Small rainfall changes drive substantial changes in plant coexistence

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Although precipitation patterns have long been known to shape plant distributions[1], the effect of changing climate on the interactions of species and therefore community composition is far less understood[2,3]. Here, we explored how changes in precipitation alter competitive dynamics via direct effects on individual species, as well as by the changing strength of competitive interactions between species, using an annual grassland community in California. We grew plants under ambient and reduced precipitation in the field to parameterize a competition model[4] with which we quantified the stabilizing niche and fitness differences that determine species coexistence in each rainfall regime. We show that reduced precipitation had little direct effect on species grown alone, but it qualitatively shifted predicted competitive outcomes for 10 of 15 species pairs. In addition, species pairs that were functionally more similar were less likely to experience altered outcomes, indicating that functionally diverse communities may be most threatened by changing interactions. Our results highlight how important it is to account for changes to species interactions when predicting species and community response to global change.

For centuries, ecologists and biogeographers have understood that plants respond to climate[1], and this forms the foundation for our understanding of plant responses to global change. However, we know much less about how changing interactions between species may help or hinder the capacity of species to persist given the shifting location of their preferred climate[2,5]. For a species to persist in a community affected by global change, it must not only survive the direct physiological effects of climate change but also the effects of altered densities, interaction strengths and identities of neighbours[2,3]. Although it has long been clear that the abiotic context influences interactions between species[3,6–8], predicting how these changes will impact population growth and community composition in a robust manner has proven challenging. Overcoming this challenge requires an understanding of how each individual species will respond directly to climate, how species interactions will be altered, as well as a theoretically justified framework for predicting the longer-term outcome of the altered species interactions[4,9,10].

Pioneering studies on the effects of rainfall on competitive outcomes have used climate manipulations such as rainout shelters or natural precipitation gradients to quantify precipitation-driven changes in biomass and species composition over time; results in some cases were probably driven by altered species interactions[11–14]. However, the response variables typically measured in these studies, such as biomass change, offer limited insight into how changing species interactions will shape long-term competitive outcomes. Modern coexistence theory[4,15–17] offers a useful mathematical approach for doing just that.

In modern coexistence theory, competitive outcomes between pairs of species are determined by the relative strength of stabilizing niche differences that promote coexistence and fitness differences that drive competitive exclusion[4,18]. Stabilizing niche differences reduce interspecific competition and increase the ability of each species to recover from low density, a hallmark of stable coexistence. Fitness differences are frequency-independent advantages that favour one species over another regardless of their relative abundance in the community. For a pair of species to coexist, stabilizing niche differences must exceed fitness differences, giving both species the ability to recover from low density[4,18]. Although it may be tempting to regard niche and fitness differences as fixed properties of a pair of species, these differences depend on the abiotic conditions under which species compete[19], and thus may change as the climate changes. Quantifying how they do so will therefore provide insights into future competitive outcomes and community composition.

Separate from their ability to predict competitive outcomes, stabilizing niche differences and fitness differences lie at the heart of numerous hypotheses for how altered precipitation will influence competitive dynamics. For example, fitness differences between competitors are invoked when altered precipitation differentially harms the dominant competitor to the benefit of subordinates, increasing species diversity[11]. Alternatively, stabilizing niche differences are invoked when reduced precipitation is thought to increase competitive exclusion by compressing the growing season and reducing the phenological differences between species[20,21]. However, these hypotheses about why competitive interactions change with climate are almost never quantitatively evaluated. Thus, measuring the effect of precipitation change on niche and fitness differences can offer fundamental insights into why changes in environmental conditions affect long-term coexistence and species diversity in a plant community.

Novel approaches to quantifying stabilizing niche differences and fitness differences in field settings[9,10,22] under different climate treatments offer the opportunity to understand how environmental change

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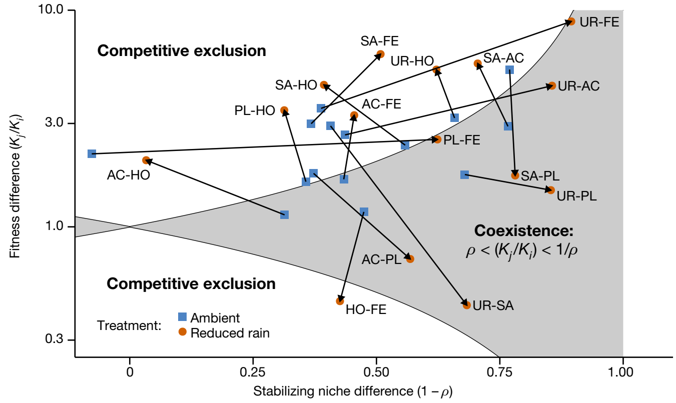

Fig. 1 | Effects of water treatment on the stabilizing niche and fitness differences of competing pairs. The stabilizing niche and fitness differences of species pairs under the ambient and reduced rain treatments predict coexistence outcomes. Pairs coexist when $\rho < K_j/K_i < 1/\rho$, indicated by the grey shaded region. When this inequality is not met, as indicated by the unshaded region, one species will exclude the other. See Extended Data Table 1 for species labels.

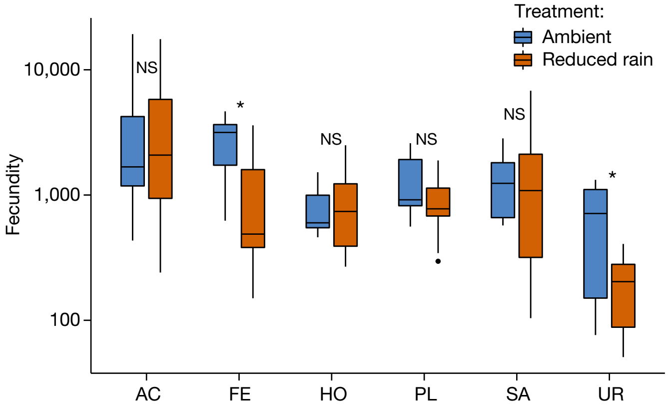

Fig. 2 | Effects of water treatment on the fecundity of species when grown without competitors. Seeds produced per germinant (fecundity; note the log scale) from plants grown without competitors under the ambient and reduced rain treatments. See Extended Data Table 1 for species codes and the number of replicates (n). The box and whiskers plot represents the median, the 25th and 75th percentiles, and the minimum and maximum values in the data. Differences were assessed using a generalized linear mixed-effects model: fecundity ~ species × treatment + plot (*$P < 0.001$; NS, not significant).

affects plant performance, competitive interactions and the long-term consequences of those interactions. Although these approaches are nearly impossible to execute in any diverse community with long-lived species, annual plant communities lend themselves to just this kind of work. Lifetime fitness is attained in just 1 year, many plants can be feasibly grown in a field plot and the simple life cycles are reasonably described by the mathematical models necessary for quantifying stabilizing niche and fitness differences and predicting competitive outcomes[9,10,22]. Although annual plants have less complex demography than perennials, they are nonetheless part of the same continuous global spectrum of plant function[23] that is widely used to extrapolate findings from one system or set of species to another[24].

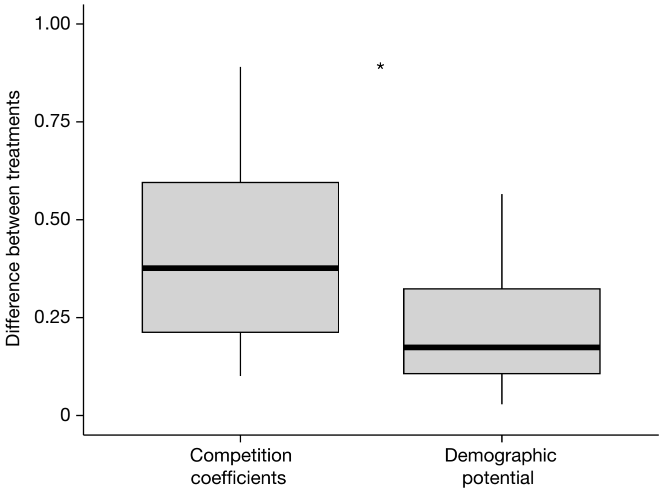

Fig. 3 | Effect of water treatment on components of the invasion growth rates of species. Changing precipitation differentially altered two quantities that shape the invasion growth rate of species across all species pairs. These are (1) competition coefficients, defined as a log ratio of the intraspecific and interspecific competition effects of resident species, and (2) the demographic potential, defined as a log ratio of the demographic potential of the invader relative to resident species. See Methods for full details and theoretical justification for this analysis (*$P = 0.044$). The box and whiskers plot represents the median, the 25th and 75th percentiles, and the minimum and maximum values.

