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Growth form and lifespan of herbaceous species mediate the role of traits in short-term drought response

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A list of authors and their affiliations appears at the end of the paper

Increased climate variability is expected to intensify short-term drought events. Plants have evolved stress tolerance strategies involving trade-offs in resource conservation, mycorrhizal collaboration and plant size, yet how these strategies promote drought resistance across different herbaceous plant groups remains unknown. Leveraging 63 globally distributed grassland and shrubland sites from the International Drought Experiment, we identified plant traits linked to drought resistance in 661 populations of 421 species after 1 year of extreme drought. We assessed how traits, site precipitation and drought severity affected cover change across growth forms and lifespans, and how trait–environment interactions influenced drought resistance. Across all species, leaf N (an acquisitive trait) was associated with drought resistance, whereas in forbs, drought resistance was also associated with a conservative root trait and plant size. In addition, interactions among traits mediated drought resistance; root traits predicted performance only in concert with other traits. Environmental variables influenced trait effects on drought resistance, notably for annuals in wetter sites, suggesting that drought-escape strategies in annuals may be advantageous only under mild stress. Our study highlights variability in traits that predict drought resistance across herbaceous plant groups, emphasizing the importance of species context, environmental stress and the selection of traits in research and management.

Global climate shifts are causing increasingly variable weather patterns, characterized by drier conditions in some regions and years and more frequent, intense episodes of extreme precipitation in others[1,2]. Extreme short-term droughts are projected to increase in frequency and intensity, resulting in substantial impacts on plant communities with consequences for ecological and social systems[3–5]. Plants have evolved a range of drought survival strategies, which are linked to morphological, physiological and phenological traits contributing to their performance and fitness[6]. Analysing the effectiveness of these strategies in the face of extreme short-term drought conditions can provide a framework for better understanding and predicting plant responses to changing climate[7,8].

Trait-based approaches have the potential to predict responses to pulse dynamics[9] and biomass-altering factors, such as drought[10]. Trait frameworks can be useful for conceptualizing trade-offs among traits involved in these responses[11]. A proposed framework[12] includes trait gradients related to resource conservation, mycorrhizal collaboration and plant size, describing gradual linear changes between opposing ecological strategies. The conservation gradient is defined by the leaf[13] and root[14] economics spectra. One end of the gradient is comprised of ‘fast’ traits linked to resource acquisition and shorter lifespan, while the other end features ‘slow’ traits related to conserving resources and longer lifespans. Along the collaboration gradient, root traits of plants are characterized by a ‘do it yourself’

e-mail: sworthy@holdenfg.org; rpp6@iu.edu; funk@ucdavis.edu

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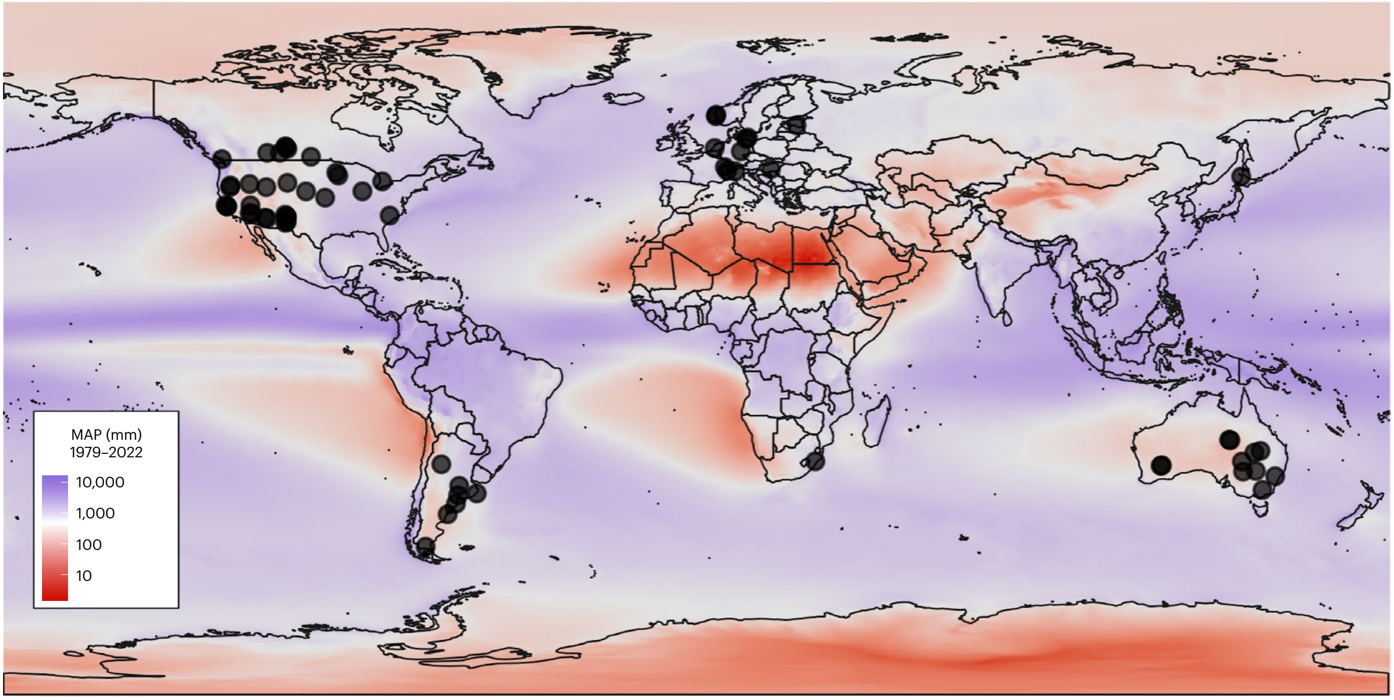

Fig. 1 | Map of the study sites. Global distribution of the 63 study sites (dots) and MAP (mm) from 1979 to 2022 at 0.25° resolution[85,86].

strategy versus an 'outsourcing to fungal partners' strategy for acquiring resources[15]. In the latter, trade-offs are between root diameter, which provides habitat for mycorrhizal fungal colonization, and mass-specific root length (or surface area), which facilitates nutrient foraging and acquisition via long, thin absorptive roots[15]. Lastly, there are size gradients associated with plant vegetative height and rooting depth—taller plants compete better for light and deeper roots access water from deep soil[16], but both strategies require greater resource investment.

A range of phenotypic strategies will probably confer drought resistance. With respect to the resource conservation gradient, species with slow resource-return traits, such as thicker and denser leaves and roots, may help minimize water loss and increase drought survival[8,17]. Across the collaboration and plant size gradients, multiple traits can enhance water uptake including greater investment in root surface area[18,19], mycorrhizal associations to access water beyond root depletion zones, or first- and second-order roots (or taproots) in deep soils[8,20]. The gradients of conservation and collaboration are orthogonal to each other and to plant size. This suggests that plants may adopt a specific conservation strategy while varying their collaboration and size strategies, creating a multifaceted strategy to drought adaptation[12]. In support of this idea, recent studies have shown that plants combine traits in unexpected ways (for example, acquisitive aboveground traits with conservative belowground traits[21]) to increase growth, survival and fecundity[22,23] and that different combinations of traits optimize these performance metrics across environments[24,25].

We used a network of drought experiments, the International Drought Experiment (IDE)[5], which are broadly distributed across grasslands and shrublands (Fig. 1 and Supplementary Table 1) to address our first aim of determining which traits or combination(s) of traits are related to resistance to short-term (single-year) drought for a diverse set of herbaceous plant species. We define drought resistance here as lower reductions in plant cover with drought. On the basis of plant economic theory, we hypothesize that traits aligned with the slow end of the resource conservation gradient would increase drought resistance[13]. While root traits are a recent addition to trait strategy frameworks, we hypothesize that belowground traits aligned with resource conservation (for example, thicker, more robust roots) would more often be associated with increased drought resistance than aboveground traits[16,26]. In addition, we posited that traits could combine in complex ways to achieve similar drought resistance, supporting alternative design theory[27,28]. We hypothesize that traits from different trade-off gradients or allocation strategies would interact such that the association of one trait with cover change is mediated by another trait. For example, mass-based leaf nitrogen concentration could interact with rooting depth where low leaf nitrogen, a 'slow' resource conservation strategy, confers drought resistance only in combination with deeper rooting depth, a size gradient trait. We also hypothesize that how traits are associated with cover change may differ with the magnitude of drought (drought severity; Methods) and mean annual rainfall[29,30]. For instance, resource conservative traits such as denser roots and lower specific leaf area may be more strongly associated with drought resistance under high drought severity than low drought severity[17].

The second aim of this work was to explore how trait–performance relationships vary across species groups and elucidate strategies used for drought resistance. We hypothesize that species with different growth forms (graminoids versus forbs) and lifespans (annuals versus perennials) would respond differently to short-term drought, complicating the development of a global framework for drought response. For example, grasses may develop extensive fine roots that are shorter for optimal water uptake in shallow soil layers, whereas forbs may rely on deeper roots[31,32], and these morphological differences may underlie differences in drought strategies and the relatively larger negative effects of drought on grasses than forbs[33]. Annual and perennial species may respond to short-term drought using different strategies to enhance performance. Perennial species are generally expected to adopt a drought-resistant strategy corresponding to the slow end of the conservation gradient, but this group appears to use a variety of strategies in response to drought[34,35]. By contrast, annual species may use a drought-escape strategy characterized by traits associated with the fast end of the conservation gradient designed to maximize growth rate and expedite flowering and reproduction[6,36].

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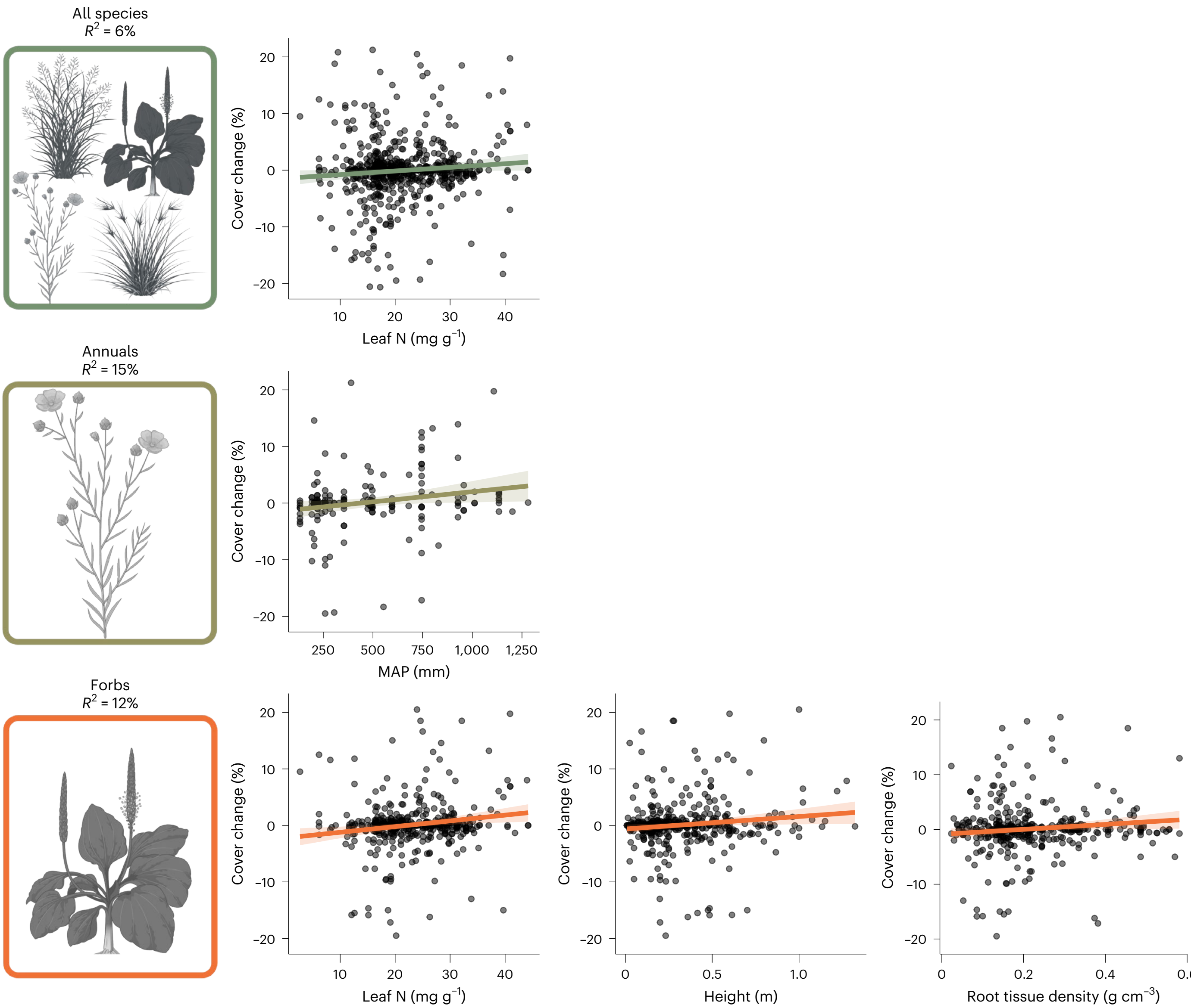

Fig. 2 | Relationships in which traits or environmental variables had a significant effect on cover change. Higher drought resistance was associated with higher leaf N when all plant groups (n = 661 populations) were pooled and for forbs (n = 410 populations). In addition, taller forbs or those with higher RTD were associated with higher drought resistance. Annuals (n = 178 populations) from sites with higher MAP also had higher drought resistance. Trend lines represent the mean conditional effects of the trait or environmental variable, coloured envelopes represent 95% credible intervals and opaque grey points are observed data points in which darker points indicate overlap among the points. Values on the x-axes are back transformed. For each plant group, R^2 values indicate the percentage of the variance in cover change explained by the full model. Plant graphics created with BioRender.com.

