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### Authors

Copeland, Stella M  
Harrison, Susan P  
Latimer, Andrew M  
[et al.](#)

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# Ecological effects of extreme drought on Californian herbaceous plant communities

STELLA M. COPELAND,<sup>1,9</sup> SUSAN P. HARRISON,<sup>1</sup> ANDREW M. LATIMER,<sup>2</sup> ELLEN I. DAMSCHEN,<sup>3</sup> ANU M. ESKELINEN,<sup>1,4,5</sup>  
BARBARA FERNANDEZ-GOING,<sup>6</sup> MARKO J. SPASOJEVIC,<sup>7</sup> BRIAN L. ANACKER,<sup>8</sup> AND JAMES H. THORNE<sup>1</sup>

<sup>1</sup>*Department of Environmental Science and Policy, University of California, Davis, California 95616 USA*

<sup>2</sup>*Department of Plant Sciences, University of California, Davis, California 95616 USA*

<sup>3</sup>*Department of Zoology, University of Wisconsin, Madison, Wisconsin 53706 USA*

<sup>4</sup>*Department of Ecology, University of Oulu, Oulu Finland*

<sup>5</sup>*Department of Physiological Diversity, Helmholtz Center for Environmental Research – UFZ, German Centre for Integrative Biodiversity Research (iDiv) Halle-Jena-Leipzig, Deutscher Platz 5e, D-04103, Leipzig Germany*

<sup>6</sup>*Department of Ecology, Evolution, and Marine Biology, University of California, Santa Barbara, California 93106 USA*

<sup>7</sup>*Department of Biology and Tyson Research Center, Washington University in St. Louis, St. Louis, Missouri 63105 USA*

<sup>8</sup>*Open Space and Mountain Parks Department, City of Boulder, Boulder, Colorado 80303 USA*

**Abstract.** Understanding the consequences of extreme climatic events is a growing challenge in ecology. Climatic extremes may differentially affect varying elements of biodiversity, and may not always produce ecological effects exceeding those of “normal” climatic variation in space and time. We asked how the extreme drought years of 2013–2014 affected the cover, species richness, functional trait means, functional diversity, and phylogenetic diversity of herbaceous plant communities across the California Floristic Province. We compared the directions and magnitudes of these drought effects with expectations from four “pre-drought” studies of variation in water availability: (1) a watering experiment, (2) a long-term (15-yr) monitoring of interannual variability, (3) a resampling of historic (57-yr-old) plots within a warming and drying region, and (4) natural variation in communities over a broad geographic gradient in precipitation. We found that the drought was associated with consistent reductions in species richness and cover, especially for annual forbs and exotic annual grasses, but not with changes in functional or phylogenetic diversity. Except for total cover and cover of exotic annual grasses, most drought effects did not exceed quantitative expectations based on the four pre-drought studies. Qualitatively, plant community responses to the drought were most concordant with responses to pre-drought interannual rainfall variability in the 15-yr monitoring study, and least concordant with responses to the geographic gradient in precipitation. Our results suggest that, at least in the short term, extreme drought may cause only a subset of community metrics to respond in ways that exceed normal background variability.

**Key words:** *California Floristic Province; drought; experimental water addition; functional traits; plant community; precipitation.*

## INTRODUCTION

Climate change is leading to increasingly frequent and extreme droughts in many arid and semiarid parts of the world (Sheffield and Wood 2008, Cook et al. 2015, Williams et al. 2015). Observed ecological consequences include widespread increases in tree mortality (Breshears et al. 2005, van Mantgem et al. 2009, McDowell and Allen 2015), loss of primary productivity at both local and regional scales (Ciais et al. 2005, Zhao and Running 2010, Knapp et al. 2015), and reduced species richness in herbaceous communities, with disproportionate losses of rare species (Tilman and El Haddi 1992) and/or shallowly rooted species (Harte et al. 2006). Experimental

water manipulations have been shown to mimic the productivity-reducing effects of drought (Harte et al. 2006, Penuelas et al. 2007, Potts et al. 2012, Hoover et al. 2014, Koerner and Collins 2014) and have also suggested the potential for droughts to disproportionately affect particular functional groups and/or vegetation types (Penuelas et al. 2007, Baez et al. 2013, Hoover et al. 2014). However, opportunities for better understanding drought impacts on plant communities remains scarce due to the infrequency and unpredictability of droughts; inferences from many studies are constrained by observations across a limited geographic area, lack of pre-drought observations, and/or a relatively small species pool. It therefore remains unclear how often droughts or other climatic events are “extreme” in the sense of producing ecological effects that exceed the normal range of variability (Smith 2011), across diverse ecosystems and multiple dimensions

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<sup>9</sup>E-mail: scopeland@ucdavis.edu

of biodiversity, including the species, functional, and phylogenetic diversity of communities.