To assess the effect of precipitation change on species coexistence, we grew six California annual grassland plant species in pairwise competition in the field under ambient and 20% reduced rainfall and quantified their competitive dynamics. The six species were selected from our previous work[9,10] to span the breadth of ecological strategies found in the annual plant community at the site. Climate forecasts for the region over the next century predict increases in interannual variability and modestly less rainfall[25,26], a change mimicked by a rainfall exclusion treatment in our experimental design. We used results from the field experiment to parameterize a plant competition model that describes the dynamics of annual plant populations as a function of the intrinsic demographic rates of species and the effects of pairwise competition[27]. We used fitted germination rates, plant fecundity in the absence of competition and pairwise competition strengths, all under the two rainfall treatments (Methods) for six interacting species to quantify their stabilizing niche and fitness differences[22]. These metrics allowed us to predict the long-term outcome of competition for each pair of species under different rainfall treatments (Fig. 1).

Our results revealed qualitative effects of rainfall change on the predicted coexistence of 10 of 15 species pairs in our study (Fig. 1), changes that were driven by rainfall exclusion effects on stabilizing niche and fitness differences (Extended Data Table 2). For these 10 species pairs, coexistence was predicted in one rainfall treatment but not in the other. Specifically, four pairs were predicted to coexist under an ambient regime, but not the reduced rainfall treatment. Six other pairs were predicted to coexist under reduced rainfall but not under the ambient treatment (Fig. 1, Extended Data Table 2 and Extended Data Fig. 1). Four pairs were not predicted to coexist in either treatment, and one pair was predicted to coexist in both.

Notably, although reducing rainfall had substantial effects on predicted competitive outcomes, it had smaller effects on each species when grown alone (Fig. 2 and Extended Data Table 1). Four of the six species showed no difference in fecundity in the two treatments, whereas only two species, *Festuca microstachys* and *Uropappus lindleyi*, experienced lower fecundity (by an average of 62% and 71%, respectively) in the reduced rainfall treatment. The fact that four species were insensitive to reduced rainfall was surprising as decreasing water availability often decreases growth and fecundity[14,28]. However, these species are adapted to a Mediterranean climate with frequent dry years. For these four species, reduced rainfall may not limit fecundity without neighbours also competing for that same water and further reducing soil water to

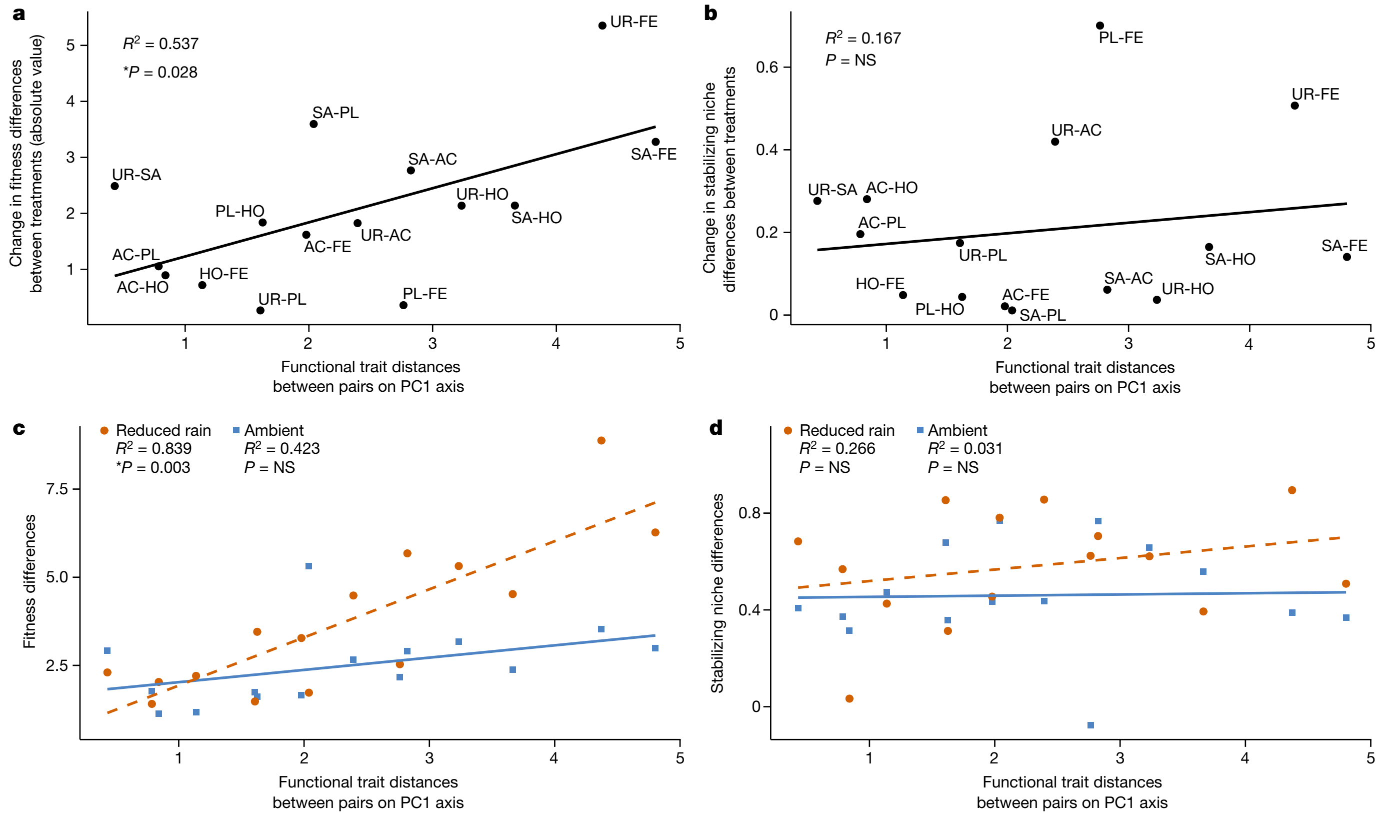

Fig. 4 | Effect of differences in functional traits on pairwise competition outcomes within and between water treatments. a, Change in fitness differences with rainfall treatment plotted against the functional trait distance between species pairs along the PC1 axis. **b**, Change in stabilizing niche differences with rainfall treatment plotted against the functional trait distance between species pairs along the PC1 axis. For the species labels in **a**,**b**, see Extended Data Table 1. **c**, Fitness differences between species pairs plotted against their functional trait distance along the PC1 axis, for each of the two rainfall treatments. **d**, Stabilizing niche differences between species pairs plotted against their functional trait distance along the PC1 axis, for each of the two rainfall treatments (* indicates significant *P* value from the Mantel test; NS indicates not significant).

a truly limiting level. In addition, the year in which we conducted our study was a relatively wet one, meaning that our 20% reduction treatment and ambient treatment fell within the typical rainfall range for this community[29]. Together, these results highlight how even modest changes in rainfall (20% reduction) that have minimal effects on the fecundity of most species in the absence of competitors (Fig. 2) can nonetheless drive substantial changes in competitive outcomes (Fig. 1).

To evaluate the degree to which precipitation effects on coexistence resulted from changing competitive interactions versus changing demographic potential (driven by fecundity in the absence of neighbours), we quantified how rainfall-driven changes to each of these quantities altered the invasion growth rates of species. The invasion growth rate of species is the rate at which it can invade a system in which their competitor is at its 'resident' equilibrium state. Invasion growth rates therefore determine competitive outcomes (Methods), and depend on both the per capita suppression of growth of the resident relative to that of the invader (a ratio of competition coefficients) and the demographic potential of the invader relative to its competitor (capturing the direct responses to the environment for the species; equation (5)). We found that reduced rainfall altered the relative strength of the competition coefficients more strongly than the differences in demographic potential (Fig. 3).

