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Can functional traits predict plant community response to global change?

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Abstract. One primary goal at the intersection of community ecology and global change biology is to identify functional traits that are useful for predicting plant community response to global change. We used observations of community composition from a long-term field experiment in two adjacent plant communities (grassland and coastal sage shrub) to investigate how nine key plant functional traits were related to altered water and nitrogen availability following fire. We asked whether the functional responses of species found in more than one community type were context dependent and whether community-weighted mean and functional diversity were significantly altered by water and nitrogen input. Our results suggest varying degrees of context dependency. We found that plants with high leaf nitrogen concentration (specifically nitrogen fixers), shallow roots, and low leaf mass per unit area and plant-level transpiration were similarly negatively influenced by added nitrogen across community types. In contrast, responses to water manipulations exhibited greater context dependency; plants with high water-use efficiency, lower plant-level transpiration rates, and shallower roots were negatively impacted by simulated drought in the shrub-dominated community, but there was no significant relationship between these traits and changes in water inputs in the grassland community. Similarly, we found context dependency in community-wide trait responses to global change. Functional diversity tended to be higher in plots with reduced water as compared to those with added water in grassland, while the opposite trend was observed in coastal sage scrub. Our results indicate that some traits are strong predictors of species and community response to altered water and nitrogen availability, but the magnitude and direction of the response may be modulated by the abiotic and biotic context.

Key words: California grassland; coastal sage scrub; community response to global change; community-weighted means; functional diversity; invasive grasses; nitrogen manipulation; rainfall manipulation.

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INTRODUCTION

Functional trait-based approaches to global change move beyond simply characterizing an

ecological response and focus on building a predictive capacity based on the differential effects of environmental change on plant functional strategies (McGill et al. 2006, Gornish and

Prather 2014, Violle et al. 2014). Focusing on traits facilitates a mechanistic understanding of how shifts in species composition will alter ecosystem processes (Garnier et al. 2004, Diaz et al. 2013), while providing a framework for maximizing resilience to global change (Laliberte et al. 2010, Sundstrom et al. 2012), and enabling the identification of environmental feedbacks (Bardgett and Wardle 2010). Identifying which traits determine response to global change factors allows for greater generalizations that enable predictions for how species with similar traits may respond in other settings (Gornish and Prather 2014).

One critical challenge in trait-based ecology is context dependency (Pennings et al. 2005, Harrison et al. 2010, Gornish and Prather 2014). Species' performances within a community are determined not only by abiotic factors (climate, resource availability), but also by a complex suite of biotic factors (competition, facilitation; Grubb 1994, Chesson 2000, Vellend 2010). Determining how the same species respond to identical global change manipulations when grown in different biotic environments may help resolve why functional traits may be strong predictors of global change in some cases and weak predictors in others (Sandel et al. 2010, Gornish and Prather 2014). Moreover, quantifying how trait distributions of biotic communities respond to climate change is useful because traits provide a mechanistic understanding of how shifts in species composition will alter ecosystem processes (Garnier et al. 2004).

Scaling from traits of individual species through the community to ecosystem functioning can be achieved by examining two complementary community-level metrics: community-weighted mean (CWM) trait values (Lavorel and Garnier 2002, Garnier et al. 2004) and functional diversity (FD; Mason and de Bello 2013). CWM trait values are based on Grime's mass ratio hypothesis (Grime 1998), which proposes that each species contributes to ecosystem function in proportion to its biomass. The overall distribution of trait values in a community is perhaps more important for ecosystem processes than its mean value, and several measures of FD allow for quantification of the variance of traits (Diaz et al. 2007, Laliberte and Legendre 2010, Mason and de Bello 2013). Both CWM and FD are useful metrics for

understanding community responses to global change (Klump and Soussana 2009, Fernandez-Going et al. 2012, Laliberte et al. 2012).

Most semi-arid regions, including the southwestern United States, are expected to experience more extreme precipitation events, more severe droughts, and increasing fire frequency with global climate change (Syphard et al. 2007, Das et al. 2013, Hufnagel and Garamvolgyi 2014). Recent precipitation trends have already shifted plant community composition in some areas, often in association with species-dependent rates of mortality (Breshears et al. 2005, Kelly and Goulden 2008). Increasing fire frequency has also been identified as altering plant community composition (Diaz-Delgado et al. 2002, Talluto and Suding 2008). In principle, plant functional traits should be related to these shifts, although in practice these relationships may be difficult to predict. For example, species with traits for tolerating drier soils, such as high water-use efficiency (WUE), may be favored under increased drought (Dudley 1996, Saldana et al. 2007, Kimball et al. 2013). Alternatively, species that escape drought, with traits such as rapid growth and early flowering, may increase under drier conditions (Franks 2011). An improved understanding of when each strategy is favored, including its context dependency, is needed for generalization to other systems.

Functional traits can also determine species' responses to nitrogen deposition (Vitousek et al. 1997, Evans et al. 2001, Fenn et al. 2010). Nitrogen deposition has been linked to decreasing biodiversity, often in association with increased abundance of non-native species (Phoenix et al. 2006, Rao and Allen 2010, Ochoa-Hueso et al. 2011). The hypothesized reason for proliferation of invasive species in response to added nitrogen is that non-natives who become invasive in their introduced range are often positioned further along the "fast-return" end of the leaf economic spectrum, possessing traits that allow them to take advantage of added nitrogen with increased growth (Leishman et al. 2010, Ordóñez and Olff 2013). Other traits, such as the ability to fix atmospheric nitrogen through symbiotic associations with microbes, can yield a negative species response to added nitrogen (Zavaleta et al. 2003, Kimball et al. 2014). Changes in abundance and community composition can influence ecosystem

processes such as litter decomposition and net primary production (Allison et al. 2013, Coomes et al. 2014). Indeed, one of the goals of linking functional traits to global change response is to understand how shifting community composition affects nutrient cycling (Lavorel and Garnier 2002, Garnier et al. 2004, McGill et al. 2006).

We measured traits of dominant species in adjacent Southern California grassland and coastal sage scrub ecosystems and related those traits to species responses to precipitation and nitrogen manipulations over 6 years following wildfire. Our overarching goal was to examine context dependency in response to global change by examining how specific plant traits related to shifts in community composition, and by scaling trait responses to the community level. Specifically, we addressed the following questions: (1) Do traits related to water and nitrogen use determine species' responses to water and nitrogen manipulations after a wildfire? (2) Did species that were found in both communities exhibit consistent responses in the two ecosystem types? and (3) How do traits relate to manipulations when scaled to the community level? We hypothesized that fast-growing plant species, with traits like high carbon assimilation rates, would be more positively affected by added N and more negatively impacted by drought than more stress-tolerant plant species, with traits such as high WUE (Grime 1977, Tilman and Wedin 1991, Wright et al. 2004, Reich 2014). Less is known about the context dependency of response to abiotic manipulations, so we did not have any specific hypotheses regarding the response of species found in more than one community (Arft et al. 1999, Pennings et al. 2005). We hypothesized that the relationships between traits and water and nitrogen manipulations would scale up to the community level, such that drought plots would be characterized by slower nutrient cycling than added-nitrogen plots (Diaz and Cabido 1997). Our results highlight the importance of context and scale in predicting vegetation change in response to altered precipitation and nitrogen deposition.