Results

Traits from different gradients predict drought response in forbs

Leaf N, height and root tissue density (RTD) were significant predictors of cover change (Fig. 2). A positive association was observed between leaf N and drought resistance when all plant groups were pooled (Fig. 2). The other relationships were largely restricted to forb species (Fig. 2 and Extended Data Figs. 1–9), with no traits significantly associated with drought resistance in graminoids (Extended Data Fig. 5). Specifically, drought resistance (lower reductions in plant cover with drought) in forbs was positively associated with height, leaf N and RTD (particularly perennial forbs). Taller forbs were significantly more drought resistant than taller graminoids, but there was no significant difference in association between leaf N, RTD and cover change across growth forms (Extended Data Figs. 5, 6 and 10, and Supplementary Fig. 1). Associations between RTD and cover change were not significantly different among combinations of lifespans and growth forms despite RTD being significantly positively associated with drought resistance in perennial forbs (Extended Data Figs. 7–10).

Interactions between traits on different gradients mediate short-term drought response

We found evidence that traits reflecting different trade-off gradients interact to drive species' drought resistance (Supplementary Fig. 2). Taller plant species with higher leaf N showed higher drought resistance in perennials and the all-species group (Fig. 3), representing an interaction between the plant size and resource conservation gradients. In addition, plants with higher belowground biomass allocation (root mass fraction (RMF)) and higher leaf N were more drought resistant in annuals and the all-species group (Fig. 3). By contrast, plants with

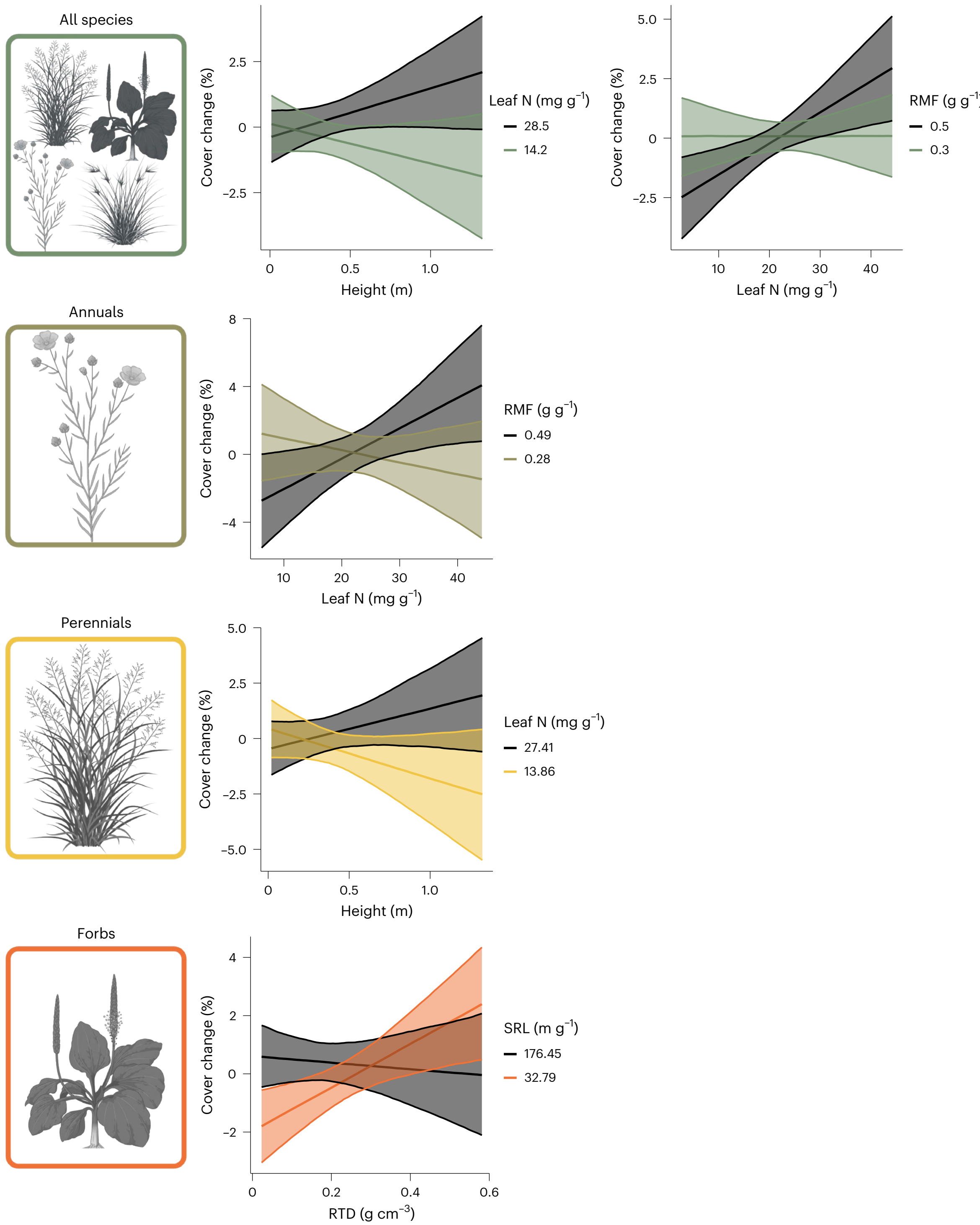

Fig. 3 | Interaction plots showing the predicted effects of significant two-way interactions between traits. Two significant interactions were found when all plant groups (n = 661 populations) were pooled: height × leaf N (R^2 = 5%) and leaf N × RMF (R^2 = 5%). The interaction between leaf N and RMF (R^2 = 13%) was also significant for annuals (n = 178 populations) while the interaction between height and leaf N (R^2 = 6%) was also significant for perennials (n = 462 populations). For forbs (n = 410 populations), RTD significantly interacted with SRL to effect cover change (R^2 = 8%). Trend lines represent the median relationships between cover change and the x-axis trait at the minimum (coloured line) and maximum (black line) values of the other trait; coloured envelopes represent 95% credible intervals. Trait values are back transformed. Plant graphics created with BioRender.com.

lower RMF showed greater drought resistance when leaf N was lower. Finally, we found interactions between the resource conservation and collaboration gradients, in which forbs could achieve higher drought resistance with a conservative strategy of low specific root length (SRL) and high RTD or an acquisitive strategy of high SRL and low RTD (Fig. 3 and Supplementary Fig. 2).

Environmental factors mediate the effects of some traits on drought resistance

Overall, the drought severity index (DSI) and mean annual precipitation (MAP) were weak predictors of drought resistance (Extended Data Fig. 1–9). Drought resistance was higher for annuals in sites with higher MAP (Fig. 2 and Extended Data Fig. 1), and

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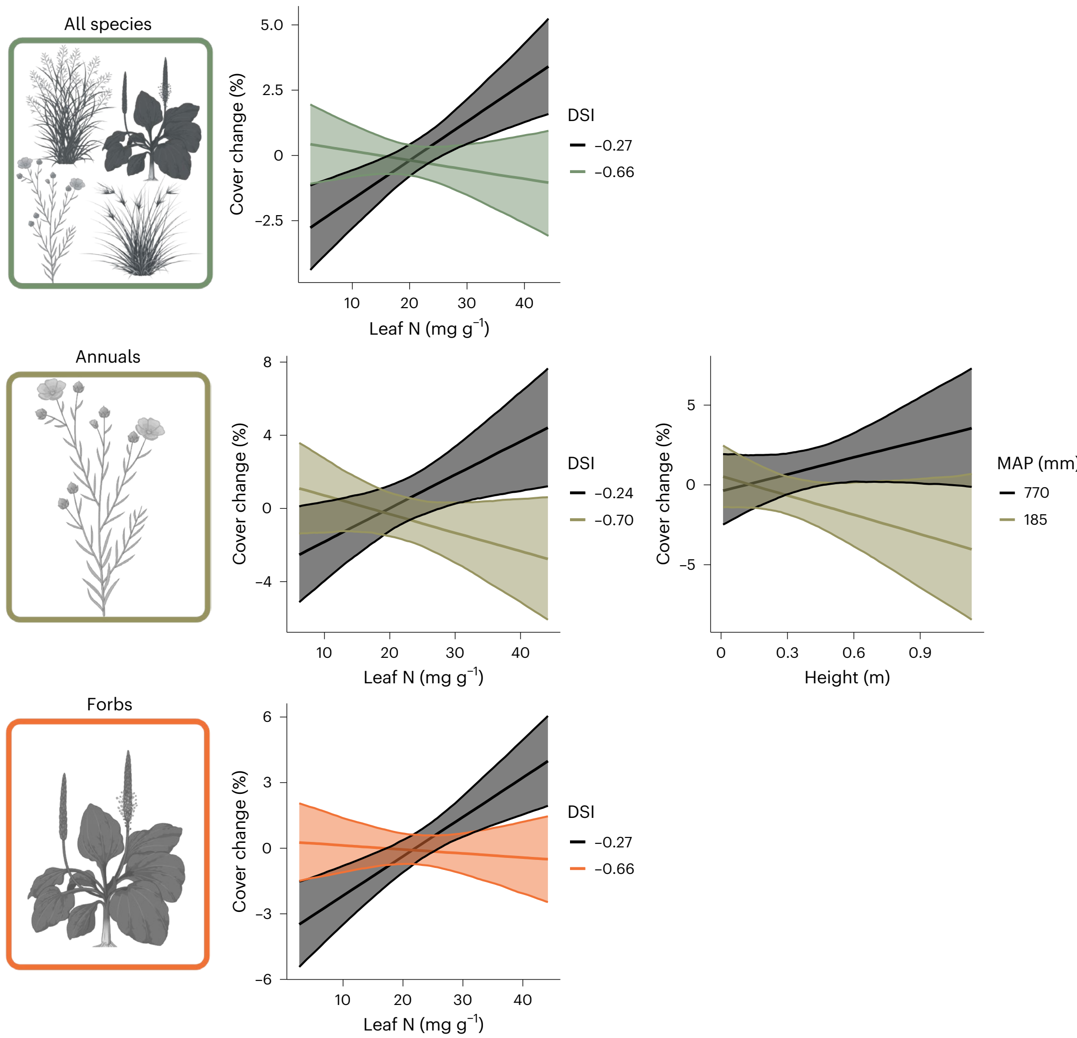

Fig. 4 | Interaction plots showing the predicted effects of significant two-way interactions between traits and the environmental variables DSI and MAP. All-species (n = 661 populations, R^2 = 6%), annual (n = 178 populations, R^2 = 17%) and forb (n = 410 populations, R^2 = 11%) plant groups had significant interactions between leaf N and DSI. More negative values of DSI correspond to more severe drought. There was also a significant interaction between height and MAP for the annual species group (R^2 = 12%). Trend lines represent the median relationships between cover change and the x-axis trait at the minimum (coloured line) and maximum (black line) values of the environmental variable; coloured envelopes represent 95% credible intervals. Values of the traits and environmental variables are back transformed. Plant graphics created with BioRender.com.

this association significantly differed from that of perennials (Extended Data Fig. 10 and Supplementary Fig. 1). We also found that environmental variables mediated the effects of traits on drought resistance, particularly in wetter sites (Supplementary Fig. 3). Drought resistance was higher for plant species in the annual, forb and all-species groups with higher leaf N in sites that experienced a less severe drought (higher DSI; Fig. 4). Similarly, taller annuals were more drought resistant in sites with higher MAP (Fig. 4).

Discussion

Few studies have examined how trait frameworks predict drought resistance while taking a whole-plant perspective across a broad range of species and sites[10]. Our study shows that forbs use diverse drought strategies, combining traits from conservation, collaboration and size gradients[12] in ways that challenge the traditional 'fast–slow' spectrum, although these patterns vary with environmental context. Leaf N concentration and height, two acquisitive (fast) traits, were related to drought resistance in forbs, which is consistent with a drought-escape strategy[6,36]. This suggests a benefit to fast-growing species that can escape drought by completing their life cycle in a short time, thus speeding up their phenology. High leaf N can also enhance water-use efficiency as greater investment in ribulose-1,5-bisphosphate carboxylase/oxygenase increases carboxylation efficiency[37]. Drought-resistant forbs, however, also showed high RTD, a conservative (slow) trait that may characterize robust taproots, particularly in perennial forbs, suggesting that these species leverage traits from both ends of the conservation gradient. These findings highlight that the capacity to deploy contrasting short-term strategies—coupling acquisitive traits for rapid growth with conservative root investments—may stabilize plant communities during intermittent drought[38]; however, prolonged drought could force shifts towards either extreme, decoupling trait coordination patterns observed under transient stress[39,40].

Taller forb species were less negatively impacted by short-term drought, significantly less so than taller graminoid species. This contradicts studies that report an advantage of small size under drought and in arid environments[38,41–44], as lower leaf area leads to less water transpired. Taller forbs may resist drought by possessing deeper roots, which is supported by positive correlations between height and rooting depth, particularly in annual forbs (r = 0.22; Supplementary Table 8). However, rooting depth was not a significant predictor of cover change in any plant group (Fig. 2 and Extended Data Fig. 1). Our inability to detect significant effects of rooting depth on drought response may stem from difficulties in accurately measuring this trait. However, the ability of this trait to predict how species will respond to drought has already been called into question (but see ref. 45). For example, using simulations, a previous study[46] showed that the distribution, functional plasticity and hydraulic conductivity of roots all influence aboveground biomass such that shifts in root distribution to surface soils without changes in rooting depth may outweigh the importance of having deeper roots.