In summary, the changes in predicted competitive outcomes between species in the rainfall manipulation were most strongly driven by changes in species interactions (Fig. 1 and Extended Data Fig. 1). As there was variation across species pairs in how the rainfall manipulation affected their coexistence, we sought to better understand the potential mechanisms underlying this diversity of competitive changes. Specifically, we tested whether the variation across species pairs in the effect of rainfall manipulation on competitive outcomes was correlated with functional or ecological strategy differences between species. We quantified strategy differences using functional trait measurements of our focal species, which capture variation in the life history strategies of species and can explain variation in species interactions[10]. To quantify aggregate functional trait differences between species, we conducted a principal component analysis (PCA) of 11 previously measured functional traits of 23 species from the community[10,30] (Extended Data Fig. 2) and extracted the scores of our six focal species along the first PC axis, which explained 22.7% of the trait variation among species. The traits measured included key leaf, stem and root functional traits that are widely sampled globally to capture a diversity of plant strategies[23] and competitive outcomes[24], as well as less widely sampled traits related to competition for water in our system, such as rooting depth, phenology and integrated water use efficiency (via carbon stable isotopes) (Extended Data Table 3). This suite of traits has also been shown to relate to niche and fitness differences[10] in our system.

We found that the greater the functional dissimilarity between species, the more their fitness differences changed with altered rainfall (Mantel $R^2 = 0.54$, $P = 0.028$; Fig. 4a and Extended Data Fig. 2). Underlying this finding was a weak relationship between trait dissimilarity and fitness differences in the ambient rainfall treatment and a much stronger relationship when rainfall was reduced (Fig. 4c). Consistent with previous work in this system showing that fitness differences but not niche differences between species are correlated with their functional trait differences[10], we did not find any relationship between trait dissimilarity and stabilizing niche differences either within or between treatments (Fig. 4b,d). Together, these results suggest that there is a functional basis to how rainfall affects fitness differences and therefore competitive outcomes, an area worthy of further investigation. This aligns with our understanding of trait variation, as species with similar functional traits often respond to the environment in similar ways[12,30] and thus their interactions should be less likely to change. It also suggests that communities with high functional diversity, and therefore a greater proportion of pairwise interactions between functionally distinct species, may be most at risk for climate-driven changes in interaction outcomes in the future.

A great diversity of processes are known to contribute to species coexistence in communities[4,19,31–33], including numerous potential mechanisms of coexistence that our study was not able to quantify. For example, broader-scale spatial and temporal heterogeneity probably affect coexistence in this community, and this explains the fact that not all pairs are predicted to coexist in the ambient rainfall treatment. Although these and other factors contribute to coexistence at larger landscape scales and are worthy of future study, understanding the long-term predicted competition outcomes at a neighbourhood scale under different rainfall conditions as we have done here provides an important template on which we can overlay other coexistence mechanisms in conjunction with future abiotic changes.

Finally, although community ecology has frequently assumed that the pairwise interactions of species can be combined to predict whole-community outcomes, higher-order interactions challenge this assumption. Unfortunately, it is often logistically daunting to properly quantify these interactions empirically[34], let alone do so in different rainfall environments. Nonetheless, as a step towards a multispecies perspective on our results, we applied a previously developed structural approach[35] to our pairwise interaction results to assess how the rainfall treatment affected the potential for coexistence in systems with three or more of the study species. This analysis quantifies structural analogues of niche and fitness differences, which can be used to assess the potential for any number of species to coexist. Consistent with past work in our system[35], we found that the fraction of possible pairs coexisting (11 of 15 in at least one treatment; Fig. 1 and Extended Data Tables 2 and 4) was greater than the fraction of coexisting triplets (4 of 20; Extended Data Table 5), which was greater than the fraction of quadruplets, quintuplets and sextuplets (always 0; Extended Data Table 6). However, just as 10 of 11 pairs predicted to coexist only coexisted in one rainfall treatment (Fig. 1 and Extended Data Tables 2 and 4), four of four triplets predicted to coexist only coexisted in one of the two rainfall treatments (Extended Data Table 5). This suggests that the pairwise results that we reported above extend to systems with more than two species, although more work on the multispecies implications of our findings are warranted.

Our results demonstrate the importance of accounting for species interactions when predicting the effects of global change. Our rainout experiment generated a modest 20% reduction in precipitation with insignificant effects on the fecundity of four of our six species when grown without competitors (Fig. 2 and Extended Data Table 1). These responses are small enough to be inconsequential in any global change forecast built on the direct responses of species to changes in climate. However, this small change in rainfall strongly affected species competitive interactions, so much so that the predicted coexistence outcome changed for 10 of 15 species pairs (Fig. 1). Of these pairs, we found that species with more similar functional traits showed smaller shifts in their competitive imbalance. Thus, our results show that studies that rely solely on the direct climate responses of species to predict future communities or species distributions may miss critical changes in the effect of competitive interactions. Our results suggest that scenarios in which global change alters resource availability (such as water) may have fundamentally different consequences for species interactions and community structure than cases in which temperature alone is altered. If this is true, consumer–resource models[36,37] may be particularly powerful for exploring the community consequences of such changes. Although the logistical challenge of assessing changes in species interactions is not trivial, especially when considering longer-lived organisms, our results show just how important such changes can be for predicting the consequences of global change.

Online content

Any methods, additional references, Nature Research reporting summaries, source data, extended data, supplementary information, acknowledgements, peer review information; details of author contributions and competing interests; and statements of data and code availability are available at https://doi.org/10.1038/s41586-022-05391-9.

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Methods

Field experiment

The experiment was conducted at the University of California, Santa Barbara's Sedgwick Reserve in Santa Barbara County, CA, USA (34° 40′ N, 120° 00′ W), 730 m above sea level. Precipitation determines the growing season in this Mediterranean climate, which is characterized by cool, wet winters and hot, dry summers. The landscape is heterogeneous with patches of serpentine soil that support diverse native flora, in part because they are resistant to invasion by European annual grasses, which dominate much of the grasslands in this region[38]. Most of the annual species in this grassland community germinate after early season rainfall in December and January and senesce sometime between February and June. From surveys of the area, we have recorded and identified 55 species of annual forbs or grasses[30]. We chose six species for the experiment that differ in core functional traits[10,30,39] as well as their phenology across the growing season, and were known to germinate and grow reliably in previous studies (Extended Data Table 1). We collected seed for the experiment in spring and summer 2018 from the reserve. In autumn 2018, we planted a pairwise competition experiment with two different precipitation regimes.

Experimental competition plots (each 60 × 75 cm) were cleared of vegetation and any visible seeds and then sown with seed from our six focal species in late October 2018 before the onset of winter rains. The plots were located within a fenced area, which excludes deer and gophers. Each plot was randomly assigned to receive seeds of one of six focal species in the background at one of five sowing densities ranging from 0 to 12 g of seed per m^2 with four replicate plots per density per background species. As the 0 g m^{-2} plots are identical in composition across background species, for efficiency, we only sowed a total of ten 0 g; m^{-2} plots, resulting in 106 plots (10 plots with 0 g m^{-2}, 96 plots with 2–12 g m^{-2}). The natural density of this grassland community corresponds to roughly 8 g m^{-2} in a typical year, so our treatments range from no competitors to approximately 150% of typical density[9]. The central region of each plot was divided into 12 15 × 15-cm subplots, with a 7.5-cm buffer around the edges. The centre point of each subplot was sown with 25 viable seeds from one of our six focal species, with each focal species sown into two subplots per plot. Germination in the subplots allowed us to measure the average germination rate of each focal species, and following germination, the focal plant species in each subplot was thinned to a single focal individual, located no closer than 15 cm to a focal individual in neighbouring subplots to minimize competitive interactions among focal plants. If one of the six species emerged at an undesignated spot in the plot but was at least 10 cm away from another focal and the edge, we included it in the data collection. This design then results in each of the six focal species competing against intraspecific and all interspecific competitors at five different densities. Seed viability was quantified before sowing using methods from previous experiments with these species[10]. Our 106 plots were evenly divided between ambient and reduced rain treatments and randomly assigned to a rainout shelter. Fourteen large rainout shelters (1 m tall) were built around groups of adjacent plots. The shelters consisted of wooden frames that could be covered with plastic sheeting that channelled water into gutter systems that transported the rain away from the experimental plots. The sheeting was only deployed during rain events to minimize unwanted treatment effects in between storms. To further reduce artefacts between treatments, we opted to exclude rain for all plots in the experiment regardless of treatment and then return the appropriate amount of water based on rainfall during the storm to the ambient plots using collected rainwater. We deployed plastic sheeting over our rainout shelter frames during 15 of the 18 rain events that occurred between 15 February 2019 and 1 June 2019, immediately returning collected rainwater to the ambient plots using backpack sprayers at the end of the storm at a watering rate equal to the rainfall total of the storm.