METHODS

Study site

This experiment was conducted in a Mediterranean-climate grass-shrubland ecotone, in the

foothills of the Santa Ana Mountains in Orange County, California (117.704° W, 33.742° N). The exact amount of precipitation at the study site varies greatly from year to year, with an annual mean of 30 cm that falls between November and April, and a fairly predictable summer drought from May through October (Kimball et al. 2014, Parolari et al. 2015). The observations are part of a large manipulative experiment established in 2007 to assess the effects of drought, nitrogen deposition, and fire on community and ecosystem properties. The original experimental design included a controlled burn in February 2007, which was applied to half of the plots. However, the remaining plots, along with the previously burned grassland plots, burned in a natural, high intensity wildfire on 22 October 2007. Previous analyses have shown that there were no significant differences in plant community composition between the areas with contrasting burn histories (Kimball et al. 2014). Our analysis therefore lumps these areas and focuses on the relationship between functional traits and response to precipitation and nitrogen manipulations following fire.

Details of the experiment are included in previous publications (Potts et al. 2012, Allison et al. 2013, Kimball et al. 2014). Briefly, we established eight replicate blocks of three plots in each plant community (6.7 × 9.3 m in grassland and 18.3 × 12.2 m in coastal sage scrub) that received ambient, reduced (approximately 40% less than ambient), or increased (approximately 40% more than ambient) precipitation (Fig. 1). Steel frames with retractable clear polyethylene sheets were used to shield precipitation from reduced-precipitation plots during a subset of storms. Runoff from the covered plots was collected and subsequently applied to the added-water plots using high-pressure gasoline-driven pumps. The water-input manipulation began in the 2006–2007 growing season for grassland plots and in 2008–2009 for coastal sage scrub plots.

Each plot was divided into half length-wise and randomly assigned to ambient or added (6 g N·m⁻²·yr⁻¹) nitrogen. The flush of N that occurs at the beginning of the wet season was simulated by adding 2 g of quick-release calcium nitrate (15.5% N, 0% P, 0% K, 19% Ca) immediately prior to the first storm of the season. The remaining 4 g was applied as slow-release

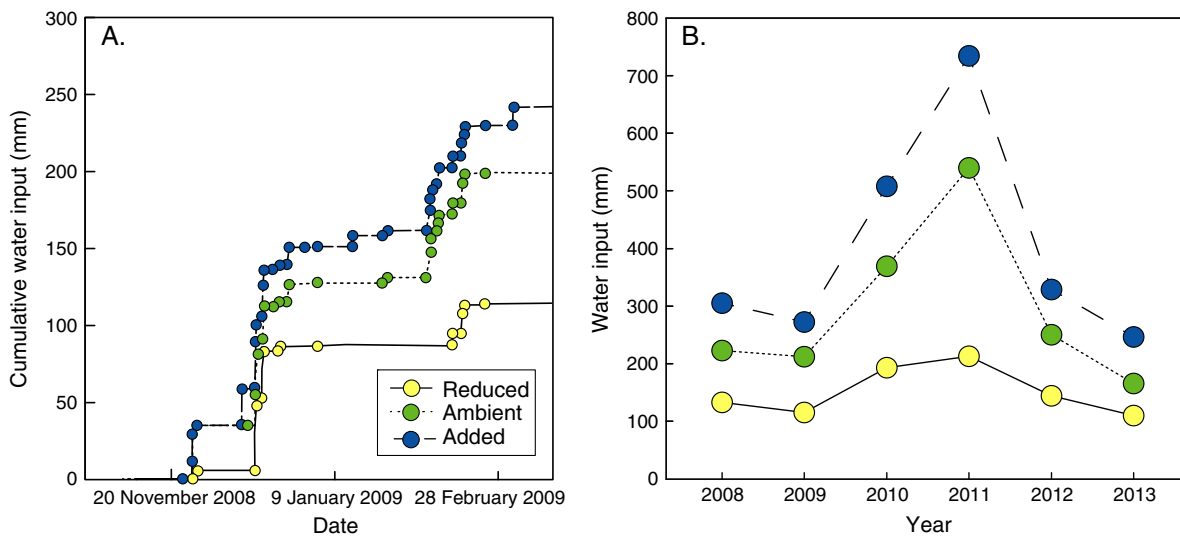


Fig. 1. (A) Cumulative water input during the 2008–2009 wet season for the three water treatments (reduced, ambient, and added). (B) Total water input for each growing season, indicated as the year when the season ended.

(4 months) calcium nitrate (14% N, 0% P, 0% K, 17% Ca) 1 month into the growing season.

Functional trait survey

From January to April 2010, we collected functional trait data from five replicate individuals of 15 common species occurring in the manipulative field experiment (Table 1). Individuals were sampled outside of the manipulated plots in order to address our primary research question of whether trait values may be used to predict response to water and nitrogen manipulations. Our third research question, on how manipulations altered community-weighted trait values, could not have been addressed by sampling traits through time within plots because changes in community composition in response to experimental manipulations were so extreme that replicates of the same species did not occur in all treatments (Kimball et al. 2014). We selected traits known to influence water and nitrogen use, as those were our manipulated environmental variables, as well as traits correlated with growth and reproductive output (Tjoelker et al. 2005, Reich 2014). Measured traits included photosynthetic capacity (A), light-use efficiency (ϕ PSII), WUE, leaf nitrogen (N) concentration, leaf mass per unit area (LMA), plant height, plant-level transpiration (E_p), root depth, and specific root

length (SRL). Physiological and chemical analyses were performed on recently matured leaves.

Photosynthesis, transpiration, and chlorophyll fluorescence were measured with a LI-6400 portable gas exchange system (LI-COR, Lincoln, Nebraska, USA). All measures were collected between 08:00 and 14:00 local time with chamber relative humidity between 40% and 60%. Ambient CO_2 concentration, leaf temperature, and irradiance level were held constant at 400 $\mu\text{L/L}$, 25°C, and 2000 $\mu\text{mol photon/s}$. The effective quantum yield of PSII (ϕ PSII) was calculated as $(F_m' - F_s)/F_m'$, where F_s is the fluorescence yield of a light-adapted leaf and F_m' is the maximal fluorescence during a saturating light flash. Measurements were taken after 10 min, by which time photosynthesis and transpiration had achieved steady state. When leaves were too small to fill the chamber, the cuvette leaf area was determined and used to area-correct gas exchange data. WUE was measured as photosynthetic rate divided by transpiration rate.