Given the central role of roots in water uptake, we hypothesized that root traits would be strong predictors of drought response. However, our findings indicate that root traits generally predicted performance only in concert with other traits. Being taller was particularly advantageous in combination with high leaf N, and the benefits of high leaf N were amplified when more biomass was allocated belowground. RTD, which enhanced drought resistance in forbs, mediated the effect of SRL, such that species could achieve resistance through either high SRL and low RTD (thinner, less dense roots) or the opposite strategy. This supports the idea that multiple strategies can yield similar performance outcomes[24,25], and may explain discrepancies across studies that focus on single root traits or report weak relationships between root traits and performance[10,38,47,48]. Alternatively, root traits may play a larger role in long-term drought responses, rather than short-term extreme drought as analysed here[45]. While many of our trait values were sourced from site principal investigators or trait databases, several root traits (for example, N, RMF) are underrepresented in databases and were estimated through imputation. Databases and imputation do not capture the plasticity that species may show in response to variation in water availability in the field or genetically driven variation in traits across populations[49]. Incorporating trait plasticity into future studies, along with improved representation of sites from Africa, Asia and South America, will be important for understanding its impacts on resource acquisition, drought resistance and the predictive power of trait-based approaches[42,50].

Our results show that the relationship between plant traits and drought resistance is context dependent, with environmental conditions altering which strategies confer resistance. Specifically, the positive effect of leaf N on drought resistance in annuals and forbs was evident only under mild drought severity, and taller annuals were more drought resistant only at sites with higher MAP. These results suggest that the drought-escape strategy characteristic of many annuals is advantageous primarily under moderate stress, while at drier sites or under severe drought, more conservative traits probably play a greater role in drought resistance. Traits not examined here, such as osmotic potential, root distribution or root hair abundance, may become increasingly important as stress intensifies[42,51] and may also explain the high unexplained variance in our models. Our finding that complex interactions among traits and environmental variables shape drought resistance underscores the context dependency of trait–performance relationships, echoing and extending recent work in this area[24,25,52].

Trait–performance relationships were generally weaker or absent in graminoids and perennials, which may reflect the influence of additional factors such as stored reserves, clonal growth or unmeasured traits, which buffer their short-term drought responses[53]. The performance of perennial species, in particular, may require longer-term observation to capture how storage and economic traits interact to mitigate drought effects. By contrast, annuals did show links between traits and drought response, possibly because their fitness is more directly tied to immediate environmental conditions[54]. While our study did not incorporate intraspecific trait variation, local-scale variation and plastic responses may contribute to the variability observed in graminoid and perennial groups[39,42] and the low variance explained by these and other models in the study. Overall, these findings suggest that growth form and lifespan are important considerations when interpreting drought resistance traits, and that integrating these factors can improve predictions of species and community responses to increasing drought stress.

Our study, leveraging a globally distributed network of sites to identify how traits predict short-term drought response across a range of habitats and plant species types, shows that traits can predict plant performance in some plant species groups and that trait–performance relationships vary across environments and with drought severity. There is a growing consensus that the choice of trait matters in deciphering species' growth strategies[55,56], and our results suggest further context dependency in how trait frameworks can be applied to understand ecological processes. While individual traits contributed to drought resistance, our findings also highlight that interactions among key traits can further enhance plant performance during short-term drought. Although this analysis does not delve into the mechanisms by which abiotic and biotic factors drive variation in drought resistance across plots within sites, it opens up promising avenues for future research. Within-site analyses provide an opportunity to explore how microclimate, soil texture, drought history and the functional composition of neighbouring plants, for example, influence drought performance at community-level scales. To fully capture the variability of plant trait responses to drought, a combined understanding from detailed local-scale studies and globally replicated experiments can be pivotal.

Methods

Experimental design

We measured changes in plant species cover in response to experimentally imposed, short-term drought in Drought-Net's IDE. The IDE is a coordinated, distributed experiment, in which precipitation inputs are reduced passively across a range of grassland and shrubland sites to target a common level of statistical extremeness by allowing the proportional reduction in precipitation across sites to vary[5]. Precipitation reductions were determined individually for each site to impose statistically extreme levels (comparable to a 1-in-100-year drought at each site) based on historical precipitation records from the site or by using the Terrestrial Precipitation Analysis Tool[57]. Precipitation levels were reduced with passive rain-out shelters (with v-shaped or corrugated polycarbonate roofs), which work especially well in ecosystems with small-statured plants[58]. Percentage aerial cover was estimated for each species separately within a 1 × 1-m subplot located within each plot at each site[5]. As such, total absolute cover estimates could be greater than 100% for a plot and were used to calculate the change in cover. All sites participating in the IDE are required to use the same Drought-Net experimental protocols (https://droughtnet.weebly.com).

While there are over 140 sites participating in the IDE, only a subset of the sites met our criteria for inclusion in this analysis: (n = 63 sites; Fig. 1 and Supplementary Table 1) availability of pre- and post-treatment plant cover data, complete identification of plant species, and trait data. Like most grasslands and shrublands, many of these sites (62%) have a history of management (Supplementary Table 1). Only 9 of these sites have active management: mowing (4), burning (4) and grazing (1). We excluded plant cover and trait data for woody species in this study as cover change of woody species can be difficult to measure and their traits vary greatly across different life stages[59,60]; we could not ascertain the life stage associated with traits from trait databases[61,62]. In our full dataset, which included woody species, 53% of populations excluded by outlier trait analysis were woody populations, suggesting that woody species have more extreme trait values. Furthermore, due to their larger size and stored energy, woody species may be buffered from drought-induced effects in a single year[63,64].

All sites included in this study experienced approximately 1 year of experimental drought treatment and had both pre- and post-drought species cover data available. MAP was reported by site principal investigators for each of their sites[5]. The magnitude of drought experienced by each site differed, so we calculated an index to represent the actual

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severity of drought imposed at each site during the experimental period. Following a previous study[5], we calculated the amount of precipitation each site received in the year before plant cover collection, corrected for the number of days during which drought shelters were in place. We then multiplied this value by the site-reported percentage reduction in precipitation imposed by the drought treatment to estimate the total amount of precipitation received at each site ($\text{Precipitation}_{\text{drought}}$). We then compared the estimated precipitation received with the MAP and calculated the deviation from this number: DSI = ($\text{Precipitation}_{\text{drought}}$ − MAP)/MAP[5]. More negative values of DSI correspond to more severe drought (Supplementary Table 1).

Cover change quantification

We used a BACI (before, after, control, impact) design to determine the change in cover for each species at each site following ~1 year of drought[65]. We quantified the change in cover due to drought effects by subtracting the change in cover within control plots from the change in cover in droughted plots (($\text{Drought}_{\text{after}} - \text{Drought}_{\text{before}}$) − ($\text{Control}_{\text{after}} - \text{Control}_{\text{before}}$))[66]. If a population was absent at one time point, before or after the drought, but present at the other, its cover was set to zero when it was absent. Input percentage cover values were the means of each species across all replicated plots within each site. Outlier values of cover change (± 3 s.d. from the mean) were removed to prevent their skewing of model interpretation (2.5% of values). Final cover change values represent the effects of drought on droughted plots relative to control plots. Positive values indicate increased percentage cover in drought compared with control plots whereas negative values indicate decreased percentage cover in drought compared with control plots. Cover change varied between −21% and 21% across populations (Supplementary Table 2).

Functional traits

Nine traits were included in this study, namely, height, mass-based leaf nitrogen concentration (leaf N), mass-based root nitrogen concentration (root N), RMF, rooting depth, mean fine root diameter, fine RTD, specific leaf area (SLA) and fine SRL (Supplementary Table 2). Mean root diameter, RTD and SRL values were from fine root samples, those less than or equal to 2 mm in diameter. Values of root N came from total root samples. Different data sources often report different measurements of SLA, with the petiole included, an unknown status of petiole inclusion or the petiole excluded. We included all observations, regardless of measurement type, to maximize data coverage. If multiple types of measurements were available, we took the average. The traits were selected to balance above- and belowground traits, organ level and biomass allocation traits, and to capture integrated whole-plant strategies and trait trade-offs[12].

Trait data were gathered for species in a stepwise manner (Supplementary Table 3). First, IDE principal investigators were queried for trait data that corresponded to species at their local site; measurements were made according to ref. 67. Second, trait databases were queried including TRY[68], AusTraits[69], Global Root Traits (GRooT)[70] and observed values from CoRRE[71]. Approximately 52% of all trait data were sourced from IDE investigators (14%) or trait databases (38%). TRY, GRooT and CoRRE are global databases, while AusTraits includes data only for Australian plant species. CoRRE focuses on grassland species and combines data from various databases, including TRY, BIEN[72], AusTraits, TiP Leaf[73] and the China Plant Trait Database[74]. From AusTraits and GRooT, we used database-supplied mean values for each species. For TRY and CoRRE, we calculated mean values when multiple database submissions were available for a given trait of a species. More specifically, for TRY, we first calculated the mean within each dataset and then within each species. Lastly, we conducted comprehensive literature searches to populate remaining missing trait data for species when possible (Supplementary Table 3). We included only trait data for species from studies without experimental manipulations and those coming from mature individuals, omitting traits from seedlings.

Missing trait values were imputed using Bayesian hierarchical probabilistic matrix factorization (BHPMF[75]). This methodology imputes trait values based on the taxonomic hierarchy of the species and the correlation structure of the traits. Before imputation, all traits were $\log_{10}$- and z-transformed. Then, 50 imputations were performed, and the mean of these imputations was taken[76]. Imputation was performed using the default settings of the 'GapFilling' function in the BHPMF[77] package in R programming language[78]. Cross-validation was used during imputation such that observed data were randomly removed and imputed values were created for all populations, including those with observed measurements. This methodology allowed for the estimation of the quality of the imputed values; observed values were regressed against their imputed values and R^2 values were evaluated. Imputed trait values were of high quality with R^2 values ranging from 0.89 to 0.99 (Supplementary Fig. 4).

Finally, we removed outlier trait values (±3 s.d. from the mean). Overall, few trait data were removed, with 2.5% of rooting depth values being the highest percentage of data removed for any trait. If a species had observed cover data at multiple IDE study sites, we assigned the same trait values for all its occurrences. The R package Taxonstand[79] was used to verify that species' names were used consistently. Interspecific trait variation differed across traits, with some traits (leaf N, root N, SLA, SRL) showing wider ranges across species than others (height, rooting depth, RMF, RTD, mean root diameter; Supplementary Table 2).

We evaluated the effects of the nine traits, site MAP and DSI, and selected trait–trait and trait–environment interactions on cover change for 661 populations, from 421 species, across 63 IDE sites. We were also interested in understanding how these effects differed depending on lifespan (annuals: $n = 178$; perennials: $n = 462$) and growth form (graminoids: $n = 251$; forbs: $n = 410$). Thus, we analysed responses for eight plant groups: annuals, perennials, graminoids, forbs, annual forbs, perennial graminoids, perennial forbs and all species (Supplementary Tables 2 and 4–7). The annual group consisted of graminoids ($n = 44$), forbs ($n = 124$) and legumes ($n = 10$), while the larger perennial group included graminoids ($n = 205$), forbs ($n = 224$) and legumes ($n = 33$). Populations classified as biennial (10) or uncertain lifespan (11) were excluded from strictly annual or perennial plant groups. Analysis of the annual graminoids ($n = 44$) was not completed owing to limited sample size.

Statistical analyses

We fit a linear mixed-effects model using a Bayesian approach to each of the eight datasets to analyse trait effects on changes in cover between control and droughted plots of widely distributed sites. If a predictor in these models was significant, we then evaluated whether the relationship between the predictor and cover change significantly differed between the sets of groups, that is between lifespans, growth forms or the combinations of lifespans and growth forms. In addition, we fit models to each dataset to evaluate how interactions of traits associated with different trade-off gradients and allocation strategies are related to drought resistance, specifically interactions of leaf N versus height and rooting depth (conservation versus size[12,13]), leaf N versus RMF (conservation versus allocation[12,13,18]), and RTD versus SRL (conservation versus collaboration[12,14,15]). We also sought to understand how the environment influenced the association between these traits and drought resistance. To do so, we fitted models in which the trait interacted with MAP and DSI, separately for leaf N, height, rooting depth, RMF, RTD and SRL. All models were fitted using the brms package[80] with traits or trait combination, MAP and DSI as fixed effects or trait–environment interactions as fixed effects along with site and species as random effects. All predictors were centred and scaled before analysis. Fixed effects were given diffuse normal priors for slopes and default Student-t priors for intercepts; random effects were also given default Student-*t* priors. For each model, we ran four independent chains with random initial values for 2,000 iterations and a warm-up period of 1,000 iterations. All parameters were assessed for convergence (Rhat = 1) and were considered significant if their 95% credible interval did not overlap zero. In models evaluating the relationships among lifespans, growth forms or their combinations, the emmeans package[81] was used to estimate and compare marginal means among the sets of species. For each of the plant groups, we checked whether predictor variables were correlated with all correlations between −0.47 and 0.39 (Supplementary Table 8). We also checked for multicollinearity among model predictors using the performance package[82]; all variance inflation factors were <1.8, indicating low correlation[83]. For each model, we also visually inspected the residuals to ensure that model assumptions of normality of residuals and homogeneity of variance were met. We further tested for homogeneity of variance using the performance package[82].

Reporting summary

Further information on research design is available in the Nature Portfolio Reporting Summary linked to this article.

Data availability

All data used in this study are openly available via Zenodo at https://doi.org/10.5281/zenodo.17724111 (ref. 84). Source data are provided with this paper.

Code availability

Analyses in this study were conducted using customized scripts in R. The scripts are available via Zenodo at https://doi.org/10.5281/zenodo.17724111 (ref. 84).