Both rainfall regimes received identical ambient rain until mid-February 2019, which allowed plants to germinate and establish under similar conditions, thereby focusing the effects of our reduced rain treatment on the post-germination growth and reproduction phase. In January 2019, we recorded germination rates and thinned each of the focal seedlings that resulted from the original 25 seeds to a single individual. Any recruits from the seed bank were weeded out throughout the season unless the recruit was designated a focal because of its identity and position within the plot (or if the recruit was the background competitor species). We then recorded lifetime fecundity for each focal individual and censused the number of competitors in a 10-cm radius around each focal plant. We tracked germination, fecundity and number of neighbours for over 1,600 plants in our plots.

Ultimately, the reduced rain treatment received 12.75 cm less rain than the ambient plots, which corresponded to a 20% reduction in total rain over the lifetime of the plants. Soil gravimetric water content ((wet weight − dry weight)/dry weight) was measured three times during the experiment from our 8 g m^{-2} plots on 27 March, 21 April and 17 May 2019 (Extended Data Table 7). Soil samples were taken from three different plots in each treatment in March and from eight different plots in each treatment in April and May. Soil was weighed and then dried in a 60 °C oven for 3 days and weighed again. According to Welch two-sample t-tests, the reduced rain plots experienced significantly lower gravimetric water content than the ambient plots on all three dates (Extended Data Table 7), with the reduced rainfall plots measuring a gravimetric water content that was 68%, 71% and 78% of the ambient plots, respectively. The site received above average rainfall in the 2018–2019 growing season[29], resulting in the reduced rain treatment receiving 2.25 cm of rainfall below the average and the ambient treatment receiving 10.5 cm above the average.

Model parameterization

To quantify the niche and fitness differences critical to understanding coexistence between species pairs, we parameterized an annual plant demographic model that describes the dynamics of annual plant populations with a seed bank, and includes species-level variation in germination rates, seed survival in the seed bank, fecundity and pairwise competition coefficients (equation (1)). The population dynamic model allowed us to calculate stabilizing niche and fitness differences from the fitted parameters using a previously developed approach[9,10]. In brief, the per capita growth rate of species i in year t (left side of equation (1)) is modelled as a function of its germination rate (g_i), seed survival rate (s_i) and per germinant fecundity (F_i):

$$\frac{N_{i,\,t+1}}{N_{i,t}} = \left(1 - g_i\right)s_i + g_iF_i \tag{1}$$

The model tracks the growth of $N_{i,t}$, the density of species i in the autumn of year t before germination, as the sum of two terms. The first is the growth contributed by seeds that do not germinate that year, a function of the seed germination and survival rate, as these seeds will remain in the seedbank. Previous work at this site measured seed survival for each species by testing their viability before and after burying bags of seed in the ground for a year, and we assumed these rates were unchanged from previous years. The germination rates were determined from averaging the germination rate for each species across plots from the 25 viable seeds sowed for each focal. The second term, g_iF_i describes the growth contributed by seeds that do germinate. The term F_i refers to the per germinant fecundity or the amount of seeds added to the following autumn seed bank by each germinated individual of species i. F_i can be expressed as a function that describes how fecundity decreases with increasing density of intraspecific and interspecific competitors[4,10,27].

$$F_i = \frac{\lambda_i}{1 + \alpha_{ii} g_i N_{i,t} + \alpha_{ij} g_j N_{j,t}} \tag{2}$$

The numerator (λ_i) denotes the fecundity of a germinated individual of species *i* when it is grown in the absence of any competition. The interspecific and intraspecific competition parameters (α_{ii} and α_{ij}) represent the competitive effect of species *i* on itself and the competitive effect of species *j* on species *i*, respectively. The $g_j N_{j,t}$ term represents the density of germinated competitors of species *j*.

We used the collected data to fit the parameters in equation (2) in R using the non-linear least squares method (nlstools package in R version 4.2.0). We allowed lambda (low-density seed production (λ_i)) and alphas (competition interaction coefficients for each pair (α_{ii}, α_{ij}, α_{jj}, α_{ji})) to vary as a function of rainfall treatment, competitor density and competitor identity, and used the non-linear least squares test to estimate each parameter. We bootstrapped the data and re-estimated the parameters 1,000 times to estimate error for the parameters. Given previous work at the site showing strong competition between species, we constrained all the competition parameters to be positive (>0.001), which eliminates the possibility of facilitation (that is, via a negative interaction coefficient estimate). Of the 72,000 alphas estimated from the bootstrapped data, less than 0.02% of them were equal to the constrained value of 0.001.

Stabilizing niche differences between two species were calculated as $1 - \rho$, where ρ measures niche overlap[4,10,27], described as:

$$\rho = \sqrt{\frac{\alpha_{ij}}{\alpha_{jj}} \frac{\alpha_{ji}}{\alpha_{ii}}} \tag{3}$$

Niche overlap therefore captures the extent to which a species limits conspecific individuals (represented by the intraspecific interaction coefficients in the denominator of equation (3) more than it limits heterospecific individuals (captured by the interspecific interactions in the numerator of equation (3)), and relates to the ability of species to increase when rare. If a species limits conspecific individuals more than heterospecifics, niche overlap is low, and invasion growth rates are more positive[10,22].

Similarly, fitness differences between two species can be described by a ratio ((κ_j/κ_i), which is calculated by the following equation[10]:

$$\frac{\kappa_j}{\kappa_i} = \left(\frac{\eta_j - 1}{\eta_i - 1}\right) \sqrt{\frac{\alpha_{ij}}{\alpha_{jj}} \frac{\alpha_{ii}}{\alpha_{ji}}} \tag{4}$$

where

$$\eta_i = \frac{\lambda_i g_i}{1 - (1 - g_i)(s_i)} \tag{5}$$

The fitness ratio compares species inherent competitive abilities and is the product of two terms: the 'demographic ratio' $\left(\frac{\eta_j - 1}{\eta_i - 1}\right)$ and the 'competitive response ratio' $\sqrt{\frac{\alpha_{ij}}{\alpha_{jj}} \frac{\alpha_{ii}}{\alpha_{ji}}}$ [10]. Therefore, high competitive fitness can come either from a species producing a large total number of seeds when not experiencing competition (that is, a favourable demographic ratio), or by being relatively insensitive to the total effects of competitors (that is, a favourable competitive response ratio)[10].

Long-term coexistence is predicted when stabilizing niche differences (ρ) and fitness differences $\left(\frac{\kappa_j}{\kappa_i}\right)$ satisfy the following inequality (equation (6)):

$$\rho < \frac{\kappa_j}{\kappa_i} < 1/\rho \tag{6}$$

To assess the direct effect of rainfall on individual species, we compared the low-density plot fecundities of each species under each precipitation treatment (Fig. 2). We then compared the estimated competitive interaction parameters (α_{ii}, α_{ij}, α_{jj}, α_{ji}) for each pair of species under each precipitation treatment. Note that the germination rate did not differ by treatments because the rainfall exclusion was started after the germination-inducing rain event, and the seed bank survival was taken from previous work at the site. Finally, we used equations (3, 4 and 5) to calculate stabilizing niche and fitness differences and thus predicted long-term competitive outcomes between pairs under each treatment (Fig. 1). To estimate error, we calculated stabilizing niche and fitness differences 1,000 times from each of the 1,000 bootstrapped parameter estimates (Extended Data Fig. 1).