Following physiological measurements, leaves were harvested, scanned for leaf area, and dried to calculate LMA and average leaf size. Total leaf N concentration was determined with an elemental analyzer (Costech 4010 elemental combustion system, Valencia, California, USA). Plant height was measured from the ground to the tip

Table 1. Species used in these analyses, along with their four-letter species code, plant family, life form, and the plant communities (CSS or GL) in which they are found.

Species	Code	Family	Life form	Plant community
<i>Amsinckia menziesii</i>	amme	Hydrophyllaceae	Annual forb	GL
<i>Artemisia californica</i>	arca	Asteraceae	Woody shrub	CSS
<i>Avena fatua</i> *	avfa	Poaceae	Annual grass	CSS and GL
<i>Bromus diandrus</i> *	brdi	Poaceae	Annual grass	CSS and GL
<i>Bromus madritensis</i> *	brma	Poaceae	Annual grass	CSS and GL
<i>Brassica nigra</i> *	brni	Brassicaceae	Annual forb	CSS and GL
<i>Dichelostemma capitatum</i>	dica	Liliaceae	Bulb	CSS and GL
<i>Erodium cicutarium</i> *	erci	Geraniaceae	Annual forb	CSS and GL
<i>Festuca perennis</i> *	fepe	Poaceae	Annual grass	CSS and GL
<i>Acmispon glaber</i>	acgl	Fabaceae	Subshrub	CSS
<i>Lupinus bicolor</i>	lubi	Fabaceae	Biennial nitrogen-fixing forb	CSS and GL
<i>Lupinus truncatus</i>	lutr	Fabaceae	Biennial nitrogen-fixing forb	CSS
<i>Malosma laurina</i>	mala	Anacardiaceae	Woody shrub	CSS
<i>Medicago polymorpha</i> *	mepo	Fabaceae	Annual nitrogen-fixing forb	CSS and GL
<i>Stipa lepida</i>	stle	Poaceae	Perennial grass	CSS
<i>Salvia mellifera</i>	same	Lamiaceae	Woody shrub	CSS

Note: Invasive species are denoted with an asterisk.

of vegetative material rather than inflorescences, which can be much taller than leaves in many herbaceous species. We counted the number of leaves on each replicate individual (five per species). Plant-level transpiration rate was estimated as $E_{\text{plant}} = E_{\text{leaf}} \times \text{leaf size} \times \text{leaf number}$. For herbaceous species, entire plants were harvested by digging up the entire root system. Root depth was measured as the length of the deepest root. A representative subsample of the root system (including absorbing and conducting roots) totaling 60 cm was weighed to determine SRL (cm/mg). For woody shrub species, root depth was difficult to determine and we used species means from the literature (Hellmers et al. 1955). We dug a 30-cm hole adjacent to each shrub and excavated a portion of the root system to determine SRL as described above.

Plant cover

Plant cover in the grassland plots was determined by point intercept, using a 1 × 1 m frame divided into a 10 × 10 cm grid positioned above the canopy. All species at each intersection point on the frame's grid (100 points) were recorded. Plant cover in coastal sage scrub plots was determined in a permanent 4 × 4 m subplot located in the center of each plot. These subplots were divided into 64 0.25-m² sections, and species presence in each section was noted. The number

of sections that each shrub species occupied was recorded, and the species' total fractional cover was calculated for the plot. The cover of species that were present but occupied less than the total area of one section was visually estimated and recorded as <1.6% or <1%. Our previous publications for the site focused on the effects of water and nitrogen manipulation after fire on the composition of coastal Sage Scrub (Kimball et al. 2014) and grassland (Matulich et al. 2015) communities. Here, we use these data to calculate species' responses to manipulations and investigate relationships between cover data and functional traits to address whether traits may be used to predict response to changes in water and nitrogen availability.

Data analysis: species' traits and responses in different contexts

To understand how each species responded to nitrogen manipulations (RR_N), we calculated response ratios (lnRR) as $\ln(\text{mean cover in nitrogen addition plots}/\text{mean cover in control plots})$. Separate lnRRs were calculated for each water condition (added, ambient, or reduced) and for each year. Response to added water (RR_{+w}) was calculated as $\ln[(\text{mean cover in water-addition plots})/(\text{mean cover in ambient-water plots})]$, and response to reduced water (RR_{-w}) was calculated as $\ln[(\text{cover in water-reduction plots})/$

(cover in ambient-water plots)]. RR_{+w} and RR_{-w} were calculated separately for ambient and added nitrogen.

For species with more than 5% cover in at least one treatment, we used separate linear regressions to evaluate relationships between species' $\ln RR$ and trait values for each trait and year. In some cases where residuals were not normally distributed, traits were \ln -transformed (height, root depth, SRL, LMA, and E_p). To simplify the complexity in trait variation, we conducted a principal components analysis of all traits. Species found in both grassland and coastal sage scrub communities were included in the analysis. We used linear regression to calculate the relationship between $\ln RR$ s and the first two principle component axes.

For all species with at least 5% cover in both grassland and coastal sage scrub communities, we used two-way ANOVAs to determine whether RR_N varied depending on plant community or on water treatment. Similarly, we used two-way ANOVAs to determine whether RR_{+w} and RR_{-w} varied depending on plant community or on nitrogen treatment.

Data analysis: community-level traits

We calculated CWM trait values (Garnier et al. 2004) and functional dispersion (FD_{is} ; Laliberte and Legendre 2010) to understand how water and nitrogen manipulations influenced trait distributions at the community level. For individual grassland and coastal sage scrub plots, CWM trait values were calculated for each trait as the sum of species-level traits weighted by the species relative abundances. FD_{is} was calculated as the mean distance of each species, weighted by relative abundances, to the centroid of all species in a plot for each trait (Laliberte and Legendre 2010). Our 15 species captured, on average, 90% of the species present in coastal sage scrub plots. Grassland plots were more diverse and plots where our 15 species amounted to less than 25% of total cover were excluded from the functional dispersion calculations. Plots in which we only had trait values on one species were excluded from calculations of FD_{is} . We used mixed model, repeated measures ANOVAs with water, nitrogen, and the water-by-nitrogen interaction as fixed factors, and with block and the block-by-water interaction as random factors (which takes

into account the split-plot design), and year as a repeated factor to determine whether CWM and FD_{is} trait values changed through time and with water and nitrogen manipulations (SAS Institute, version 9.3, Cary, North Carolina, USA). We used the first-order autoregressive covariance structure in the REPEATED statement of the model because it treats successive years as being more correlated and allows correlations to decline exponentially with time. Grassland and coastal sage scrub plots were analyzed separately.

