term responses of ecosystems to repeated and/or longer droughts. Regardless, the key role of aridity in driving the response to a short-term drought suggests that management strategies focusing on specific traits or biodiversity (e.g. Cadotte et al., 2011; Laughlin, 2014) need also to account for the abiotic context and recognize that biotic drivers can operate differently in

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arid versus humid sites. Integrating these considerations will help to conserve grassland biodiversity and maintain critical ecosystem services.

AUTHOR CONTRIBUTIONS

Diana Bertuol-Garcia, Daniel C. Laughlin, Gustavo Brant Paterno, and Nancy Shackelford conceived the study; Michele Carbognani, Manjunatha H. Chandregowda, Amber C. Churchill, Jeffrey S. Dukes, Mary Ellyn DuPre, Nico Eisenhauer, T'ai Gladys Whittingham Forte, Yann Hautier, Andrew Hector, Hugh A. L. Henry, Anke Jentsch, Sally Koerner, María Grisel Longo, Alejandro Loydi, Akira S. Mori, Seth M. Munson, Uffe N. Nielsen, Timothy J. Ohlert, Rafael Otfinowski, Meelis Pärtel, Josep Peñuelas, Pablo L. Peri, Alessandro Petraglia, Juan Manuel Piñeiro, Sally A. Power, William E. Rogers, Braulio A. Santos, Melinda D. Smith, Andreas Stampfli, Michelle Tedder, George R. Wheeler, Jennifer Williams, and Michaela Zeiter coordinated data collection, Diana Bertuol-Garcia and Timothy J. Ohlert curated and managed the data; Liesbeth van den Brink, Michele Carbognani, Jeffrey S. Dukes, Mary Ellyn DuPre, Nico Eisenhauer, T'ai Gladys Whittingham Forte, Hugh A. L. Henry, Angelika Kübert, Emma Ladouceur, Daniel C. Laughlin, Alejandro Loydi, Akira S. Mori, Seth M. Munson, Gastón R. Oñatibia, Gustavo Brant Paterno, Pablo L. Peri, Sally A. Power, Yolanda Pueyo, Nancy Shackelford, Andreas Stampfli, Jennifer Williams, and Michaela Zeiter provided feedback on the analytical framework; Diana Bertuol-Garcia performed data analysis; Diana Bertuol-Garcia, Liesbeth van den Brink, Emma Ladouceur, Uffe N. Nielsen, and Rachel J. Standish wrote the manuscript; Michele Carbognani, Manjunatha H. Chandregowda, Amber C. Churchill, Daniela F. Cusack, Maren Dubbert, Nico Eisenhauer, T'ai Gladys Whittingham Forte, Yann Hautier, Andrew Hector, Hugh A. L. Henry, Anke Jentsch, Sally Koerner, Angelika Kübert, María Grisel Longo, Alejandro Loydi, Akira S. Mori, Seth M. Munson, Timothy J. Ohlert, Gastón R. Oñatibia, Rafael Otfinowski, Meelis Pärtel, Gustavo Brant Paterno, Josep Peñuelas, Pablo L. Peri, Alessandro Petraglia, Juan Manuel Piñeiro, Sally A. Power, Yolanda Pueyo, William E. Rogers, Braulio A. Santos, Nancy Shackelford, Andreas Stampfli, Michelle Tedder, George R. Wheeler, and Jennifer Williams provided feedback on the manuscript; Diana Bertuol-Garcia, Liesbeth van den Brink, Michele Carbognani, Daniela F. Cusack, Maren Dubbert, Hugh A. L. Henry, Daniel C. Laughlin, Seth M. Munson, Meelis Pärtel, Alessandro Petraglia, Sally A. Power, William E. Rogers, Braulio A. Santos, Nancy Shackelford, Andreas Stampfli, Rachel J. Standish, and Michaela Zeiter revised and edited the manuscript. All authors read and agreed with the final version of the manuscript.

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CONFLICT OF INTEREST STATEMENT

Andrew Hector is a Senior Editor and Yann Hautier is an Associate Editor of *Journal of Ecology*, but neither took part in the peer review and decision-making processes for this paper.

PEER REVIEW

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DATA AVAILABILITY STATEMENT

Data and code used for analysis are available from the Borealis repository at https://doi.org/10.5683/SP3/X4UI3E (Bertuol-Garcia et al., 2026).

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SUPPORTING INFORMATION

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

Appendix S1. International drought experiment sites.

Appendix S2. ANPP in drought and control plots.

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Appendix S3. Taxonomic standardization.
Appendix S4. Trait availability.
Appendix S5. Comparing genus versus species-level trait data.
Appendix S6. Trait imputation.
Appendix S7. Main axes of variation in plant functional composition.
Appendix S8. Soil groups.
Appendix S9. Variables.
Appendix S10. SEM specification and selection.
Appendix S11. SEM statistical validation.
Appendix S12. Variable distribution.
Appendix S13. Full results for ANPP resistance.
Appendix S14. Species versus genus-level analysis.
Appendix S15. Alternative resistance metric (same-state resistance).

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