Invasion growth rate analysis

We decomposed the invasion growth rates of species pairs to determine the extent to which changes in the interaction strengths of species versus changes in fecundity drove the widespread changes to species coexistence (Fig. 1) with rainfall manipulation. For a species pair to coexist, each species must be able to invade an equilibrium population of the other from low density. In our annual plant model, species *i* can invade species *j* when[40]:

$$\frac{\alpha_{jj}}{\alpha_{ij}} > \frac{(\eta_j - 1)}{(\eta_i - 1)} \tag{7}$$

where α_{ij} describes the competitive effect of species *j* on species *i*, and η_i captures the seeds produced per seed lost from the seed bank for species *i*, which is a function of seed production in the absence of competitors (λ), germination rate (*g*) and seed survival in the seed bank (*s*) (equation (5)). This inequality can be rearranged into the following expressions:

$$\frac{(\eta_i - 1)}{(\eta_j - 1)} \times \frac{\alpha_{jj}}{\alpha_{ij}} > 1 \tag{8}$$

$$\log_{10}\left(\frac{\eta_i - 1}{\eta_j - 1}\right) + \log_{10}\left(\frac{\alpha_{jj}}{\alpha_{ij}}\right) > 0 \tag{9}$$

where the capacity for species *i* to invade species *j* depends on both the relative demographic potential of the competitors (ratio of the etas (η_i and η_j) that reflects the direct responses of species to the environment) and the degree to which the resident species harms itself relative to the invader (ratio of the alphas (α_{jj} and α_{ij}) that reflect interspecific and intraspecific competition). We investigated which of these two elements changed more with the rainfall exclusion treatment by calculating the absolute value of the differences in each term between treatments. We then performed a paired Student's *t*-test on the magnitudes (absolute value) of the two differences and found that across species pairs, the competition coefficients term (α ratios) changed significantly more than the demographic potential (η ratios) (Fig. 3; $P = 0.044$). This indicates that the changes in species coexistence that we observed in our experiment were driven more by shifts in species interactions than by changes in the direct responses of species to the environment.

Functional trait analysis

Eleven functional traits including leaf nitrogen content, phenology, leaf dry matter content, leaf area, specific leaf area, maximum height, seed mass, rooting depth, specific root length, integrated water use efficiency (estimated with leaf tissue δ^{13}C) and canopy shape index were measured for 23 species, including our six focal species, at the site in a previous year[10,30,39] (for units and descriptions, see Extended Data Table 3). In selecting traits, we sought to include both traits that are widely sampled (such as specific leaf area, seed mass and maximum height measures), as well as traits that can be harder to sample but that we expect matter more for competitive interactions among annuals, including rooting depth, phenology and measures of canopy architecture (via canopy shape index). In terms of competition for water, we sampled rooting depth, fine-root structure (via specific root length) and integrated water use efficiency (via carbon stable isotopes). We created a PCA with the measured traits of 23 annual plant species from the site (Extended Data Fig. 2) to determine the extent to which species differed in their functional traits. We used differences between species on the PC1 axis (which explained 22.68% of the variability) as an overall measure of trait dissimilarity between the six species. The study species broadly span the functional trait spectrum of the annual plant community with considerable variation in traits, including, for example, a 40-fold difference in leaf area and a sixfold difference in seed mass. Given the pairwise nature of our data, following previous work at the site[10], we used Mantel tests to test whether either stabilizing niche or fitness differences between species pairs were correlated with trait dissimilarity, both within and between treatments.

Multispecies structural analysis

Following recent methodological developments[35], we used a structural approach to derive metrics analogous to niche (Ω) and fitness (θ) differences that determine the range of demographic rates sufficient for multispecies coexistence given their intrinsic growth rates and their pairwise interaction coefficients scaled by germination. This allowed us to include the indirect interaction effects on competitive outcomes that can occur when more than two species are competing. It also allowed us to see how these structural analogues of niche and fitness differences changed with rainfall for all possible pairs, triplets, quadruplets, quintuplets and one sextuplet (Extended Data Tables 4–6). When analysing the species pairs, consistent with our main analysis (Extended Data Table 2), we found that the same 10 of 15 pairs (67%) had altered coexistence outcomes in the rainfall manipulation treatment (Extended Data Tables 2 and 4). Extending the structural approach to all species triplets showed that 4 of 20 (20%) of the triplets experienced altered coexistence outcomes with rainfall manipulation (Extended Data Table 5), which extends the overall pairwise results into a multispecies context. When we explored coexistence of species quadruplets, quintuplets and the sextuplet of all species, we noted changes in the parameters between rainfall treatments (for example, Ω and θ; Extended Data Table 6), although the method did not predict stable coexistence of any of the larger species groupings in either treatment.

Reporting summary

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

Data availability

Data are available on Zenodo (https://doi.org/10.5281/zenodo.7083314). Data were recorded in Microsoft Excel (v.16.63.1) and analysed in R (v.4.2.0).

Code availability

Codes are available on Zenodo (https://doi.org/10.5281/zenodo.7083314). Figures and tables were created in R (v.4.2.0).

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Author contributions M.N.V.D. and N.J.B.K. conceived and led the project. M.N.V.D., J.M.L. and N.J.B.K. developed the methods. M.N.V.D. carried out the field experiment and collected the data. Data were analysed and visualized by M.N.V.D. The initial manuscript was written by M.N.V.D. and N.J.B.K., with substantial contributions from J.M.L.

Competing interests The authors declare no competing interests.