RESULTS

Species' traits and responses in different contexts

The effect of the manipulations on species abundance was significantly related to the species' traits, although these relationships varied by year, factors manipulated, and plant community. We hypothesized that plant species with traits characteristic of fast-growing plants would be more positively affected by added nitrogen and more negatively impacted by reduced water than plant species with traits characteristic of stress tolerance. PC1 was generally correlated to traits that influence stress tolerance, while PC2 was generally correlated with traits characteristic of faster growth (Table 2). Specifically, the first principal component (PC1) was positively correlated with root depth and leaf mass per unit area (LMA), and negatively correlated with leaf N and photosynthetic capacity (A, Table 2). The

Table 2. Correlation of individual traits with the first two principle component functions resulting from principal components analysis.

Trait	PC1	PC2
Height	0.202116	0.194485
Leaf N	-0.332326	0.443161
LMA	0.476417	0.148197
E_p	0.443059	0.329253
$\phi PSII$	-0.133154	0.52562
root_depth	0.511438	0.205044
SRL	0.17443	-0.354097
A	-0.251926	0.423808
WUE	0.228565	0.109982

Notes: The first principle component function accounted for 35% of the variation, and the second function accounted for 27% of the variation. LMA, leaf mass per unit area; E_p , plant-level transpiration; $\phi PSII$, light-use efficiency; SRL, specific root length; A, photosynthetic capacity; WUE, water-use efficiency.

second principle component (PC2) was positively correlated with light-use efficiency (ϕ PSII), photosynthetic capacity (A), leaf N, and plant-level transpiration (E_p , Table 2).

We found unexpected significant positive relationships between PC1 and RR_N (Fig. 2A, B), likely due to the negative response of nitrogen fixers to added nitrogen. Significant positive relationships between PC2 and RR_{+w} in CSS plots in both ambient-nitrogen (Appendix S1: Table S1) and added-nitrogen (Fig. 2D) plots generally supported our hypothesis that fast-growing plants would respond more positively to added water. However, the relationship between PC2 and RR_{+w} was negative in GL plots in all years in ambient-nitrogen plots and in the majority of years in added-nitrogen plots (Appendix S1: Table S1; Fig. 2C), indicating the importance of biological context on relationships between traits and response to manipulations. Relationships between PC scores and RR_{-w} were generally not significant and did not support our hypothesis (Appendix S1: Table S1).

The relationship between individual trait values and response to manipulations varied with context (year, community, and combination of manipulations; Appendix S1: Table S1). Plants with higher leaf N concentration (specifically nitrogen fixers) were more negatively impacted by added nitrogen than plants with lower leaf N (Fig. 2E, F; Appendix S1: Table S1). This result was entirely driven by the nitrogen-fixing species in the community, such that removing those species from the analyses resulted in no significant relationship between leaf N and response to nitrogen ($R^2 < 0.03$ and $P > 0.06$ for analyses without nitrogen-fixing species). In 2009 under ambient-nitrogen conditions and in 2009 and 2010 under added-nitrogen conditions, grassland species with thinner or less dense roots (higher SRL values) had stronger positive responses to water addition (Fig. 2G). Contrary to our hypothesis, species with higher WUE were more negatively impacted by water reduction in the coastal sage scrub plots in most years with added nitrogen, and there was no relationship between WUE and response to water reduction in the grassland plots (Appendix S1: Table S1; Fig. 2H). In coastal sage scrub plots, plants with higher plant-level transpiration rates (E_p) and deeper roots had greater positive responses to added

water in most years under ambient nitrogen (Appendix S1: Table S1).

For species regularly found in both grassland and coastal sage scrub plots, responses to manipulations varied significantly depending on the community in which the species was found and sometimes depending on the nitrogen or water treatment (Fig. 3; Appendix S1: Table S2). For *Bromus madritensis*, the response to adding nitrogen was more negative under reduced-water conditions in grassland plots, but was not significantly influenced by water availability in coastal sage scrub plots (Fig. 3A). For the nitrogen-fixing forb *Lupinus bicolor*, the negative response to added nitrogen was muted in reduced-water plots (Fig. 3B). Non-native grasses, including *B. madritensis*, *B. diandrus*, and *Festuca perennis*, responded positively to added water (and likewise sometimes negatively to reduced water) in grassland plots, but they responded negatively to added water in coastal sage scrub plots (Fig. 3C–E, G). The native forb *L. bicolor* responded more negatively to added water in grassland than in coastal sage scrub plots (Fig. 3F).

Community-level traits

CWM values of all traits changed significantly through time in both grassland and coastal sage scrub (Fig. 4; Appendix S1: Tables S3 and S4). Grassland plots, dominated by annual plants, had CWM trait values that fluctuated from year to year (Fig. 4, left-hand column), presumably representing changes in community composition that tracked inter-annual changes in precipitation (Fig. 1) and due to time since the 2007 wildfire. In coastal sage scrub plots, CWM values of most traits tended to increase through time, changing continually along with post-fire community recovery (Fig. 4, right-hand column). In grassland plots, the main effects of water and nitrogen on CWM values of WUE (Fig. 4A), root length (Fig. 4C), and E_p (Appendix S1: Table S3) were not significant, while in coastal sage scrub plots, CWM values of these traits (Fig. 4B, D; Appendix S1: Tables S3 and S4) were significantly higher in added-water plots than in reduced-water plots. Although we hypothesized that CWM values of fast-growing plants would increase with added nutrients in the grassland, instead we found that SRL (Appendix S1: Tables