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Author contributions

S.J.W., R.P.P. and J.L.F. conceived of the study. S.J.W., J.C.L., B.E.W., J.A., A.C.B., K.E.B., J.E.C., E.C.E., R.A.F., A.K.G., D.J.M.-W., R.P.P. and J.L.F contributed to early-stage discussions. S.J.W., J.C.L., B.E.W., J.A., A.C.B., K.E.B., J.E.C., E.C.E., R.A.F., A.K.G., D.J.M.-W. and J.L.F. collected and preprocessed trait data. T.J.O. and M.D.S. collected and preprocessed site data. H.A., A.B., K.H.B., E.W.B., K.M.B, J.F.C., M.C., C.N.C., K.C., M.H.C., S.X.C., J.C., A.C.C., T.D., J.S.D., A.E., N.E., T.G.W.F., F.A.F., S.V.H., Y.H., H.A.L.H., F.I., A.J., S.E.J., S.E.K., J.K., G.K.-D., A.K., E.G.L., M.E.L., M.G.L., A.L., C.M., J.W.M., A.S.M., S.M.M., G.S.N., U.N.N., R.C.O'C., T.J.O., B.B.O., R.O., M.P., P.L.P., G.P., A.P., J.M.P.-G., L.W.P., C.P.-R., S.A.P., S.M.P., Y.P., C.R., B.A.S., M.D.S., L.A.S., A.S., R.J.S., M.S., M.J.T., P.T., K.T., A.V., L.v.d.B., V.V., L.G.V., J.L.W., A.A.W., L.Y., A.L.Y., J.M.Z. and M.Z. contributed plant cover data. S.J.W. performed the analyses. S.J.W., J.C.L., B.E.W., R.P.P. and J.L.F. interpreted the results and drafted the initial paper. All co-authors reviewed the results and contributed to the writing and revision of the paper.

Competing interests

The authors declare no competing interests.

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Correspondence and requests for materials should be addressed to Samantha J. Worthy, Richard P. Phillips or Jennifer L. Funk.

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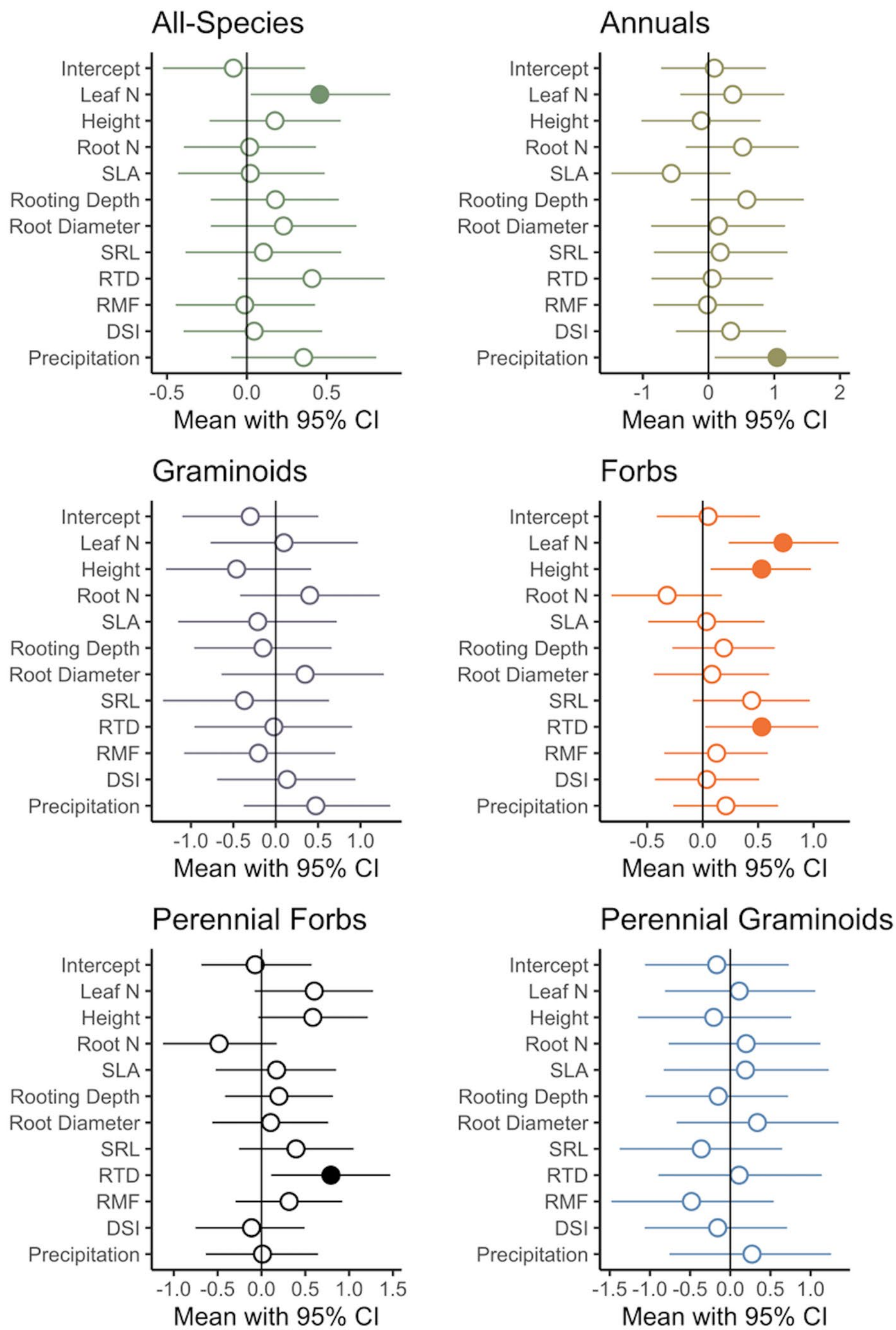
Samantha J. Worthy [1,2] ✉, **Justin C. Luong** [3,4], **Brooke E. Wainwright** [4], **Jonathan Aguiñaga** [1,5], **Harald Auge** [6,7], **Anca C. Barcu** [4], **Amgaa Batbaatar** [8,9], **Karen H. Beard** [10], **Edward W. Bork** [8], **Katherine E. Brafford** [4], **Kerry M. Byrne** [11], **James F. Cahill** [9], **Michele Carbognani** [12], **Cameron N. Carlyle** [8], **Karen Castillioni** [13], **Manjunatha H. Chandregowda** [14], Scott X. Chang [15], Jeff Chieppa[14], Amber C. Churchill [13,16], Jennifer E. Cribbs [4], Thomas Deola [17], Jeffrey S. Dukes [18,19], Anne Ebeling [20], Nico Eisenhauer [7,21], Elise C. Elwood[1], Regina A. Fairbanks[1,5], T'ai G. W. Forte [12], Flavia A. Funk[22,23], Anjum K. Gujral[4,5], Siri V. Haugum[24,25], Yann Hautier[26], Hugh A. L. Henry[27], Forest Isbell [13], Anke Jentsch [17], Samuel E. Jordan[28], Sally E. Koerner [29], Juergen Kreyling [30], György Kröel-Dulay [31], Andrew Kulmatiski [10], Eric G. Lamb [32], Michael E. Loik[33], María G. Longo[34], Alejandro Loydi [22,23], Dylan J. MacArthur-Waltz [5,35], Clara Milano [22], John W. Morgan[36], Akira S. Mori [37], Seth M. Munson [38], Gregory S. Newman[39], Uffe N. Nielsen [14], Rory C. O'Connor[40], Timothy J. Ohlert[41,42], Brooke B. Osborne[43], Rafael Otfinowski [44], Meelis Pärtel [45], Pablo L. Peri [46], Guadalupe Peter [47], Alessandro Petraglia [12], Juan M. Piñeiro-Guerra[48,49], Laura W. Ploughe[50], Cristy Portales-Reyes[51], Sally A. Power [14], Suzanne M. Prober[52], Yolanda Pueyo[53], Christiane Roscher [7,54], Bráulio A. Santos [49], Melinda D. Smith [42,55], Lara A. Souza [39], Andreas Stampfli [56,57], Rachel J. Standish [58], Marie Sünnemann [7,21], Michelle J. Tedder [59], Pål Thorvaldsen[60], Katja Tielbörger [61], Alejandro Valdecantos [62,63], Liesbeth van den Brink [61,64], Vigdis Vandvik [24], Liv G. Velle [60], Jennifer L. Williams [65], Amelia A. Wolf [66], Laura Yahdjian [67], Alyssa L. Young [29], Juan M. Zeberio[47], Michaela Zeiter[56,57,68], Richard P. Phillips [69] ✉ & Jennifer L. Funk [4] ✉

[1]Department of Evolution and Ecology, University of California, Davis, CA, USA. [2]The Holden Arboretum, Kirtland, OH, USA. [3]Department of Environmental Science, Policy, and Management, University of California, Berkeley, CA, USA. [4]Department of Plant Sciences, University of California, Davis, CA, USA. [5]Center for Population Biology, University of California, Davis, CA, USA. [6]Department of Community Ecology, Helmholtz Centre for Environmental Research—UFZ, Halle, Germany. [7]German Centre for Integrative Biodiversity Research (iDiv) Halle–Jenna–Leipzig, Leipzig, Germany. [8]Department of Agricultural, Food and Nutritional Science, University of Alberta, Edmonton, Alberta, Canada. [9]Department of Biological Sciences, University of Alberta, Edmonton, Alberta, Canada. [10]Department of Wildland Resources and the Ecology Center, Utah State University, Logan, UT, USA. [11]Department of Environmental Science and Management, California State Polytechnic University, Humboldt, Arcata, CA, USA. [12]Department of Chemistry, Life Sciences and Environmental Sustainability, University of Parma, Parma, Italy. [13]Department of Ecology, Evolution and Behavior, University of Minnesota, St. Paul, MN, USA. [14]Hawkesbury Institute for the Environment, Western Sydney University, Penrith, New South Wales, Australia. [15]Department of Renewable Resources, University of Alberta, Edmonton, Alberta, Canada. [16]Environmental Studies Program, Binghamton University—State University of New York, Binghamton, NY, USA. [17]Disturbance Ecology and Vegetation Dynamics, University of Bayreuth, Bayreuth Center of Ecology and Environmental Research (BayCEER), Bayreuth, Germany. [18]Department of Global Ecology, Carnegie Institution for Science, Stanford, CA, USA. [19]Department of Forestry and Natural Resources, Purdue University, West Lafayette, IN, USA. [20]Institute of Ecology and Evolution, University of Jena, Jena, Germany. [21]Institute of Biology, Leipzig University, Leipzig, Germany. [22]Centro de Recursos Naturales Renovables de la Zona Semiárida (CERZOS)—Consejo Nacional de Investigaciones Científicas y Técnicas de la República Argentina (CONICET), Bahía Blanca, Argentina. [23]Departamento de Biología, Bioquímica y Farmacia, Universidad Nacional del Sur (UNS), Bahía Blanca, Argentina. [24]Department of Biological Sciences, University of Bergen, Bergen, Norway. [25]The Heathland Centre, Alver, Norway. [26]Ecology and Biodiversity Group, Department of Biology, Utrecht University, Utrecht, Netherlands. [27]Department of Biology, University of Western Ontario, London, Ontario, Canada. [28]Chelan-Douglas Land Trust, Wenatchee, WA, USA. [29]Department of Biology, University of North Carolina Greensboro, Greensboro, NC, USA. [30]Institute of Botany and Landscape Ecology, Department of Experimental Plant Ecology, University of Greifswald, Greifswald, Germany. [31]HUN-REN Centre for Ecological Research, Institute of Ecology and Botany, Vácrátót, Hungary. [32]Department of Plant Sciences, University of Saskatchewan, Saskatoon, Saskatchewan, Canada. [33]Department of Environmental Studies, University of California, Santa Cruz, CA, USA. [34]Licenciatura en Diseño del Paisaje, Centro Universitario Regional Este, Universidad de la República Uruguay, Rocha, Uruguay. [35]Department of Entomology and Nematology, University of California, Davis, CA, USA. [36]Department of Ecological, Plant and Animal Sciences, La Trobe University, Melbourne, Victoria, Australia. [37]Research Center for Advanced Science and Technology, The University of Tokyo, Tokyo, Japan. [38]US Geological Survey, Southwest Biological Science Center, Flagstaff, AZ, USA. [39]School of Biological Sciences, University of Oklahoma, Norman, OK, USA. [40]USDA-ARS, Range and Meadow Forage Management Research Unit, Burns, OR, USA. [41]Department of Ecology and Evolutionary Biology, University of Colorado at Boulder, Boulder, CO, USA. [42]Department of Biology, Colorado State University, Fort Collins, CO, USA. [43]Department of Environment and Society, Utah State University, Logan, UT, USA. [44]Department of Biology, The University of Winnipeg, Winnipeg, Manitoba, Canada. [45]Institute of Ecology and Earth Sciences, University of Tartu, Tartu, Estonia. [46]Instituto Nacional de Tecnología Agropecuaria (INTA)–Universidad Nacional de la Patagonia Austral–CONICET, Río Gallegos, Argentina. [47]Universidad Nacional de Río Negro, Centro de Estudios Ambientales desde la NorPatagonia (CEANPa), Sede Atlántica—CONICET, Viedma, Argentina. [48]Departamento de Modelización Estadística de Datos e Inteligencia Artificial, Centro Universitario Regional Este, Universidad de la República, Montevideo, Uruguay. [49]Departamento de Sistemática e Ecologia, Universidade Federal da Paraíba, João Pessoa, Brazil. [50]Southern Colorado Plateau Network, Inventory and Monitoring Division, National Park Service, Flagstaff, AZ, USA. [51]Department of Biology, Saint Louis University, St. Louis, MO, USA. [52]Commonwealth Scientific and Industrial Research Organization (CSIRO) Environment, Canberra, Australian Capital Territory, Australia. [53]Departamento de Biodiversidad y Restauración, Instituto Pirenaico de Ecología (IPE), Consejo Superior de Investigaciones Científicas (CSIC), Zaragoza, Spain. [54]Department of Physiological Diversity, Helmholtz-Centre for Environmental Research—UFZ, Leipzig, Germany. [55]Graduate Degree Program in Ecology, Colorado State University, Fort Collins, CO, USA. [56]School of Agricultural, Forest and Food Sciences, Bern University of Applied Sciences, Zollikofen, Switzerland. [57]Oeschger Center for Climate Change Research, University of Bern, Bern, Switzerland. [58]School of Environmental and Conservation Sciences, Murdoch University, Perth, Western Australia, Australia. [59]School of Agriculture and Science, University of KwaZulu-Natal, Pietermaritzburg, South Africa. [60]Norwegian Institute of Bioeconomy Research (NIBIO), Trondheim, Norway. [61]Institute of Ecology and Evolution, Plant Ecology Group, University of Tübingen, Tübingen, Germany. [62]Departamento de Ecología, Universidad de Alicante, Alicante, Spain. [63]Instituto Multidisciplinar para el Estudio del Medio Ramón Margalef, Universidad de Alicante, Alicante, Spain. [64]ECOBIOSIS, Departamento de Botánica, Universidad de Concepción, Concepción, Chile. [65]Department of Geography, University of British Columbia, Vancouver, British Columbia, Canada. [66]Department of Integrative Biology, University of Texas at Austin, Austin, TX, USA. [67]Instituto de Investigaciones Fisiológicas y Ecológicas Vinculadas a la Agricultura (IFEVA), CONICET, Facultad de Agronomía, Universidad de Buenos Aires, Buenos Aires, Argentina. [68]Institute of Plant Sciences, University of Bern, Bern, Switzerland. [69]Department of Biology, Indiana University, Bloomington, IN, USA. ✉e-mail: sworthy@holdenfg.org; rpp6@iu.edu; funk@ucdavis.edu