Additional information

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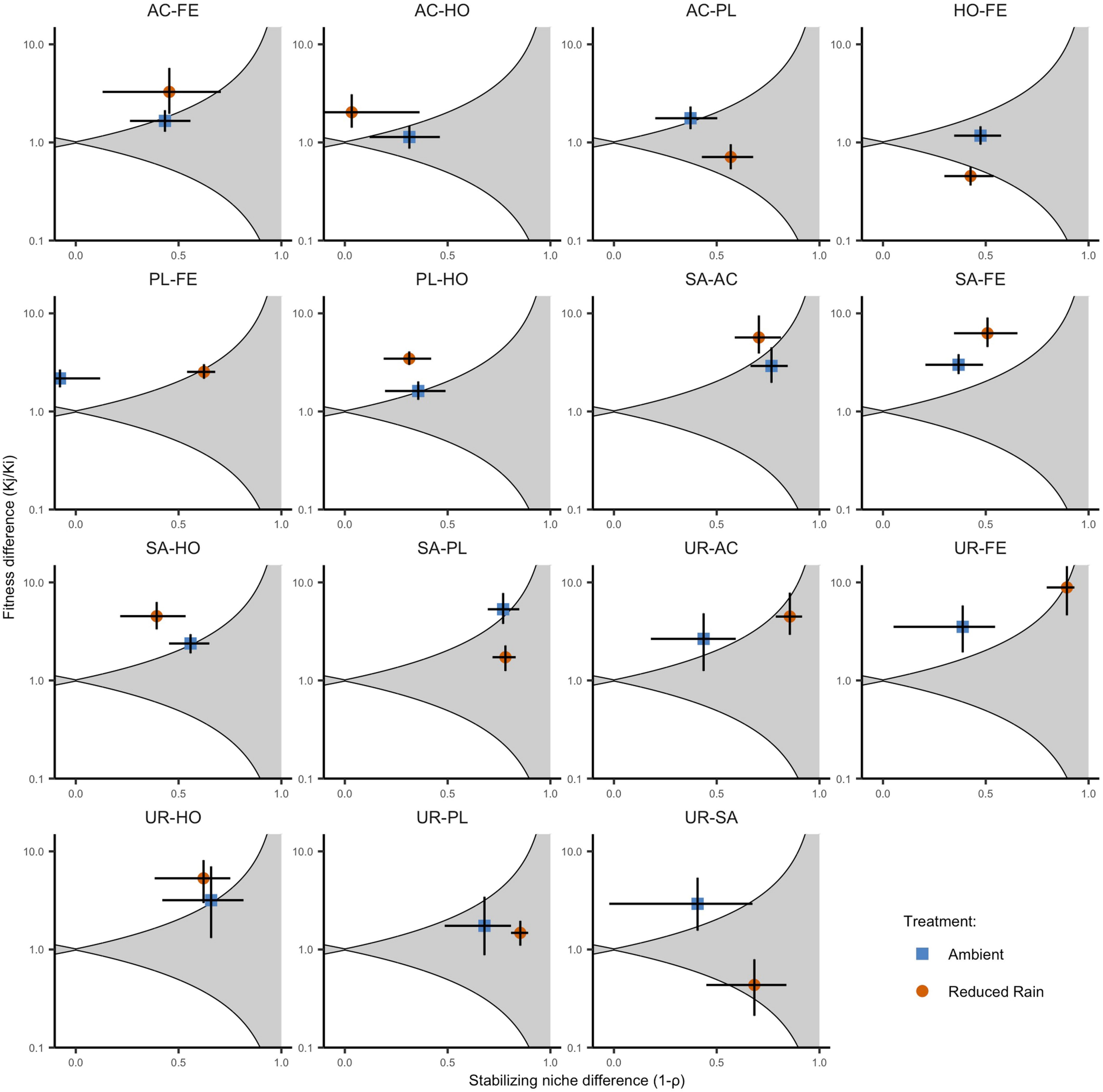
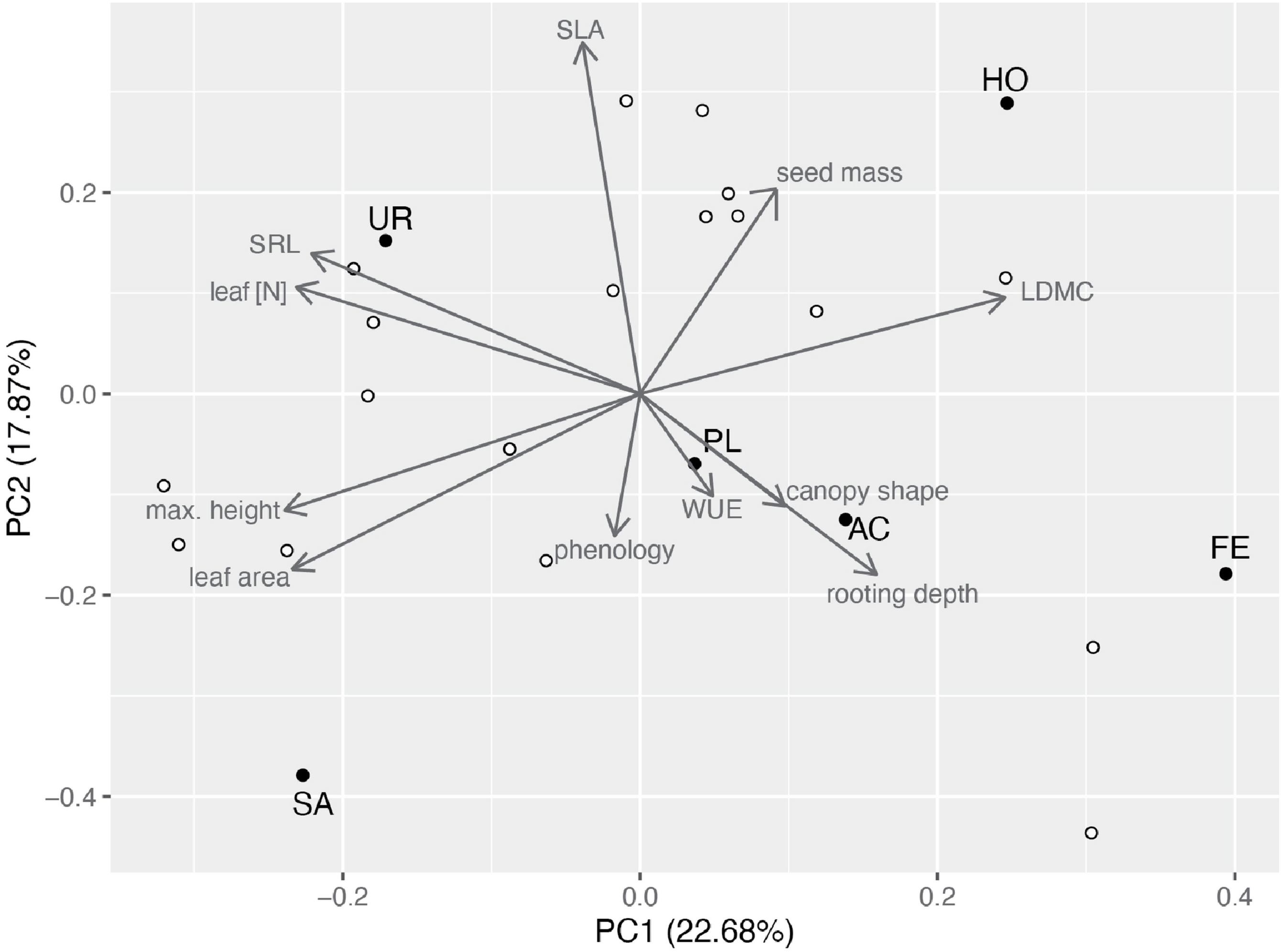


Extended Data Fig. 1 | Effects of water treatment on each competing pairs' stabilizing niche and fitness differences. Each species pair shown separately with confidence intervals (+/− 1 SD) for stabilizing niche and fitness differences obtained from bootstrapping. Inside the grey shaded region indicates coexistence, outside indicates competitive exclusion.



Extended Data Fig. 2 | Principal component analysis of functional traits from the focal plant community. Principal component analysis with 23 species and eleven functional traits from previous work at the site[10] (Methods). The six species from this study are filled in circles and labeled following Extended Data Table 1. The open circles represent other species in the community. See Extended Data Table 3 for trait descriptions.

Extended Data Table 1 | Each species' mean per capita seed production without competitors in the two treatments from the 0g/m^2 background plots ± standard error

			Ambient Rainfall			Reduced Rain			
Family	Species	Code	Mean Fecundity	Standard error	n	Mean Fecundity	Standard error	n	p-value
Fabaceae	*Acmispon wrangelianus*	AC	4,925.6	2,944.3	6	4,395.6	1,247.3	16	0.3597
Poaceae	*Festuca microstachys*	FE	2,793.0	507.9	8	1,069.1	284.8	14	0.0006*
Poaceae	*Hordeum murinum*	HO	810.9	145.8	7	944.7	198.9	12	0.6869
Plantaginaceae	*Plantago erecta*	PL	1,332.0	272.4	8	873.9	90.0	21	0.067
Lamiaceae	*Salvia columbariae*	SA	1,390.9	340.9	7	1,828.0	614.1	12	0.4452
Asteraceae	*Uropappus lindleyi*	UR	661.2	201.0	7	194.2	34.5	11	<0.0001*

P-values obtained from generalized linear mixed effects model: fecundity ~ species*treatment + plot.

Extended Data Table 2 | Stabilizing niche and fitness difference calculations for each species pair under two rainfall treatments