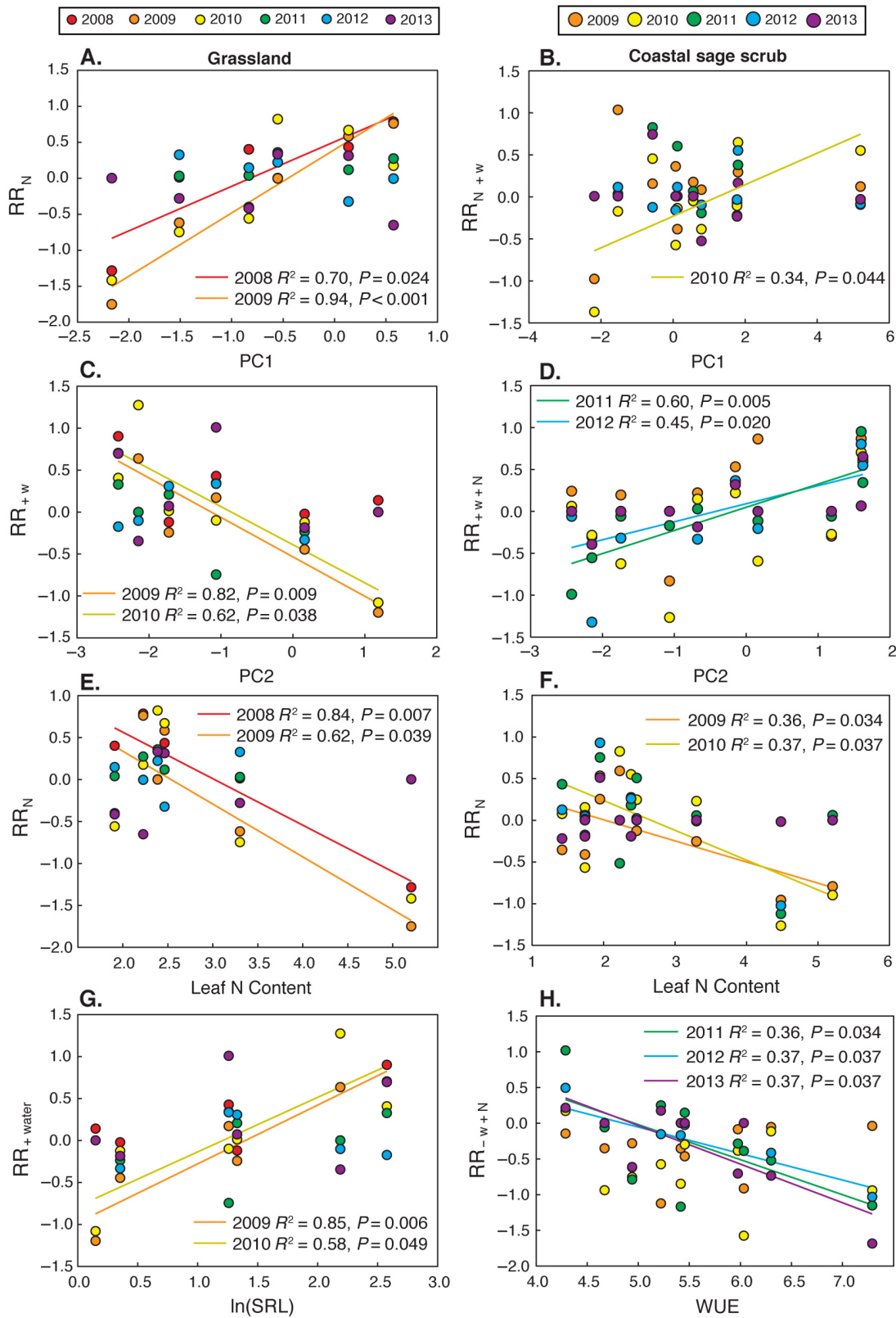


Fig. 2. Relationships between log response ratios to water and nitrogen treatments and traits in grassland (left) and coastal sage scrub (right). Each dot represents an individual species in a given year ($N = 6$ grassland species; $N = 10$ coastal sage scrub species). Panels (A) and (B) show relationships between PC1 on the x -axes and response to nitrogen treatment, RR_N , calculated as $\ln[(\text{cover in N plots})/(\text{cover in ambient-N plots})]$ under ambient-water conditions or RR_{N+w} , under added-water conditions, on the y -axes. Panels (C) and (D) demonstrate relationships between PC2 on the x -axes and RR_{+w} , calculated as $\ln[(\text{cover in water-addition plots})/(\text{cover in ambient-water plots})]$ under ambient nitrogen or added N, on the y -axes. Panels (E) and (F) indicate relationships between leaf N concentration on the x -axes and RR_N on the y -axes. Panels (G) and (H) present relationships between $\ln(\text{SRL})$ or WUE on the x -axes and RR_{+w} or RR_{-w} , calculated as $\ln[(\text{cover in water-reduction plots})/(\text{cover in ambient-water plots})]$, under added- or ambient-N conditions, on the y -axes. Relationships between all traits and all $\ln RR$ s are provided in Appendix S1: Table S1. WUE, water-use efficiency; SRL, specific root length.

S3 and S4), LMA (Fig. 4E), and plant height (Fig. 4G) were significantly higher in added-nitrogen than ambient-nitrogen plots. ϕPSII and leaf N (Fig. 4A, F) were higher in ambient-nitrogen than in added-nitrogen plots. For many traits (root length, SRL, leaf N, ϕPSII , LMA, E_p , and plant height) there was a significant water-by-year interaction (Appendix S1: Table S3). In grassland plots, the interaction indicated CWM values were higher in added-water plots in some years and higher or not significantly different in reduced-water plots in other years. In coastal sage scrub plots, the interaction (for LMA, WUE, root length, and E_p) indicated the increasing influence of water manipulations on traits through time and with fire recovery.

Functional dispersion of leaf N was significantly lower in nitrogen addition plots in both the grassland and coastal sage scrub communities (Fig. 5; Appendix S1: Tables S3 and S4). FD_{is} of ϕPSII also tended to be lower in nitrogen addition plots, especially in those with added water, while FD_{is} of all of other traits was not influenced by N addition. Functional dispersion of height was significantly influenced by water treatment and year, but the direction of the effect varied depending on community (Fig. 5; Appendix S1: Tables S3 and S4). Water-reduction plots had the greatest FD_{is} of height in grassland, and water-addition plots had higher FD_{is} of height in coastal sage scrub. Other traits showed a decrease in FD_{is} over time in coastal sage scrub plots, as the community recovered from the wildfire. In contrast, FD_{is} in grassland tended to fluctuate through time, with lowest values in 2011, the year with the greatest amount of precipitation (Figs. 1, 5).

DISCUSSION

Our observations and analyses lead us to three main conclusions: (1) Some traits were consistently related to the manipulations across community and time; for example, nitrogen-fixing species with a high leaf N concentration had a consistent negative response to added N. (2) Some traits or species exhibited context-dependent responses to the manipulations; for example, the effect of water or nitrogen availability on the abundance of some species differed markedly for individuals growing in grassland vs. coastal sage scrub. (3) Many of the CWM and functional dispersion (FD_{is}) traits varied significantly through time, presumably reflecting the patterns of post-fire recovery and changes in the abiotic and biotic environment; these patterns often interacted with the manipulations, implying that altered water or nitrogen availability can modulate post-fire recovery rate and trajectory.

Relationships between traits and response to manipulations were more complex than our simple hypotheses based on fast-growing vs. stress-tolerant plant traits, reflecting the importance of biotic and abiotic context. Patterns of CWM trait values and FD_{is} often differed between the two plant communities, indicating that the abiotic and biotic environment within each community type leads to context-dependent community responses to perturbation. Our comparison of the responses of individual species to altered water and nitrogen input and in different biotic communities provides a critical demonstration of the effect of context on species' reactions to identical manipulations.