 https://doi.org/10.1038/s41559-026-02989-4



Extended Data Fig. 1 | Model parameter estimates for each of the eight plant groups. Points represent the mean of the posterior distribution and lines represent the 95% credible intervals. Filled points indicate significant predictors of cover change where the 95% credible interval does not overlap zero. Traits include drought severity index (DSI), height (m), mass-based leaf nitrogen content (Leaf N, mg g^{-1}), mean annual precipitation (Precipitation, mm), rooting depth (m), root diameter (mm), mass-based root nitrogen content (Root N, mg g^{-1}), root mass fraction (RMF, g g^{-1}), root tissue density (RTD, g cm^{-3}), specific leaf area (SLA, m^2 kg^{-1}), and specific root length (SRL, m g^{-1}).

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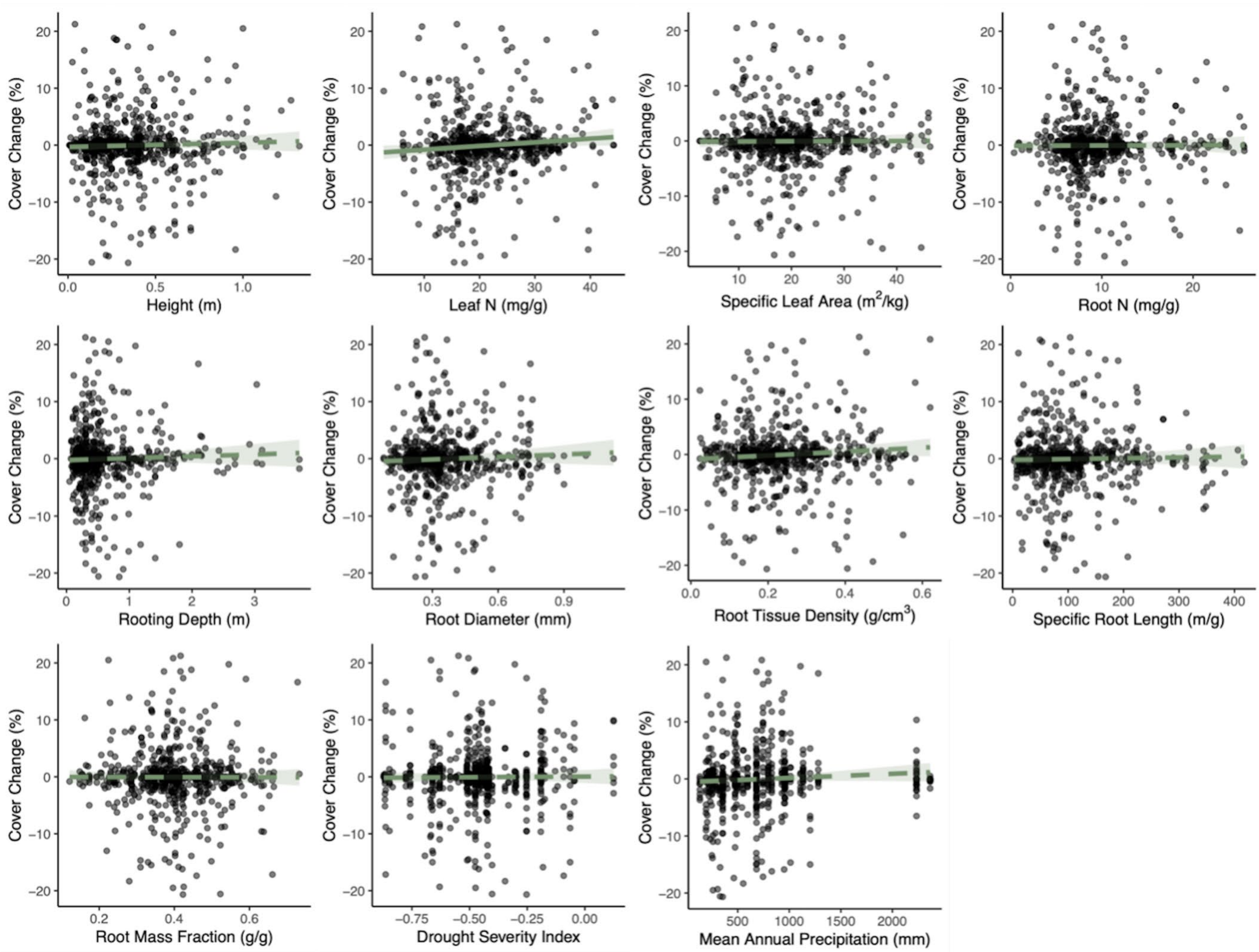

Extended Data Fig. 2 | Plots displaying the effects of traits and environmental variables on change in population cover for the all-species group (n = 661 populations, species = 421, R^2 = 6%). Trend lines represent median conditional effects of the trait, dashed lines are nonsignificant relationships and solid lines are significant relationships, colored envelopes represent 95% credible intervals. Opaque gray points are observed data points where darker points indicate overlap among points. Values on the x-axes are back-transformed.

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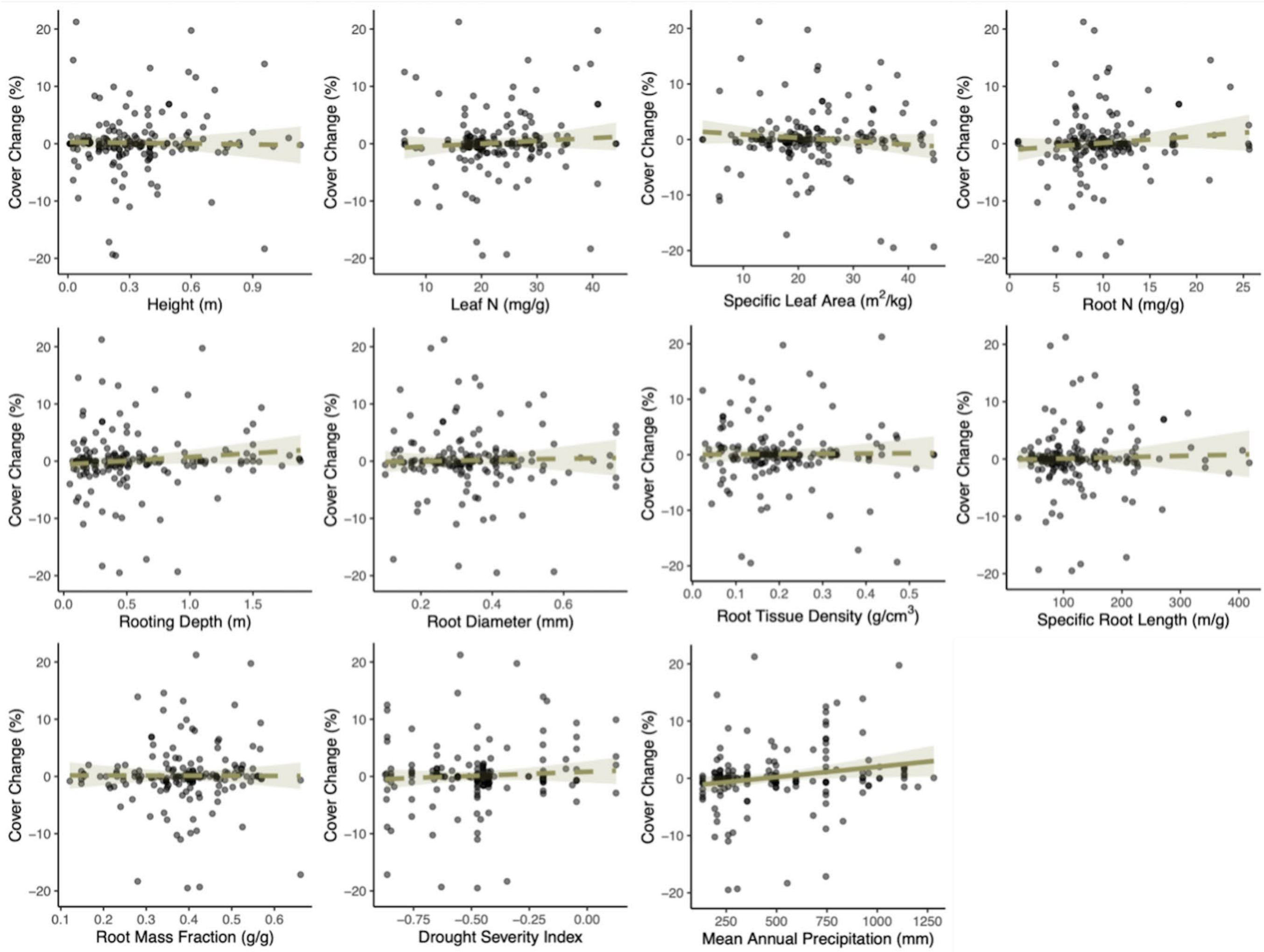

Extended Data Fig. 3 | Plots displaying the effects of traits and environmental variables on change in population cover for the annual species group (n = 178 populations, species = 121, R^2 = 15%). Trend lines represent median conditional effects of the trait, dashed lines are nonsignificant relationships and solid lines are significant relationships, colored envelopes represent 95% credible intervals. Opaque gray points are observed data points where darker points indicate overlap among points. Values on the x-axes are back-transformed.

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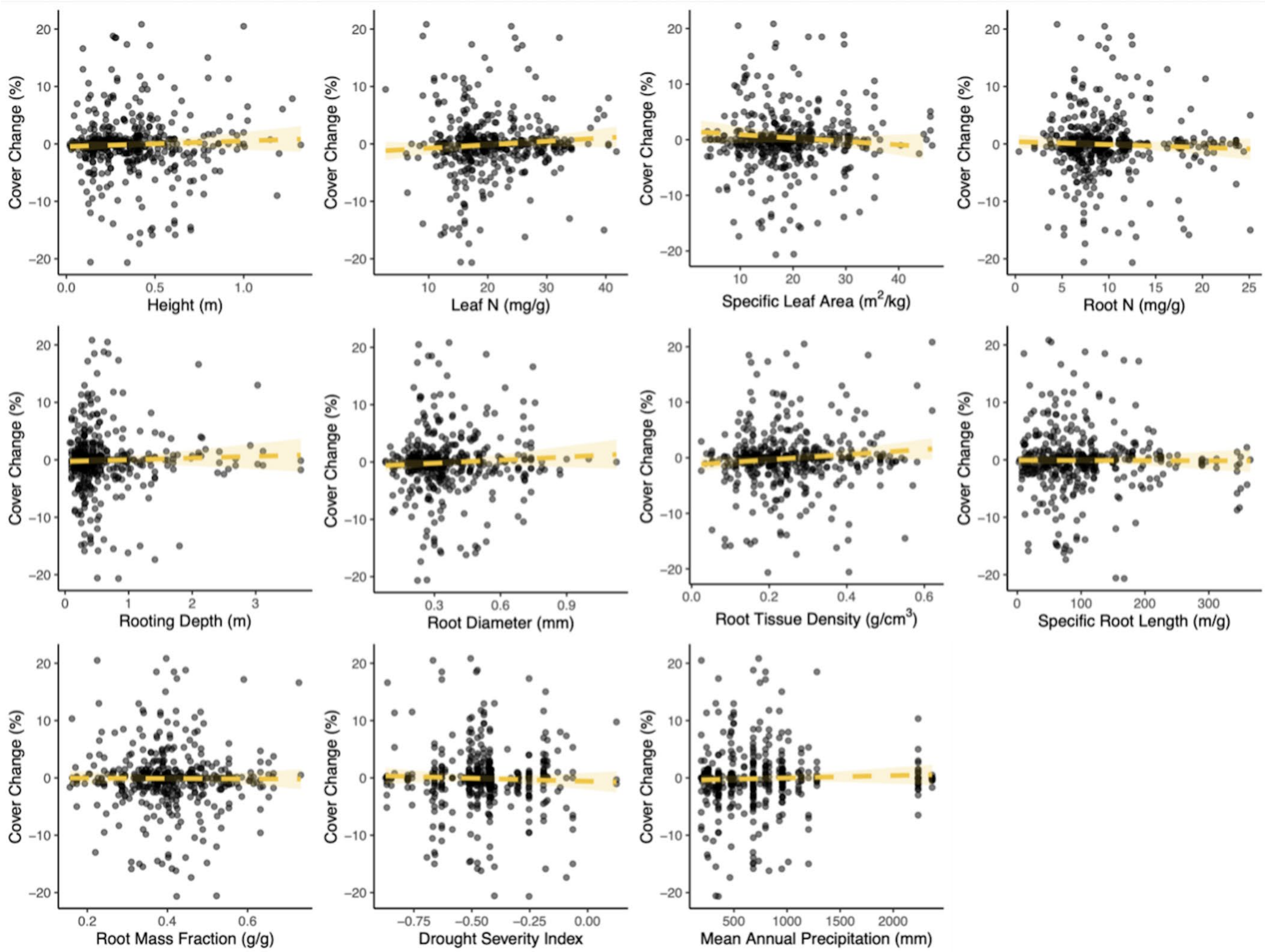

Extended Data Fig. 4 | Plots displaying the effects of traits and environmental variables on change in population cover for the perennial species group (n = 462 populations, species = 292, R^2 = 8%). Trend lines represent median conditional effects of the trait, dashed lines are nonsignificant relationships and solid lines are significant relationships, colored envelopes represent 95% credible intervals. Opaque gray points are observed data points where darker points indicate overlap among points. Values on the x-axes are back-transformed.