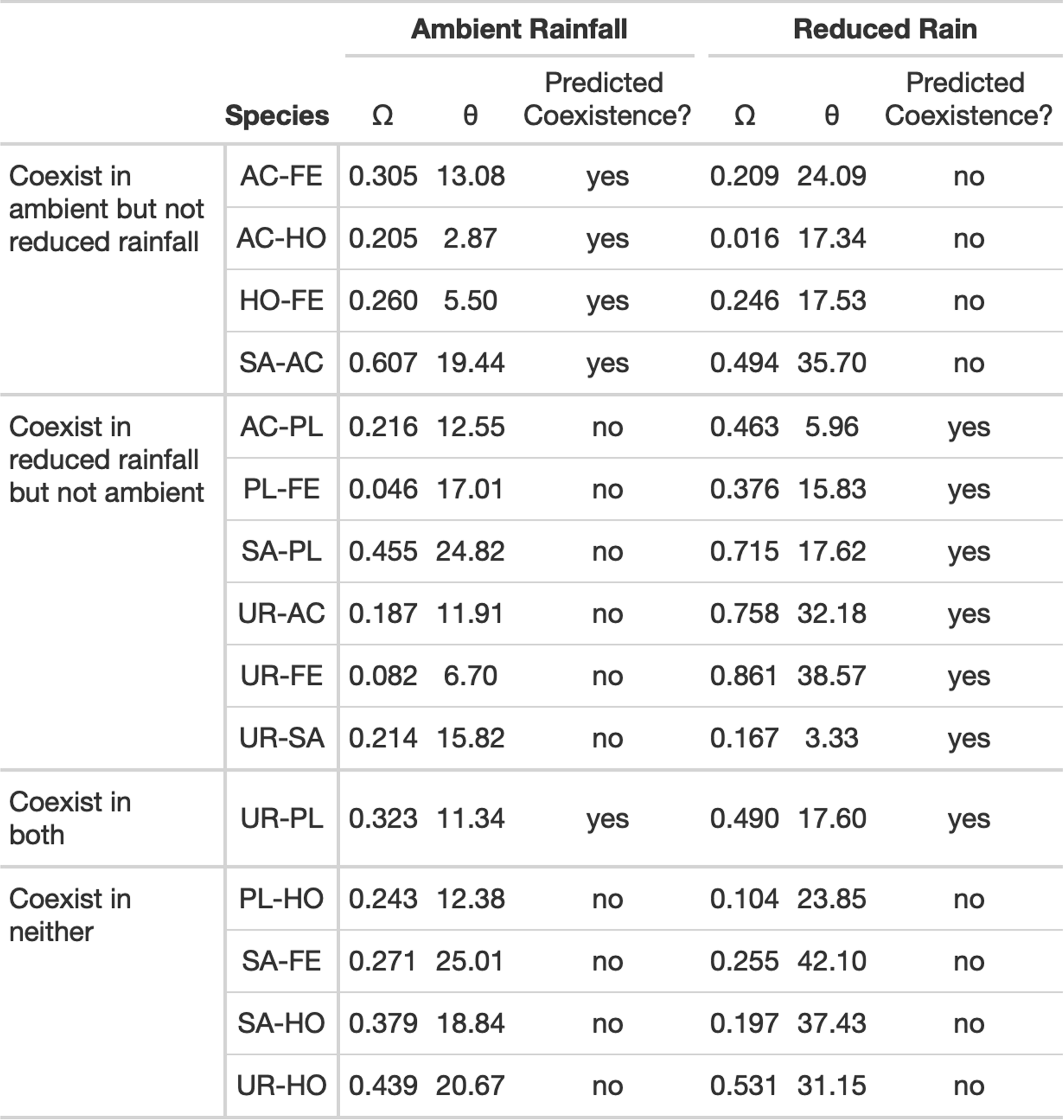
Species Pair		Ambient Rainfall			Reduced Rain		
		Stabilizing niche difference	Fitness difference	Predicted Outcome	Stabilizing niche difference	Fitness difference	Predicted Outcome
Coexist in ambient but not reduced rainfall	AC-FE	0.434	1.658	coexist	0.455	3.275	FE wins
	AC-HO	0.314	1.136	coexist	0.033	2.030	HO wins
	HO-FE	0.474	1.172	coexist	0.426	0.454	HO wins
	SA-AC	0.766	2.910	coexist	0.705	5.677	AC wins
Coexist in reduced rainfall but not ambient	AC-PL	0.373	1.765	PL wins	0.568	0.711	coexist
	PL-FE	–0.077	2.172	FE wins	0.624	2.532	coexist
	SA-PL	0.770	5.322	PL wins	0.781	1.726	coexist
	UR-AC	0.436	2.656	AC wins	0.856	4.482	coexist
	UR-FE	0.388	3.523	FE wins	0.895	8.877	coexist
	UR-SA	0.407	2.922	SA wins	0.683	0.435	coexist
Coexist in both	UR-PL	0.679	1.743	coexist	0.853	1.477	coexist
Coexist in neither	PL-HO	0.357	1.616	HO wins	0.313	3.453	HO wins
	SA-FE	0.368	2.993	FE wins	0.508	6.270	FE wins
	SA-HO	0.558	2.383	HO wins	0.394	4.522	HO wins
	UR-HO	0.658	3.180	HO wins	0.621	5.317	HO wins

Stabilizing niche differences are calculated as 1-ρ and fitness differences as κ_j/κ_i. Species pairs are predicted to coexist long term when $\rho < \kappa_j/\kappa_i < 1/\rho$. Species pairs with similar predictions of coexistence in the two treatments are grouped together.

Extended Data Table 3 | The eleven functional traits used to create the PCA in Extended Data Fig. 2 with their units and descriptions

	Trait	Units	Description
Leaf	Leaf area	cm^2	One-sided area of an individual leaf.
	Specific leaf area (SLA)	cm^2/g	Area of fresh leaf divided by oven-dry mass.
	Leaf nitrogen concentration	mg/g	Total amount of N per unit of dry leaf mass.
	Leaf dry matter content (LDMC)	mg/g	Oven-dry mass (mg) of leaf, divided by its water saturated fresh mass (g).
Root	Rooting depth	cm	Maximum soil depth from which resources can be acquired.
	Specific root length (SRL)	m/g	The ratio of root length to dry mass of fine roots - a ratio of acquisition to investment.
Whole plant	Maximum height	cm	Maximum stature a typical mature individual of a species attains in a given habitat.
	Canopy shape index	dimensionless	A measure of investment in vertical vs. lateral growth.
	Phenology (peak fruiting)	day of year	Day of peak fruiting for a species.
	Carbon isotope composition	$\delta_{13}C$	A measure of intrinsic water use efficiency (WUE).
Seed	Seed mass	g	Oven-dry mass of an average seed of a species.

Extended Data Table 4 | Ω, a structural analog of stabilizing niche differences and θ, a structural analog of fitness differences[35] for each species pair and their predicted competition outcome using the structural method under the two rainfall treatments



		Ambient Rainfall			Reduced Rain		
	Species	Ω	θ	Predicted Coexistence?	Ω	θ	Predicted Coexistence?
Coexist in ambient but not reduced rainfall	AC-FE	0.305	13.08	yes	0.209	24.09	no
	AC-HO	0.205	2.87	yes	0.016	17.34	no
	HO-FE	0.260	5.50	yes	0.246	17.53	no
	SA-AC	0.607	19.44	yes	0.494	35.70	no
Coexist in reduced rainfall but not ambient	AC-PL	0.216	12.55	no	0.463	5.96	yes
	PL-FE	0.046	17.01	no	0.376	15.83	yes
	SA-PL	0.455	24.82	no	0.715	17.62	yes
	UR-AC	0.187	11.91	no	0.758	32.18	yes
	UR-FE	0.082	6.70	no	0.861	38.57	yes
	UR-SA	0.214	15.82	no	0.167	3.33	yes
Coexist in both	UR-PL	0.323	11.34	yes	0.490	17.60	yes
Coexist in neither	PL-HO	0.243	12.38	no	0.104	23.85	no
	SA-FE	0.271	25.01	no	0.255	42.10	no
	SA-HO	0.379	18.84	no	0.197	37.43	no
	UR-HO	0.439	20.67	no	0.531	31.15	no

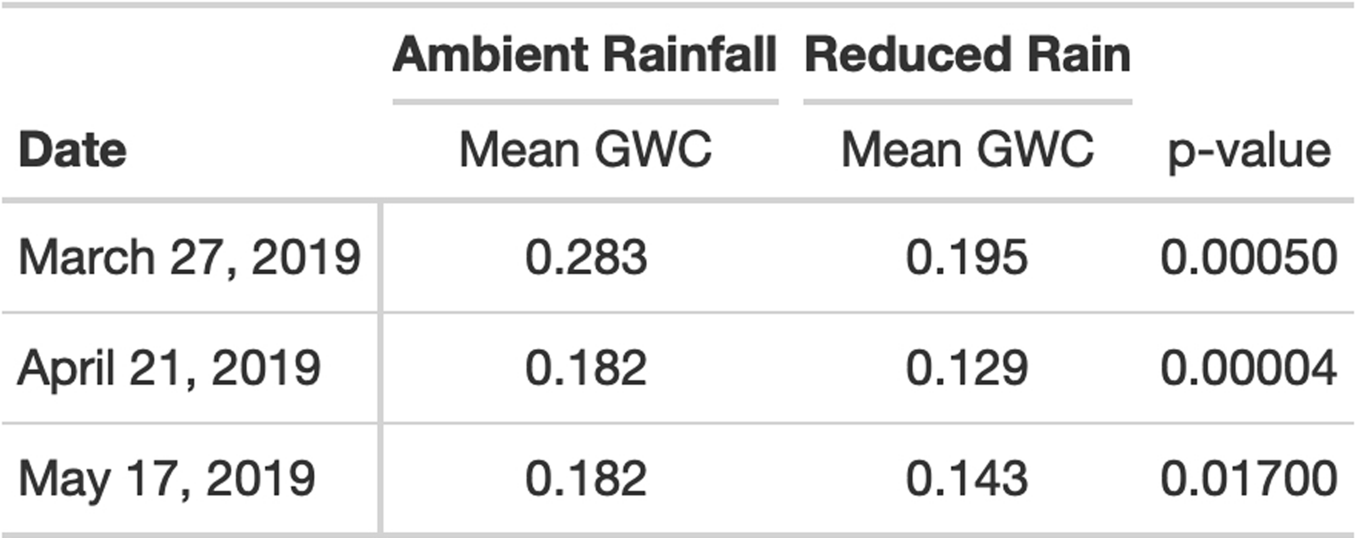
Extended Data Table 5 | Ω, a structural analog of stabilizing niche differences and θ, a structural analog of fitness differences[35] for each species triplet and their predicted competition outcome using the structural method under the two rainfall treatments