Some of the relationships we observed were consistent across the two communities; for

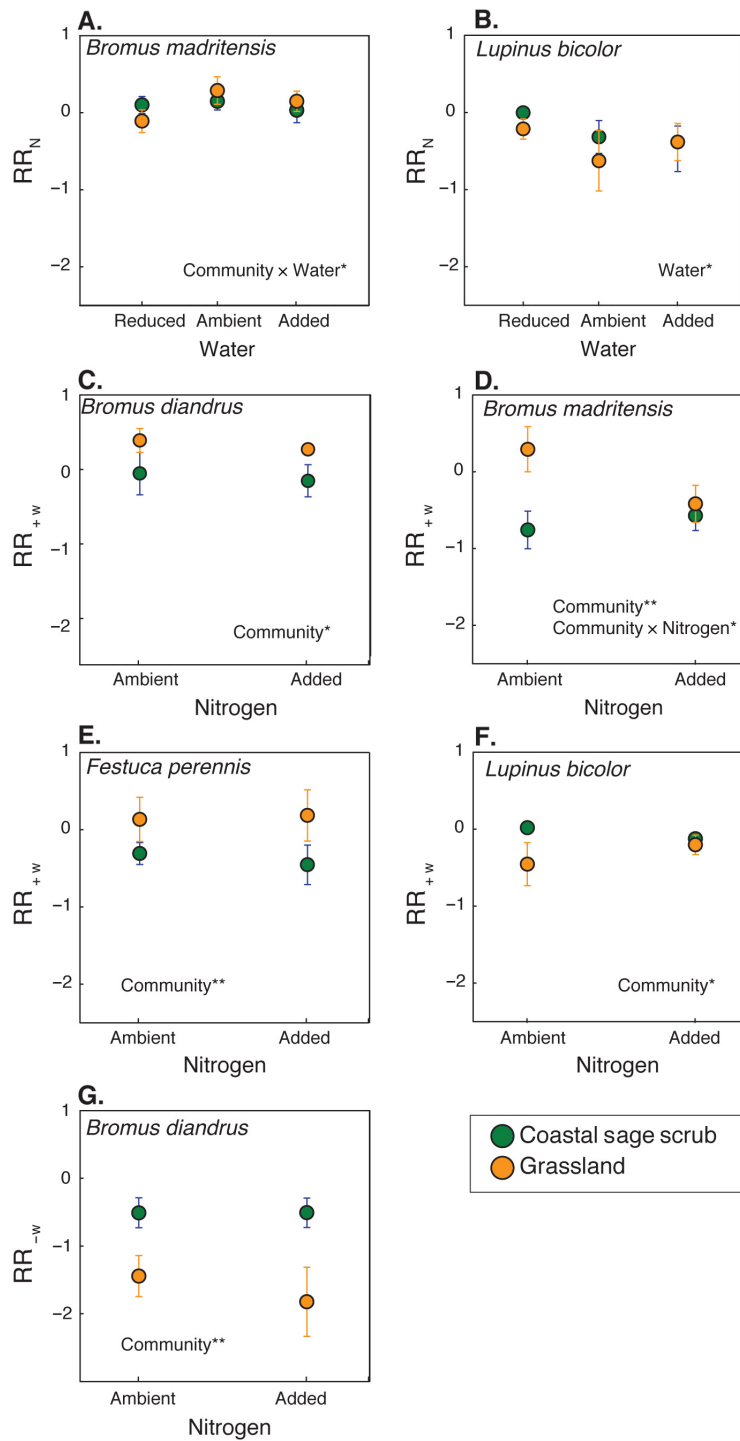


Fig. 3. Response ratios for nitrogen (RR_N) under all water treatments and for plus water (RR_{+w}), and minus water (RR_{-w}) under the two nitrogen treatments, for species that were found in both coastal sage scrub (green) and grassland (yellow) plots. Values are means $\pm 1SE$. Significantly different responses depending on the community, water, or nitrogen treatment in which they were found are listed inside graph panels, where * indicates $P < 0.05$ and ** indicates $P < 0.01$.