Plant communities are well known to be shaped by climate variation in space and time, and the well-studied effects of natural and experimental climatic variation provide a useful starting point for evaluating the effects of an extreme drought. Broadly speaking, plant productivity and species richness tend to be positively related to water availability, particularly across large-scale geographic gradients (e.g., Sala et al. 1988, Hawkins et al. 2003, Hsu et al. 2012). Some theoretical evidence suggests a “physiological tolerance” explanation for the positive water–richness relationship, in which a wider array of functional trait values (and thus, species) are compatible with wet than dry climates (Kleidon and Mooney 2000, Currie et al. 2004, Spasojevic et al. 2014). However, when climate-driven changes in plant community composition are examined in detail, comparative studies reveal many dissimilarities between the effects of geographic, temporal, and experimental gradients in climate. Interannual rainfall variability produces time-lagged and weaker effects on plant productivity, species richness, and species composition in comparison with geographic gradients (Adler and Levine 2007, Sala et al. 2012, Cleland et al. 2013, Pierre et al. 2016). Geographic gradients in climate may not resemble experimental climate manipulations because they cause a greater range of variation in plant functional traits (Sandel et al. 2010), although in other cases, geographic gradients produce qualitatively similar compositional effects to those of experimental climatic variation (Elmendorf et al. 2015). Experiments may seem ideal for predicting the effects of short-term events such as climate extremes, but they have been shown to underpredict some of the effects of ambient climatic variation (Penuelas et al. 2007, Wolkovich et al. 2012, Elmendorf et al. 2015). Given these divergent results, which likely reflect the highly multidimensional nature of climate-driven community change, it remains difficult to predict the effects of extreme drought based on either first principles (e.g., the water-availability–richness relationship) or previous evidence.

Beginning in 2012, the California Floristic Province experienced a drought that ranks among the most extreme dry periods in the last 1200 yr (Griffin and Anchukaitis 2014). It encompassed the lowest precipitation in a 12-month period in the 120-yr observational record according to multiple climate data sets (Swain et al. 2014) and is estimated as an approximately 10000-yr event based on historical reconstructions of the Palmer Drought Severity Index (Robeson 2015). The drought was exacerbated by abnormally warm temperatures, suggesting that droughts may increase in frequency in future warmer climates (Cook et al. 2015, Diffenbaugh et al. 2015, Williams et al. 2015). Warming temperatures may also amplify the effects of drought on plants, due to increased evaporative demand (Thorne et al. 2015). While effects of the Californian drought on agriculture and water storage have been well documented (e.g., Howitt

et al. 2014), many of its impacts on natural systems have yet to be assessed, including its effects on plant community diversity and composition. Here, we assess how the Californian drought during 2012–2014 affected multiple dimensions of plant diversity; we compare its effects qualitatively with those of four “pre-drought” gradients in water availability (experimental, interannual, long-term directional, and geographic); and we evaluate whether the drought is “extreme” sensu Smith (2011), i.e., whether its ecological impacts exceed the range of variability observed along the four pre-drought water gradients. Drought may uniquely affect the richness, composition, and function of plant communities, with some properties more likely than others to encounter critical thresholds and to depart from the normal range of variability (Smith 2011). Accordingly, we considered a wide array of biodiversity metrics. Based on previous evidence (already reviewed here), we anticipated that drought responses would include declines in species cover, due to lower abundance, and correlating with decreases in primary productivity, which is sensitive to water availability (e.g., Sala et al. 1988, 2012). We also expected lower species richness in response to the drought based on the general water–richness relationship identified by previous studies. We anticipated disproportionately negative effects on annual species (Tilman and El Haddi 1992, Cleland et al. 2013). Moreover, based on the widespread linkages between a suite of plant functional traits and environmental moisture gradients (Wright et al. 2005), we expected that the diminished abundances of drought-intolerant species would result in shifts toward more drought-tolerant community weighted mean trait values, such as lower specific leaf area, that show strong and consistent interspecific variation along aridity gradients (Cornwell and Ackerly 2009). Last, we expected that community functional and phylogenetic diversity would decrease in response to the drought. Functional diversity in moisture-related traits has been shown to diminish along spatial gradients of declining moisture availability that select for a drought-tolerant subset of species (Spasojevic et al. 2014). Phylogenetic diversity, which is often linked to functional diversity through conserved traits, has likewise been shown to respond to climatic gradients in space and time (Potter and Woodall 2012, Feng et al. 2014, Eiserhardt et al. 2015). In California, drought might be expected to diminish phylogenetic diversity since high phylogenetic diversity in communities is correlated with the presence of species belonging to ancient mesic lineages (Anacker and Harrison 2012).

We assessed the effects of the drought by resampling four previous studies of communities along spatial and temporal water availability gradients in 2014 after 2 yr of extreme drought. These pre-drought studies included (1) a 5-yr watering experiment in an annual-dominated grassland system, in which springtime water addition during mainly drier-than-average years led to increased biomass and shifts in community composition (Eskelinen and Harrison 2015a, b); (2) a 15-yr observational study

of interannual variability, in the same annual-dominated grassland system as the experiment, which found that drier years were associated with lower species richness and cover (Elmendorf and Harrison 2009, Fernandez-Going et al. 2012); (3) a study of long-term directional change, in which forest understory communities were resampled after a 57-yr period of declining climatic water availability and decreased species richness and altered functional composition were detected (Damschen et al. 2010, Harrison et al. 2010); and (4) an analysis of plant communities across a geographic gradient spanning the California Floristic Province, in which a nearly 10-fold range of variation in precipitation was associated with variation in species richness, functional composition, and biogeographic composition (Harrison et al. 2006, Grace et al. 2007, Anacker and Harrison 2012). While each of these data sets has marked limitations with respect to predicting drought effects, they represent four widely available forms of data from which ecologists may sometimes attempt to predict or interpret extreme climatic events.