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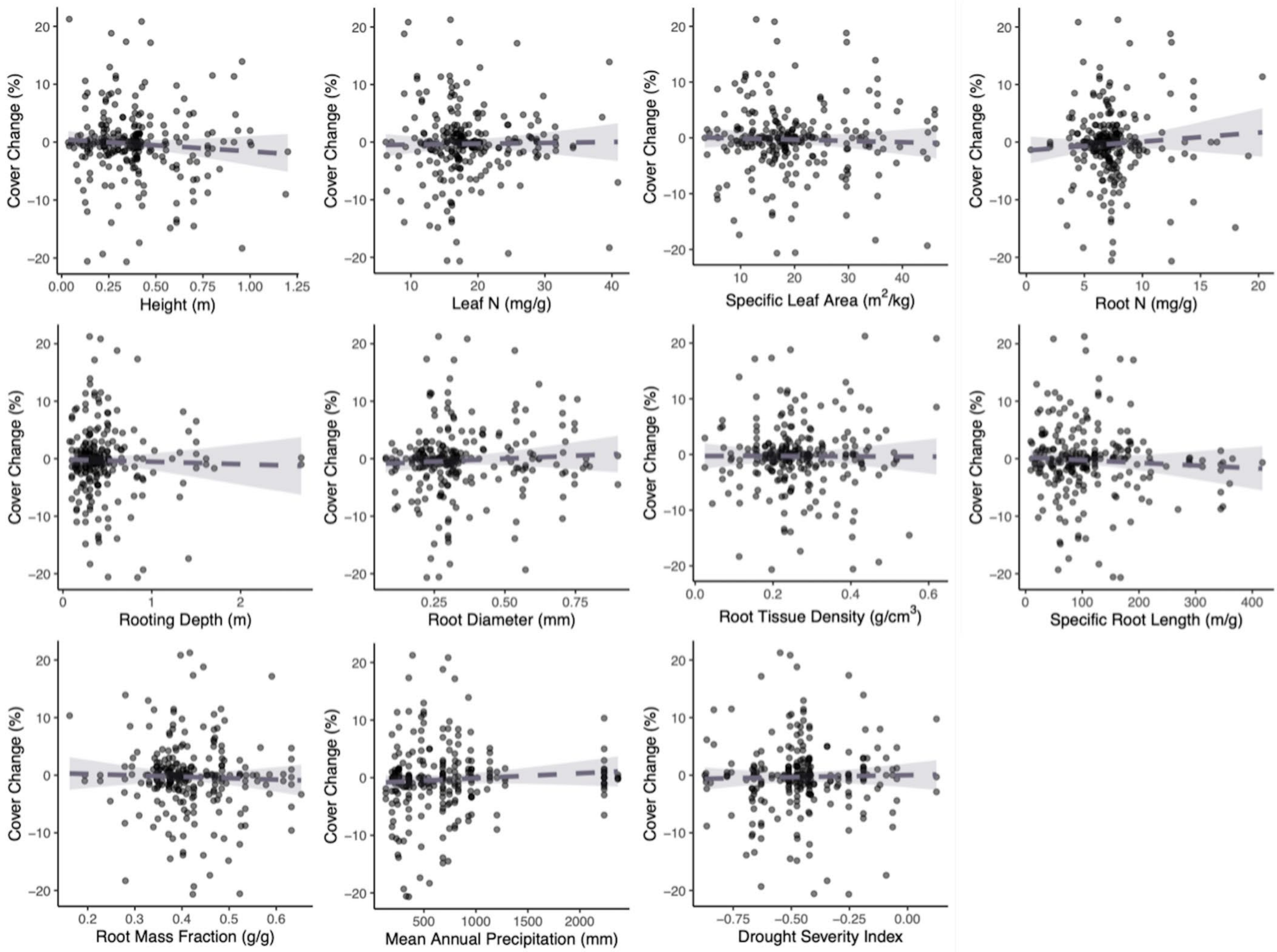

Extended Data Fig. 5 | Plots displaying the effects of traits and environmental variables on change in population cover for the graminoid species group (n = 251 populations, species = 151, R^2 = 11%). Trend lines represent median conditional effects of the trait, dashed lines are nonsignificant relationships and solid lines are significant relationships, colored envelopes represent 95% credible intervals. Opaque gray points are observed data points where darker points indicate overlap among points. Values on the x-axes are back-transformed.

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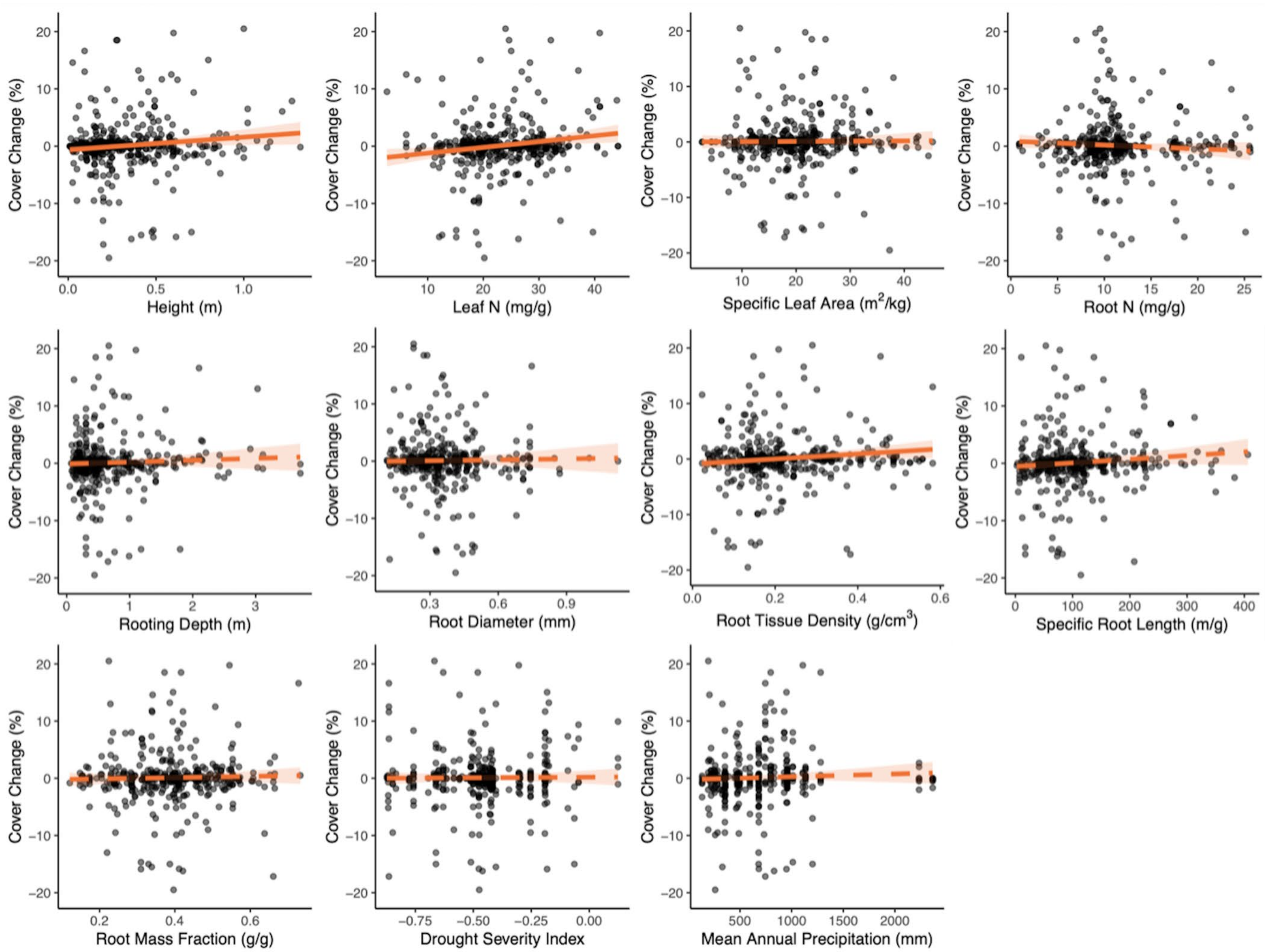

Extended Data Fig. 6 | Plots displaying the effects of traits and environmental variables on change in population cover for the forb species group (n = 410 populations, species = 270, R^2 = 11%). Trend lines represent median conditional effects of the trait, dashed lines are nonsignificant relationships and solid lines are significant relationships, colored envelopes represent 95% credible intervals. Opaque gray points are observed data points where darker points indicate overlap among points. Values on the x-axes are back-transformed.

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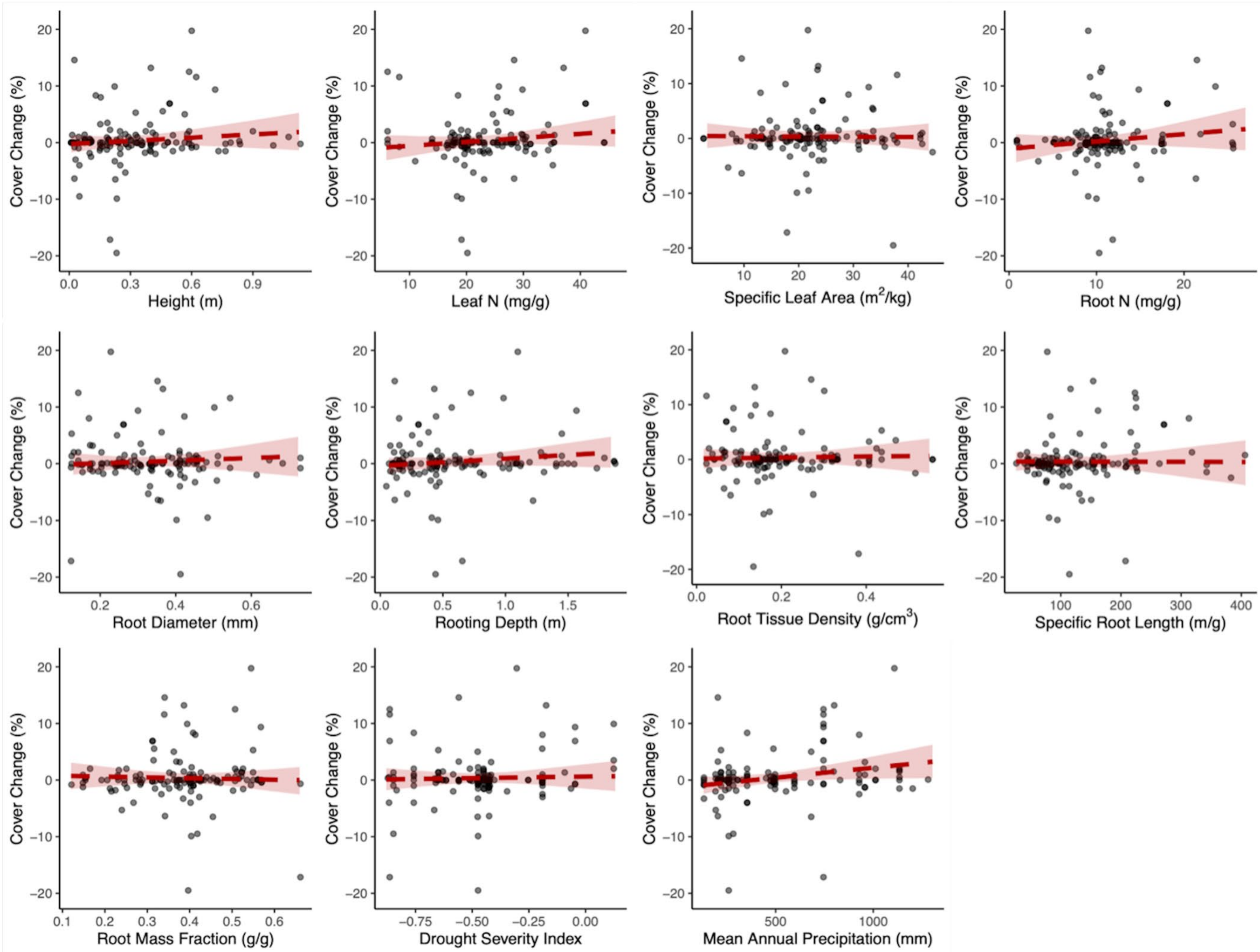

Extended Data Fig. 7 | Plots displaying the effects of traits and environmental variables on change in population cover for the annual forb species group (n = 134 populations, species = 95, R^2 = 23%). Trend lines represent median conditional effects of the trait, dashed lines are nonsignificant relationships and solid lines are significant relationships, colored envelopes represent 95% credible intervals. Opaque gray points are observed data points where darker points indicate overlap among points. Values on the x-axes are back-transformed.