		Ambient Rainfall			Reduced Rain		
	Species	Ω	θ	Predicted Coexistence?	Ω	θ	Predicted Coexistence?
Coexist in ambient but not reduced rainfall	AC-HO-PL	0.050	8.81	yes	0.000	15.87	no
Coexist in reduced rainfall but not ambient	AC-PL-UR	0.036	11.22	no	0.185	16.79	yes
	FE-PL-UR	0.007	12.67	no	0.154	24.10	yes
	PL-SA-UR	0.091	19.46	no	0.101	28.90	yes
Coexist in neither	AC-FE-HO	0.035	13.06	no	0.028	23.64	no
	AC-FE-PL	0.013	17.38	no	0.071	18.05	no
	AC-FE-SA	0.066	21.12	no	0.065	36.45	no
	AC-FE-UR	0.016	11.56	no	0.141	31.03	no
	AC-HO-SA	0.071	16.12	no	0.010	30.28	no
	AC-HO-UR	0.028	10.63	no	0.004	20.54	no
	AC-PL-SA	0.092	20.18	no	0.210	23.78	no
	AC-SA-UR	0.063	16.69	no	0.069	43.23	no
	FE-HO-PL	0.008	16.88	no	0.024	23.57	no
	FE-HO-SA	0.047	21.89	no	0.045	38.91	no
	FE-HO-UR	0.017	5.73	no	0.141	23.21	no
	FE-PL-SA	0.000	22.57	no	0.114	29.39	no
	FE-SA-UR	0.025	19.09	no	0.035	47.75	no
	HO-PL-SA	0.081	20.96	no	0.030	23.74	no
	HO-PL-UR	0.053	14.88	no	0.033	22.59	no
	HO-SA-UR	0.065	21.00	no	0.028	41.44	no

Extended Data Table 6 | Ω, a structural analog of stabilizing niche differences and θ, a structural analog of fitness differences[35] for each species quadruplet, quintuplet and sextuplet, and their predicted competition outcome using the structural method under the two rainfall treatments

		Ambient Rainfall			Reduced Rain		
	Species	Ω	θ	Predicted Coexistence?	Ω	θ	Predicted Coexistence?
Quadruplets	AC-FE-HO-PL	0.0016	16.96	no	0.0040	20.40	no
	AC-FE-HO-SA	0.0055	19.57	no	0.0078	32.61	no
	AC-FE-HO-UR	0.0018	11.37	no	0.0135	24.16	no
	AC-FE-PL-SA	0.0042	20.20	no	0.0220	27.65	no
	AC-FE-PL-UR	0.0004	14.52	no	0.0251	21.90	no
	AC-FE-SA-UR	0.0053	17.81	no	0.0084	43.18	no
	AC-HO-PL-SA	0.0170	16.36	no	0.0003	22.59	no
	AC-HO-PL-UR	0.0065	10.71	no	0.0003	17.34	no
	AC-HO-SA-UR	0.0058	15.91	no	0.0017	37.20	no
	AC-PL-SA-UR	0.0118	16.90	no	0.0256	32.22	no
	FE-HO-PL-SA	0.0002	21.31	no	0.0073	29.13	no
	FE-HO-PL-UR	0.0008	13.61	no	0.0075	24.77	no
	FE-HO-SA-UR	0.0038	18.11	no	0.0055	44.08	no
	FE-PL-SA-UR	0.0012	18.39	no	0.0142	36.46	no
	HO-PL-SA-UR	0.0123	19.56	no	0.0042	29.53	no
Quintuplets	AC-FE-HO-PL-SA	0.0003	19.35	no	0.0011	26.21	no
	AC-FE-HO-PL-UR	0.0000	14.64	no	0.0017	21.29	no
	AC-FE-HO-SA-UR	0.0002	17.13	no	0.0008	38.16	no
	AC-FE-PL-SA-UR	0.0001	17.53	no	0.0023	34.01	no
	AC-HO-PL-SA-UR	0.0012	15.49	no	0.0001	28.80	no
	FE-HO-PL-SA-UR	0.0003	18.26	no	0.0011	34.14	no
Sextuplet	AC-FE-HO-PL-SA-UR	0.0000	17.26	no	0.0002	31.09	no

Extended Data Table 7 | Gravimetric water content (GWC) measured at three different times during the experiment



	Ambient Rainfall	Reduced Rain	
Date	Mean GWC	Mean GWC	p-value
March 27, 2019	0.283	0.195	0.00050
April 21, 2019	0.182	0.129	0.00004
May 17, 2019	0.182	0.143	0.01700

P-values determined by t-tests for samples on each date.

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Corresponding author(s): Mary Van Dyke

Last updated by author(s): September 15, 2022

Reporting Summary

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☒	☐	For Bayesian analysis, information on the choice of priors and Markov chain Monte Carlo settings
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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	All data was self collected in the field by the authors and research assistants.
Data analysis	All data was analyzed in R (v.4.2.0). All code is archived on zenodo: https://doi.org/10.5281/zenodo.7083314 . The structural analysis scripts were adapted from public scripts for Saavedra et al. 2017 Ecological Monographs. This is indicated at the top of each of these scripts.

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Human research participants

Policy information about studies involving human research participants and Sex and Gender in Research.

Reporting on sex and gender	N/A
Population characteristics	N/A
Recruitment	N/A
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Note that full information on the approval of the study protocol must also be provided in the manuscript.

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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.

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Ecological, evolutionary & environmental sciences study design

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

Study description	The study aimed to understand how species competitive interactions were affected by water availability. Six species were planted in 106 pair-wise competition plots with 5 sowing densities and two precipitation treatments.
Research sample	We grew six species of annual plants including acmispon wrangelianus, festuca microstachys, hordium murinum, plantago erecta, salvia columbariae, and uropappus lindleyi.
Sampling strategy	We had 4 replicate plots per species per density ultimately resulting in 106 plots with two water treatments. Previous studies (Kraft et al. 2015) showed that this would be an adequate number of replicates to estimate the desired parameters.
Data collection	Data was collected mainly by Mary Van Dyke, with help from Kenji Hayashi, Megan Clarke, and Heather Lindsay. Data collected includes number of germinants, number of competitors within a 10cm radius of a focal plant and number of seeds produced. Functional trait data and seed survival data were collected in previous years by Dr. Nathan Kraft, Dr. Jonathan Levine, and Dr. Gaurav Kandlikar.
Timing and spatial scale	Number of germinants was counted in early January 2019, competitors were counted twice; once in February 2019 and once when the focal plant had set seed in spring 2019. Number of seeds produced was counted when more than approximately 75 percent of the plant was fruiting. Exact dates for each plant is included in the data sheet provided.
Data exclusions	No data was excluded.
Reproducibility	All methods are clearly stated in the methods section ensuring the study's reproducibility.
Randomization	106 plots were placed under 14 shelters within a fenced area. Each plot was randomly assigned to receive seeds of one of six focal species in the background at one of 5 sowing densities ranging from 0 to 12 grams of seed per meter squared with 4 replicate plots per density per background species. Half the replicates were assigned to the ambient treatment and half to the reduced precipitation treatment. A randomizer in R was used to determine plot order with each shelter having an equal number of plots in each precipitation treatment.
Blinding	It was impossible to blind all data collection because to collect the fecundity data we had to handle the plants and it was clear roughly how many competitors were around them and which water treatment the plot was assigned to but we did not let this influence our counts.

Did the study involve field work? ☒ Yes ☐ No

Field work, collection and transport

Field conditions	Over the 8 months we worked, the conditions ranged from 30 degrees to 100 degrees F with days of rain and sunshine.

Location	Sedgwick Reserve, Santa Barbara county, CA, USA (34° 40′N, 120° 00′ W), 730m above sea level.
Access & import/export	All seed used was collected locally within the reserve the season prior.
Disturbance	Study took place on a previously disturbed site where plants had been cleared and a fence surrounded the area.

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

Methods

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