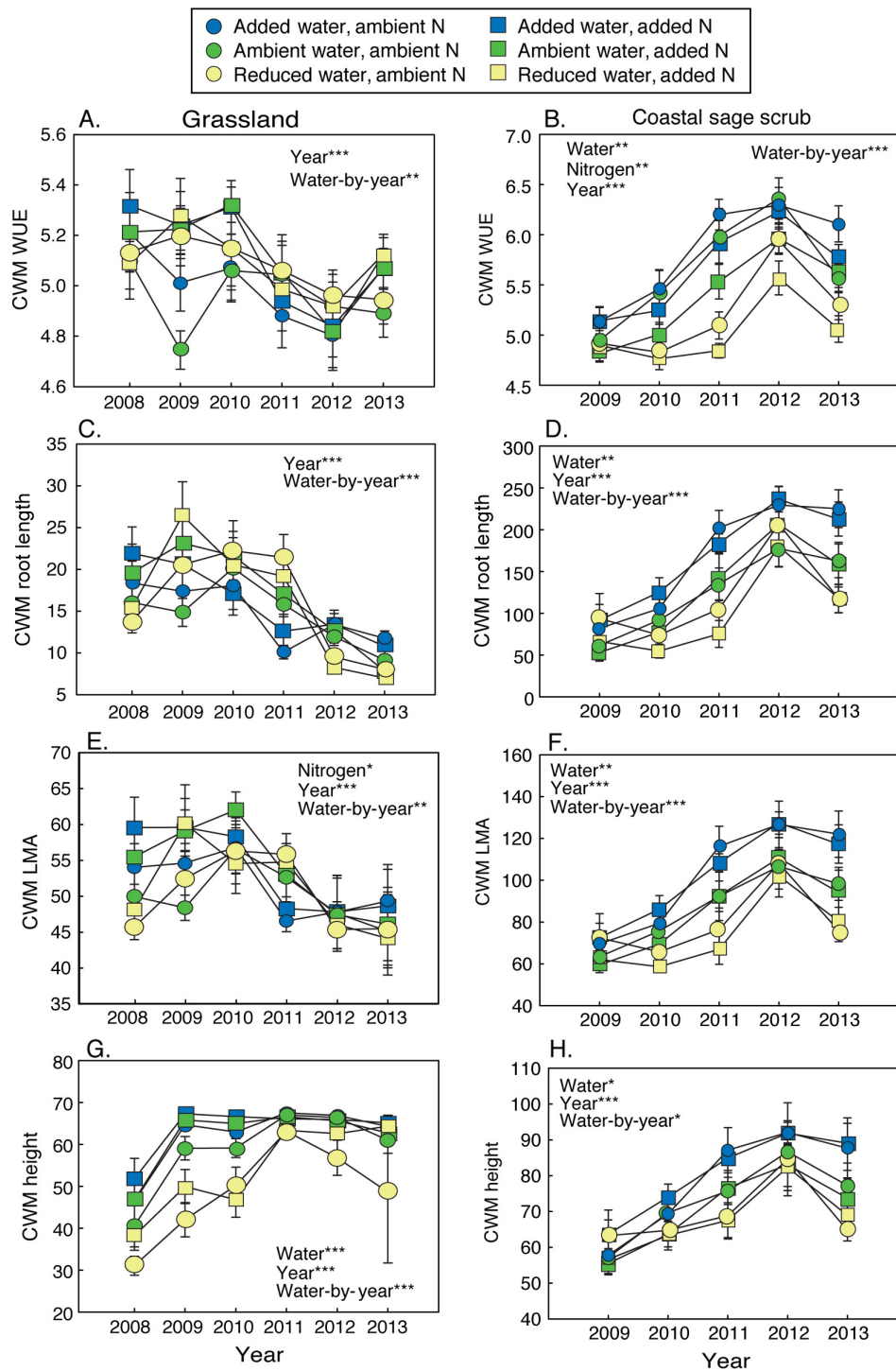


Fig. 4. Community-weighted mean (CWM) values for water-use efficiency (WUE), root length, leaf mass area (LMA), and plant height in grassland (left) and coastal Sage Scrub (right) plots in the different water and N treatments through time. Values are means \pm 1 SE. Results from all ANOVAs on CWM traits are listed in Appendix S1: Table S3. Mean and SE CWM values for all traits are listed in Appendix S1: Table S4A. * $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$; non-significant factors are not listed.

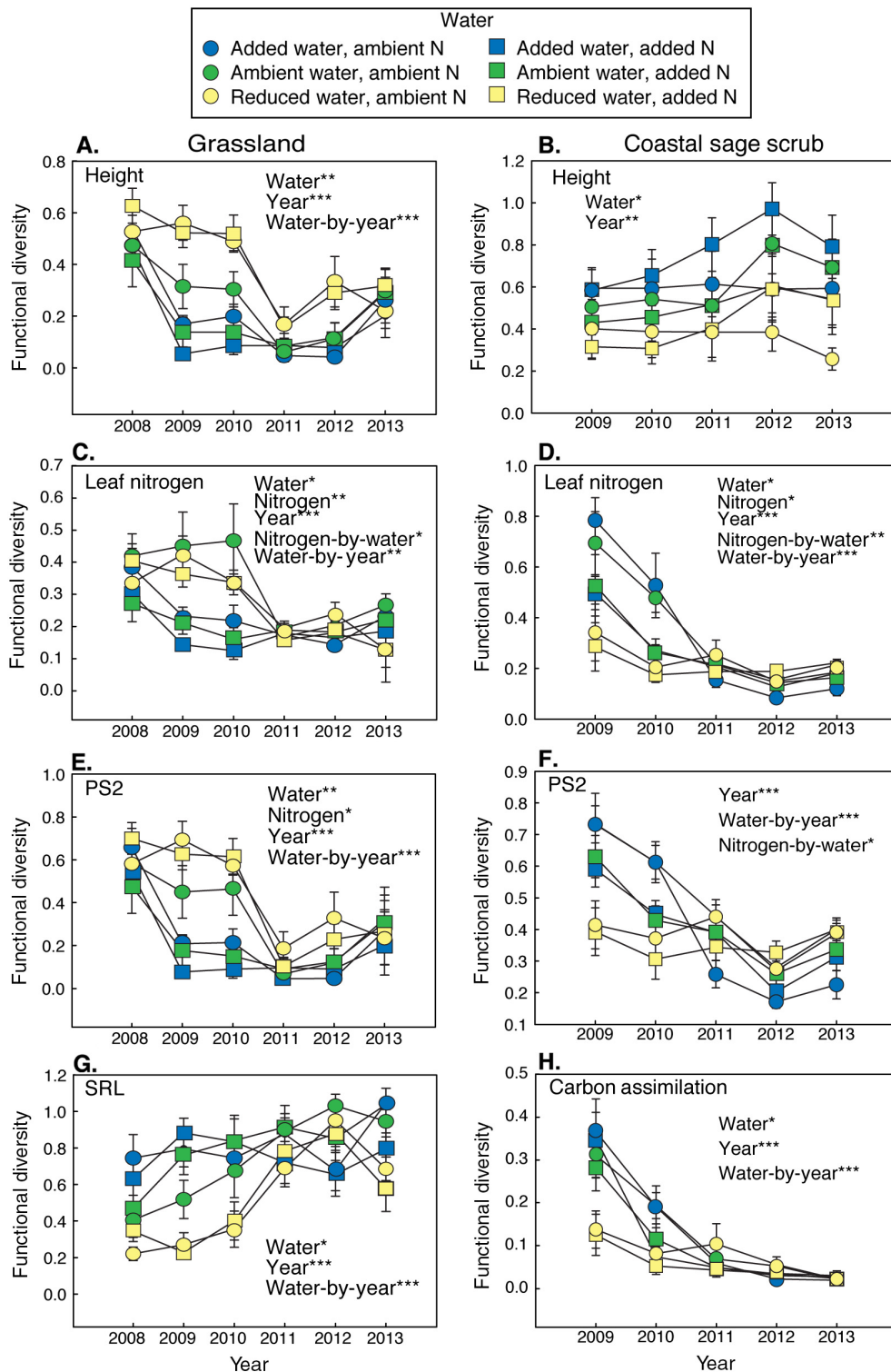


Fig. 5. Functional diversity (FD_{is}) values for height, leaf nitrogen concentration, $\phi PSII$, specific root length (SRL), and carbon assimilation (A) in grassland plots (left) and coastal sage scrub plots (right) in the different water and N treatments through time. Values are means \pm 1 SE. Results from all ANOVAs on FD_{is} traits are listed in Appendix S1: Table S4. Mean and SE FD_{is} values for all traits are listed in Appendix S1: Table S4B. * $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$; non-significant factors are not listed.

example, nitrogen-fixing species, such as *Acemispom glaber* in coastal sage scrub and *Lupinus bicolor* in grassland, performed poorly under added-nitrogen conditions. This result is consistent with previous studies showing that nitrogen-fixing forbs decrease in abundance in added-nitrogen plots (Zavaleta et al. 2003, Suding et al. 2005). Nitrogen fixation has a metabolic and non-nitrogen nutritional cost, so legumes may lose their competitive advantage with non-nitrogen fixers when nitrogen is readily available (Menge et al. 2008, Vitousek et al. 2013). For some traits, such as WUE, the relationships between traits and response ratios varied depending on the community. WUE was not significantly related to response ratios in the grassland community and was unexpectedly negatively related to response to reduced water (and likewise unexpectedly positively related to response to added water) in some conditions in the coastal sage scrub community. This result may be contrasted with other systems, in which drought favors plants with higher WUE (Ehleringer 1993, Munoz-Perea et al. 2007, Kimball et al. 2010). This unusual result is likely driven by the wildfire that burned these plots in 2007, and the altered pattern of succession in the coastal sage scrub water-reduction plots. Long-lived shrubs with high WUE and long roots were unable to recover following fire in the water-reduction plots, leaving those plots to become dominated by non-native grass species with lower WUE and shorter roots (Kimball et al. 2014).