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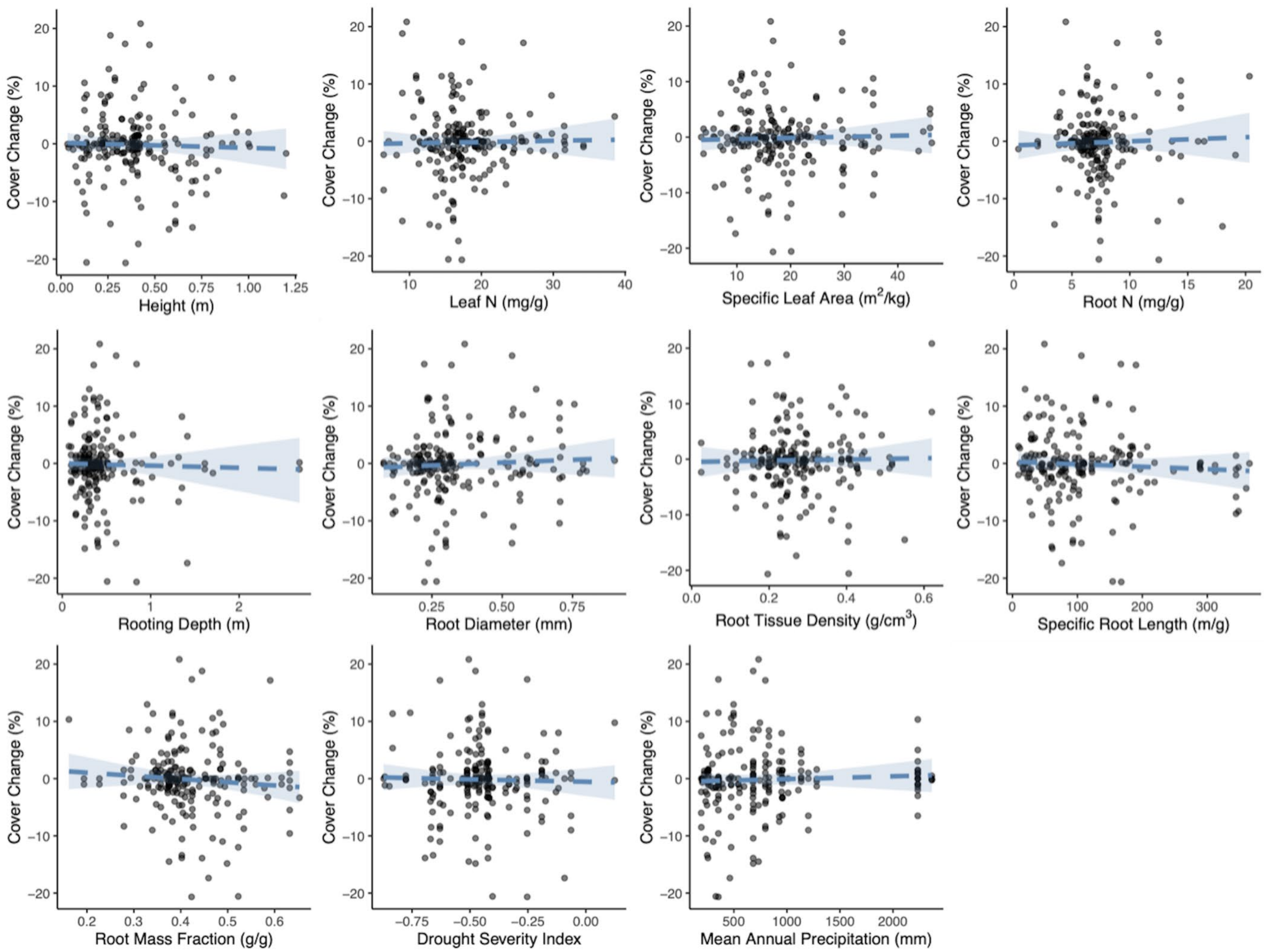

Extended Data Fig. 8 | Plots displaying the effects of traits and environmental variables on change in population cover for the perennial graminoid species group (n = 205 populations, species = 123, R^2 = 15%). Trend lines represent median conditional effects of the trait, dashed lines are nonsignificant relationships and solid lines are significant relationships, colored envelopes represent 95% credible intervals. Opaque gray points are observed data points where darker points indicate overlap among points. Values on the x-axes are back-transformed.

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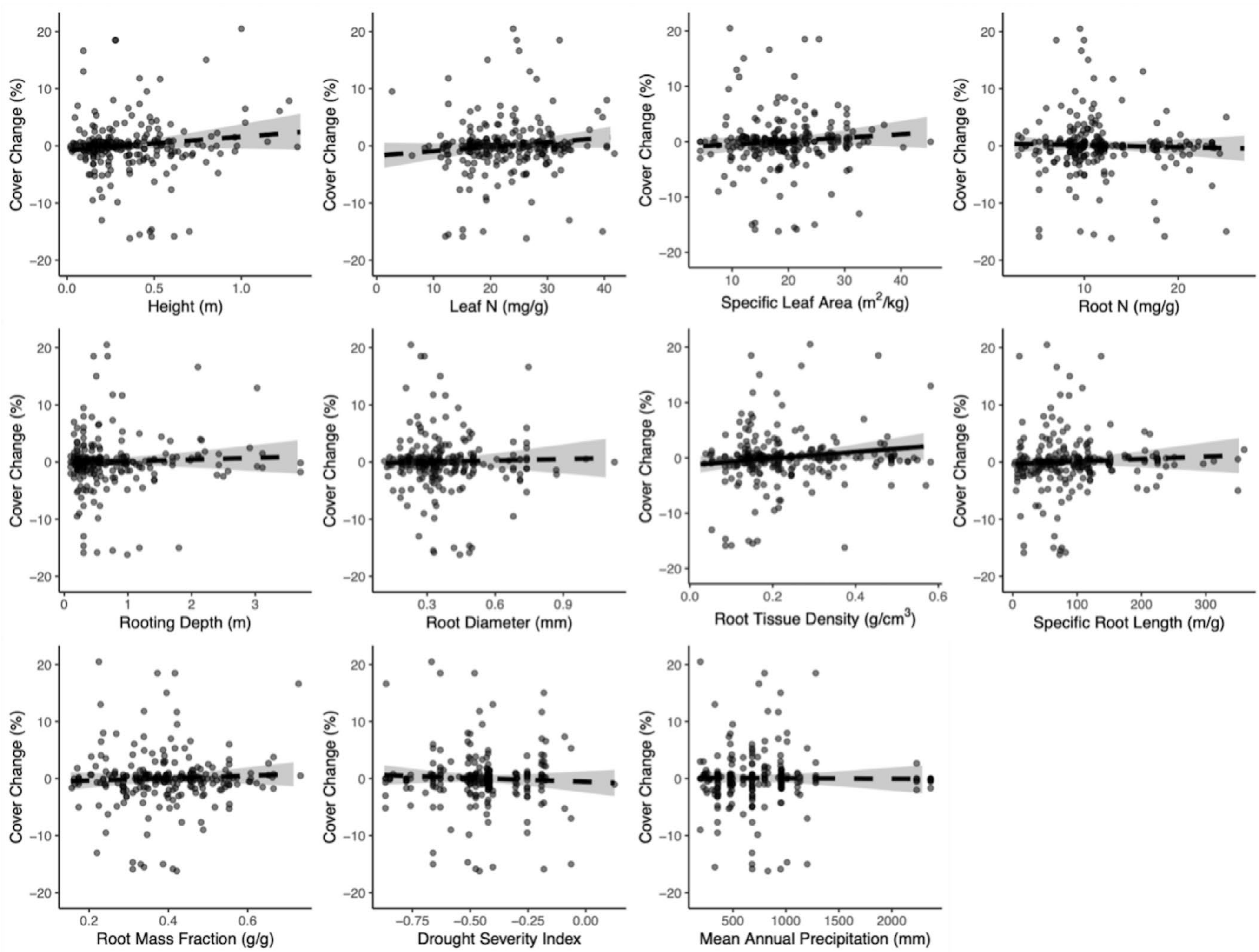

Extended Data Fig. 9 | Plots displaying the effects of traits and environmental variables on change in population cover for the perennial forb species group (n = 257 populations, species = 169, R^2 = 15%). Trend lines represent median conditional effects of the trait, dashed lines are nonsignificant relationships and solid lines are significant relationships, colored envelopes represent 95% credible intervals. Opaque gray points are observed data points where darker points indicate overlap among points. Values on the x-axes are back-transformed.

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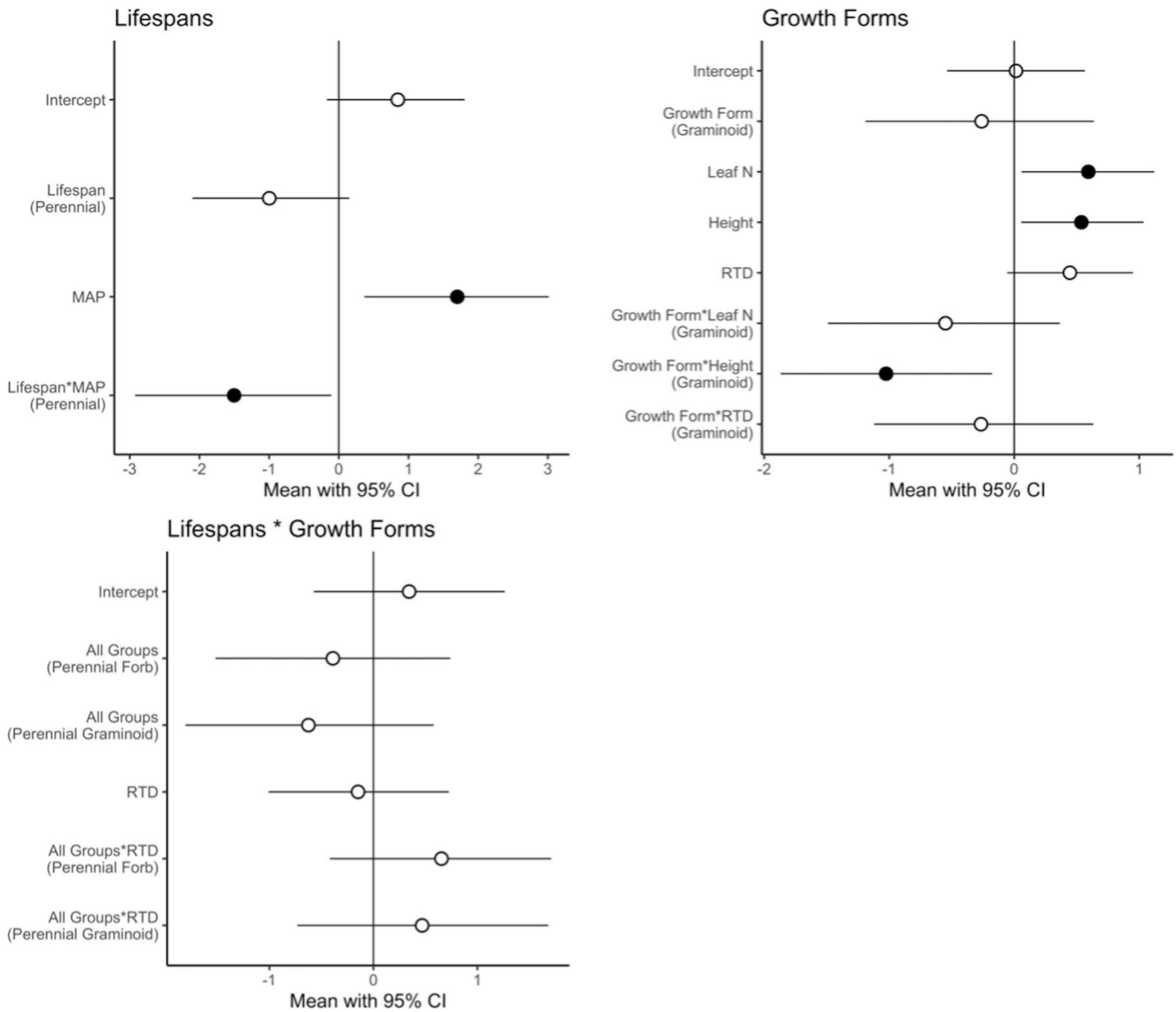

Extended Data Fig. 10 | Parameter estimates for models comparing relationships between trait or environment variables and cover change among lifespans, growth forms, or the combinations of lifespans and growth forms. These models were only fitted with predictors that were previously noted as significant in the group specific models (Extended Data Fig. 1). Points represent the mean of the posterior distribution and lines represent the 95% credible intervals. Filled points indicate significant predictors of cover change where the 95% credible interval does not overlap zero. Reference groups for the models were annual (lifespan model), forb (growth form model), and annual forb (lifespan*growth form model). Traits include height (m), mass-based leaf nitrogen content (Leaf N, mg g^{-1}), mean annual precipitation (MAP, mm), and root tissue density (RTD, g cm^{-3}).

nature portfolio

Corresponding author(s): Samantha J. Worthy

Last updated by author(s): 11/26/2025

Reporting Summary

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Statistics

For all statistical analyses, confirm that the following items are present in the figure legend, table legend, main text, or Methods section.

n/a	Confirmed	
☐	☒	The exact sample size (n) for each experimental group/condition, given as a discrete number and unit of measurement
☐	☒	A statement on whether measurements were taken from distinct samples or whether the same sample was measured repeatedly
☐	☒	The statistical test(s) used AND whether they are one- or two-sided *Only common tests should be described solely by name; describe more complex techniques in the Methods section.*
☐	☒	A description of all covariates tested
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☐	☒	A full description of the statistical parameters including central tendency (e.g. means) or other basic estimates (e.g. regression coefficient) AND variation (e.g. standard deviation) or associated estimates of uncertainty (e.g. confidence intervals)
☐	☒	For null hypothesis testing, the test statistic (e.g. F, t, r) with confidence intervals, effect sizes, degrees of freedom and P value noted *Give P values as exact values whenever suitable.*
☐	☒	For Bayesian analysis, information on the choice of priors and Markov chain Monte Carlo settings
☐	☒	For hierarchical and complex designs, identification of the appropriate level for tests and full reporting of outcomes
☐	☒	Estimates of effect sizes (e.g. Cohen's d, Pearson's r), indicating how they were calculated

Our web collection on statistics for biologists contains articles on many of the points above.