Our study design enabled us to compare species' responses to global change manipulations in different contexts. Competitive interactions likely influenced differences in the response of non-native grasses, which had increased cover in water-addition grassland plots and decreased cover in water-addition coastal sage scrub plots relative to ambient-water plots. In the coastal sage scrub water-addition plots, perennial shrub species quickly recovered following the wildfire and grew to dominate the plots (Kimball et al.

2014), leaving little room for grass germination and growth. In the grassland community where most species are annuals, the European grasses are known to be strong competitors, which likely enabled them to out-compete forbs and increase in abundance with added water (Suttle et al. 2007). There were few forbs abundant in coastal sage scrub plots, making it more difficult to compare responses to forbs in different communities. One native forb species, *L. bicolor*, was more negatively influenced by added-water conditions in the grassland plots, where European grasses were abundant, than in the coastal sage scrub added-water plots, dominated by perennial shrubs. Our results are consistent with other studies that demonstrated varying species interactions depending on water and nutrient availability, noting the importance of understanding these complexities when predicting community response to environmental change (McCluney et al. 2012, Eskelinen and Harrison 2014, Goldstein and Suding 2014).

The relationship between community-level trait distributions (CWM and FD_{is}) and our manipulations through time allows for generalization beyond the individual species' responses in our study and indicates that community-level trait patterns were significantly influenced by water and nitrogen availability. Additional information about trait distributions—beyond the CWM—is needed to predict how ecosystem functioning will shift under new environmental conditions. For instance, theory suggests that the variance of the trait distribution may reflect the capacity of the community to respond to environmental change (Norberg et al. 2001, Savage et al. 2007). Even the degree of skew and kurtosis of a trait distribution may influence a community's response (Enquist et al., 2015). Many of our focal traits, such as WUE, root length, LMA, E_p , $\phi PSII$, and leaf N, have been identified as traits that affect water, carbon, and nitrogen cycling (Diaz et al. 2013). Across the two communities, adding nitrogen resulted in an increase in abundance of species

with high A and ϕ PSII, two traits that are often ascribed to efficient competitors of light (Cornelissen et al. 2003). However, when coupled with reduced water in the coastal sage scrub plots, added N resulted in communities with lower mean SRL, LMA, WUE, leaf N, and ϕ PSII than in added-water plots and ambient-nitrogen plots, reflecting the dominance of short-statured non-nitrogen-fixing grass species. The increase in LMA in added-N plots is contrary to results found in grassland systems (Knops and Reinhart 2000, Craine et al. 2001) and may be particular to the vegetation type-conversion (from shrubs to grasses) that occurred in our semi-arid system in response to drought and N addition (Kimball et al. 2014). This shift from shrubs to grasses, reflected in the shift in CWM trait values, suggests that future drought and nitrogen deposition may reduce rates of carbon and nutrient cycling in coastal sage scrub communities.

Our CWM data also have important implications for rates of water cycling. Species that achieved high WUE did so by reducing transpiration rate, rather than increasing rates of carbon assimilation (data not shown). Thus, the result that communities in our water-reduction plots had lower WUE suggests that the dominant species may quickly deplete limited soil water in drier conditions projected for southern California. Lower values of WUE in water-reduction plots are unexpected and somewhat contradictory to the lower values of E_p , but the values are explained by the inability of shrubs to recover in those plots (Kimball et al. 2014). The water-reduction plots were characterized by high European grass cover with lower WUE, indicating a community that escapes, rather than tolerates, drought (Franks 2011). Although shrubs have higher WUE than the grasses that were more abundant in reduced-water coastal sage scrub plots, they remain active throughout a greater part of the year, potentially resulting in greater amounts of water loss to the atmosphere at the ecosystem level when scaled to a larger time period.

Concurrent with the shift in CWM trait values, we also found shifts in the functional dispersion of communities in response to our manipulations. Across the two communities, adding N resulted in communities where species were more similar in leaf N (lower FD_{is}) than under

ambient N. This decrease in FD_{is} of leaf N reflects the loss of N-fixing species and suggests that species in these communities may be employing a similar functional strategy for acquiring N. We found that functional dispersion was influenced by water availability, but this response was contingent upon community type. In coastal sage scrub plots, the FD_{is} of height, carbon assimilation, ϕ PSII, and leaf N (though to a lesser degree) was greatest in the water-addition plots, intermediate in the ambient plots, and lowest in the water-reduction plots. This pattern likely reflects the loss of shrubs and the dominance of herbaceous species in the water-reduction plots (Kimball et al. 2014). Conceptually, these results suggest a decrease in ecosystem functioning under reduced water availability due to the decrease in functional dispersion (Craine et al. 2011, Fry et al. 2013, Mariotte et al. 2013). In grassland plots, functional response to water availability was less consistent, but we generally found that the water-reduction plots had greater functional dispersion in height, leaf N, and ϕ PSII. These patterns were in contrast to our expectations and may suggest a role for facilitation among species at lower water availability (Spasojevic and Suding 2012), which may work to increase the resilience of the system to drought. In contrast, similar to patterns in coastal sage scrub, the decreased FD_{is} for carbon assimilation suggests a decrease in ecosystem functioning under reduced water availability due to the decrease in functional dispersion (Craine et al. 2011, Fry et al. 2013, Mariotte et al. 2013).

In conclusion, we identified significant relationships between species' responses to water and nitrogen manipulations and plant functional traits. The relationship between leaf nitrogen concentration and negative response to nitrogen addition was consistent across communities, suggesting predictive strength of this trait to species' responses to increases in atmospheric nitrogen deposition in systems with a high abundance of nitrogen fixers. Response to manipulations was not consistent for the majority of traits, indicating limitations to the predictive nature of traits to response to global change and a need for the development of more robust theory. Perhaps the relationships between traits and environment are interactive or non-linear functions exist that we do not yet understand. Comparisons of the

responses of the same species occurring in two contrasting biotic environments had significantly different results, giving further evidence of limitations in the utility of predictions across systems. Community trait distributions indicated reductions in rates of carbon and nutrient cycling under conditions of reduced water and added nitrogen, which are projected for large expanses of the southwest United States.

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