Software and code

Policy information about availability of computer code

Data collection	No software was used to collect the data. All data is available at https://doi.org/10.5281/zenodo.17724111.
Data analysis	All custom code is available https://doi.org/10.5281/zenodo.17724111. All analyses were completed in R version 4.2.3. Packages used to for data formatting, analyses, and plotting: tidyverse version 2.0.0, Taxonstand version 2.4, stringr version 1.5.1, corrplot version 0.94, devtools version 2.4.5, BHPMF version 1.1, abind version 1.4.8, ggpubr version 0.6.0, cowplot version 1.1.1, brms version 2.21.0, emmeans version 1.8.7, performance version 0.15.0, pRecipe version 3.0.2, giscoR version 0.6.1, raster version 3.6.26, terra version 1.7.65, rayshader version 0.35.7, classInt version 0.4.10, austraits package version 2.2.3

For manuscripts utilizing custom algorithms or software that are central to the research but not yet described in published literature, software must be made available to editors and reviewers. We strongly encourage code deposition in a community repository (e.g. GitHub). See the Nature Portfolio guidelines for submitting code & software for further information.

Data

Policy information about availability of data

All manuscripts must include a data availability statement. This statement should provide the following information, where applicable:

- Accession codes, unique identifiers, or web links for publicly available datasets
- A description of any restrictions on data availability
- For clinical datasets or third party data, please ensure that the statement adheres to our policy

All data used in this study are openly available from Zenodo at https://doi.org/10.5281/zenodo.1772411186. Source data are provided with this paper.

Research involving human participants, their data, or biological material

Policy information about studies with human participants or human data. See also policy information about sex, gender (identity/presentation), and sexual orientation and race, ethnicity and racism.

Reporting on sex and gender	NA
Reporting on race, ethnicity, or other socially relevant groupings	NA
Population characteristics	NA
Recruitment	NA
Ethics oversight	NA

Note that full information on the approval of the study protocol must also be provided in the manuscript.

Field-specific reporting

Please select the one below that is the best fit for your research. If you are not sure, read the appropriate sections before making your selection.

☐ Life sciences ☐ Behavioural & social sciences ☒ Ecological, evolutionary & environmental sciences

For a reference copy of the document with all sections, see nature.com/documents/nr-reporting-summary-flat.pdf

Ecological, evolutionary & environmental sciences study design

All studies must disclose on these points even when the disclosure is negative.

Study description	We measured changes in plant species cover in response to experimentally-imposed, short-term drought in Drought-Net's International Drought Experiment (IDE). We assessed how of nine above- and belowground traits, site mean annual precipitation and drought severity, and selected trait-trait and trait-environment interactions affected cover change across growth forms (graminoids and forbs), lifespans (annuals and perennials), and all populations. The IDE is a coordinated, distributed experiment, where precipitation inputs are reduced passively across a range of grassland and shrubland sites in order to target a common level of statistical extremeness by allowing the proportional reduction in precipitation across sites to vary. Precipitation reductions were determined individually for each site in order to impose statistically extreme levels (comparable to a 1-in-100 year drought at each site) based on historical precipitation records from the site or by using the Terrestrial Precipitation Analysis Tool. Precipitation levels were reduced with passive rain-out shelters (with v-shaped or corrugated polycarbonate roofs), which work especially well in ecosystems with small-statured plants. Percentage aerial cover was estimated for each species separately within a 1 x 1 m subplot located within each plot at each site. As such, total absolute cover estimates could be greater than 100% for a plot and were used to calculate the change in cover. All sites participating in the IDE are required to use the same Drought-Net experimental protocols (https://droughtnet.weebly.com).
Research sample	We used a BACI (before, after, control, impact) design to determine the relative change in cover for each species at each site following ~ one year of drought. We quantified the change in cover due to drought effects by subtracting the change in cover (%) within control plots from the change in cover (%) in droughted plots [(DroughtAFTER – DroughtBEFORE) – (ControlAFTER – ControlBEFORE)]. If a population was absent at one time point, before or after the drought, but present at the other, its cover was set at zero when absent. Input percent cover values were means of each species across all replicated plots within each site. Outlier values of cover change (± 3 SD from mean) were removed to prevent their skew on model interpretation (2.5% of values). We evaluated the effects of nine above- and belowground traits, site mean annual precipitation and drought severity, and selected trait-trait and trait-environment interactions on cover change for 661 populations, from 421 species, across 63 IDE sites. We were also interested in understanding how these effects differed depending on lifespan (annuals: n = 178; perennials: n = 462), and growth form (graminoids: n = 251; forbs: n = 410).). Thus, we analyzed responses for eight plant groups: Annuals, Perennials, Graminoids, Forbs, Annual Forbs, Perennial Graminoids, Perennial Forbs, and All species ((Supplemental Tables 2 and 4-7). The annual group consisted of graminoids (n = 44), forbs (n = 124), and legumes (n = 10), while the larger perennial group included graminoids (n =

205), forbs (n = 224), and legumes (n = 33). Populations classified as biennial (10) or uncertain lifespan (11) were excluded from strictly annual or perennial plant groups. Analysis of the annual graminoids (n = 44) was not completed due to limited sample size.

Sampling strategy	All sites participating in the IDE are required to use the same Drought-Net experimental protocols (https://droughtnet.weebly.com). While there are over 140 sites participating in the IDE, we chose a subset of the sites (n = 63 sites) owing to a combination of availability of pre- and post-treatment plant cover data, complete identification of plant species, and trait data. We excluded plant cover and trait data for woody species in this research as cover change of woody species can be difficult to measure and their traits vary greatly across different life stages; we could not ascertain the life stage associated with traits from trait databases. In our full dataset, which included woody species, 53% of populations excluded by outlier trait analysis were woody populations, suggesting that woody species have more extreme trait values. Further, due to their larger size and stored energy, woody species may be buffered from drought-induced effects in a single year.
Data collection	Percentage aerial cover was estimated for each species separately within a 1 x 1 m subplot located within each plot at each site. As such, total absolute cover estimates could be greater than 100% for a plot and were used to calculate the change in cover. All sites participating in the IDE are required to use the same Drought-Net experimental protocols (https://droughtnet.weebly.com). Trait data were gathered for species in a stepwise manner (Supplemental Table 3). First, IDE principal investigators were queried for trait data that corresponded to species at their local site; measurements were made according to. Second, trait databases were queried including TRY, AusTraits, Global Root Traits (GRooT), and observed values from CoRRE. Approximately, 52% of all trait data was sourced from IDE investigators (14%) or trait databases (38%). TRY, GRooT and CoRRE are global databases, while AusTraits only includes data for Australian plant species. CoRRE focuses on grassland species and combines data from various databases, including TRY, BIEN, AusTraits, TiP Leaf, and the China Plant Trait Database. From AusTraits and GRooT, we used database-supplied mean values for each species. For TRY and CoRRE, we calculated mean values when multiple database submissions were available for a given trait of a species. More specifically, for TRY, we first calculated the mean within each dataset and then within each species. Lastly, we conducted comprehensive literature searches to populate remaining missing trait data for species when possible (Supplemental Table 3). We only included trait data for species from studies without experimental manipulations and those coming from mature individuals, omitting traits from seedlings. Mean annual precipitation (MAP) was reported by site PIs for each of their sit es. Following Smith et al. (2024), we calculated the amount of precipitation each site received in the year prior to plant cover collection, corrected for the number of days during which drought shelters were in place. We then multiplied this value by the site-reported percent reduction in precipitation imposed by the drought treatment to estimate the total amount of precipitation received at each site (PrecipitationDROUGHT). We then compared the estimated precipitation received to MAP and calculated the deviation from this number: Drought Severity Index (DSI) = (PrecipitationDROUGHT – MAP)/MAP.
Timing and spatial scale	All sites included in this study experienced approximately one year of experimental drought treatment and had both pre- and post-drought species cover data available. These sites are distributed globally in grasslands and shrublands. A map is included in the manuscript and country information of each site is included in the supplement.
Data exclusions	While there are over 140 sites participating in the IDE, we chose a subset of the sites (n = 63 sites) owing to a combination of availability of pre- and post-treatment plant cover data, complete identification of plant species, and trait data. We excluded plant cover and trait data for woody species in this research as cover change of woody species can be difficult to measure and their traits vary greatly across different life stages; we could not ascertain the life stage associated with traits from trait databases. In our full dataset, which included woody species, 53% of populations excluded by outlier trait analysis were woody populations, suggesting that woody species have more extreme trait values. Further, due to their larger size and stored energy, woody species may be buffered from drought-induced effects in a single year. All sites included in this study experienced approximately one year of experimental drought treatment and had both pre- and post-drought species cover data available. We only included trait data for species from studies without experimental manipulations and those coming from mature individuals, omitting traits from seedlings. Outlier values of cover change (± 3 SD from the mean) were removed to prevent their skewing of model interpretation (2.5% of values). Finally, we removed outlier trait values (± 3 SD from the mean). Overall, few trait data were removed, with 2.5% of rooting depth values being the highest percentage of data removed for any trait.
Reproducibility	All sites participating in the IDE are required to use the same Drought-Net experimental protocols (https://droughtnet.weebly.com). All code and data used in this study are publicly available at https://doi.org/10.5281/zenodo.17724111
Randomization	We evaluated the effects of the nine traits, site MAP and DSI, and selected trait-trait and trait-environment interactions on cover change for 661 populations, from 421 species, across 63 IDE sites. We were also interested in understanding how these effects differed depending on lifespan (annuals: n = 178; perennials: n = 462), and growth form (graminoids: n = 251; forbs n = 410). Thus, we analyzed responses for eight plant groups: Annuals, Perennials, Graminoids, Forbs, Annual Forbs, Perennial Graminoids, Perennial Forbs, and All species ((Supplemental Tables 2 and 4-7). The annual group consisted of graminoids (n = 44), forbs (n = 124), and legumes (n = 10), while the larger perennial group included graminoids (n = 205), forbs (n = 224), and legumes (n = 33). Populations classified as biennial (10) or uncertain lifespan (11) were excluded from strictly annual or perennial plant groups. Analysis of the annual graminoids (n = 44) was not completed due to limited sample size.
Blinding	Blinding was not relevant to this research as we analyzed the data in groups based on plant lifespan and growth form and were specifically trying to understand the impacts of the drought treatment versus control.

Did the study involve field work? ☒ Yes ☐ No

Field work, collection and transport

Field conditions	Mean annual precipitation values and drought severity values for each site are reported in the manuscript.
Location	The 63 sites included are distributed globally. A map is included in the manuscript and country information of each site is included in

Location	the supplement.
Access & import/export	Plant samples were not imported or exported. All data were collected at each site and only these values were reported.
Disturbance	Limited disturbance was caused by the experiment.

Reporting for specific materials, systems and methods

We require information from authors about some types of materials, experimental systems and methods used in many studies. Here, indicate whether each material, system or method listed is relevant to your study. If you are not sure if a list item applies to your research, read the appropriate section before selecting a response.

Materials & experimental systems

n/a	Involved in the study
☒	☐ Antibodies
☒	☐ Eukaryotic cell lines
☒	☐ Palaeontology and archaeology
☒	☐ Animals and other organisms
☒	☐ Clinical data
☒	☐ Dual use research of concern
☐	☒ Plants

Methods

n/a	Involved in the study
☒	☐ ChIP-seq
☒	☐ Flow cytometry
☒	☐ MRI-based neuroimaging

Dual use research of concern

Policy information about dual use research of concern

Hazards

Could the accidental, deliberate or reckless misuse of agents or technologies generated in the work, or the application of information presented in the manuscript, pose a threat to:

No	Yes
☒	☐ Public health
☒	☐ National security
☒	☐ Crops and/or livestock
☒	☐ Ecosystems
☒	☐ Any other significant area

Experiments of concern

Does the work involve any of these experiments of concern:

No	Yes
☒	☐ Demonstrate how to render a vaccine ineffective
☒	☐ Confer resistance to therapeutically useful antibiotics or antiviral agents
☒	☐ Enhance the virulence of a pathogen or render a nonpathogen virulent
☒	☐ Increase transmissibility of a pathogen
☒	☐ Alter the host range of a pathogen
☒	☐ Enable evasion of diagnostic/detection modalities
☒	☐ Enable the weaponization of a biological agent or toxin
☒	☐ Any other potentially harmful combination of experiments and agents

Plants

Seed stocks	No seed stocks were used. The study only includes naturally occurring plants.
Novel plant genotypes	No novel plant genotypes were produced.
Authentication	No seed stocks were used so no authentication procedures were used.