We also asked whether drought responses (i.e., differences between 2014 and pre-2014 values) of species richness, cover, community functional trait means, functional diversity, and phylogenetic diversity in each data set matched the responses of that metric to pre-drought variation in water availability. First, we asked whether significant drought responses for community metrics were in the same direction as responses to the pre-drought water availability gradient. Second, for community metrics where significant responses to the drought and pre-drought water availability gradients were in the same direction, we asked whether the magnitude of the ecological response to drought matched, exceeded, or was less than, the magnitude of change predicted by the responses to the pre-drought water availability gradient.

Each of our four studies also included both infertile serpentine soils and fertile non-serpentine soils, allowing us to test how soil fertility and the associated differences in community composition would affect response to drought. The plant communities on these contrasting soils differed in major elements of community composition; the serpentine soils supported low-statured, low-biomass vegetation with higher diversity of native and endemic species, while the non-serpentine soils supported plant communities with higher biomass, less stress-tolerant species, and greater prevalence of exotic species. We expected infertile soils to be less sensitive to variation in water availability because of the greater prevalence of species with stress-tolerant functional traits (Harrison et al. 2014, Eskelinen and Harrison 2015b).

## METHODS

### *Pre-drought studies: methods and key prior results*

**Watering experiment.**—The watering experiment took place in grasslands at the Donald and Sylvia McLaughlin University of California Reserve in Lake and Napa Counties, California, USA (38.851° N, 123.830° W; Fig. 1).

The climate is mediterranean with cool winters, warm summers, and most precipitation falling as rain between October and April; interannual rainfall variability is high (Fig. 2A). Grasslands on serpentine soils are dominated by native perennial grasses, native annual and perennial forbs, and varying amounts of exotic annual grasses, while those on non-serpentine (sedimentary) soils are dominated by exotic annual grasses and exotic annual forbs (see Eskelinen and Harrison 2014 for a complete description).

The watering treatment was applied from 2010 to 2014 to 33 plots, while 35 plots were designated as controls. The experiment included two different types of serpentine soil (rocky hilltops and clay-rich bottomlands) that we combined into one category (serpentine) to align conceptually with other analyses (Table 1). Watered plots received locally collected rainwater via a sprinkler system from the end of March to the beginning of June, extending the natural rainy season by 8 weeks and increasing annual rainfall by approximately 18% (Fig. 2A; for details see: Eskelinen and Harrison 2014). Species identity and cover were recorded in 1 m<sup>2</sup> subplots within 4 m<sup>2</sup> plots in April and June in 2012 and 2014. This watering regime led to increased biomass, decreased diversity, and shifts toward “stress intolerant” functional trait composition, but only on soils that were either naturally fertile (non-serpentine) or experimentally fertilized (Eskelinen and Harrison 2015b). Water addition and water deficit may have asymmetrical effects, but since the final three years of the watering experiment were years of below-average rainfall (Fig. 2A), the watered vs. control treatments more

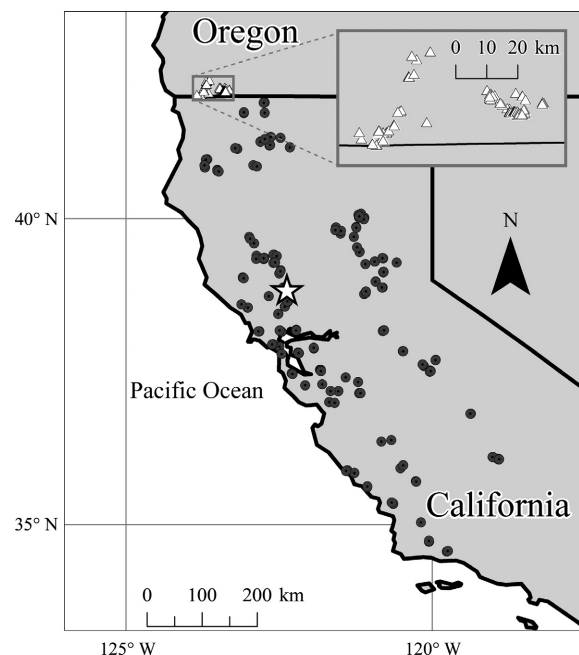


Fig. 1. Map of study locations. The location of the Watering Experiment and Interannual Variability Studies (UC McLaughlin Reserve) is marked with a star. Plot locations for the Geographic Gradient Study are represented by circles and by triangles for the Long-term Directional Change Study.

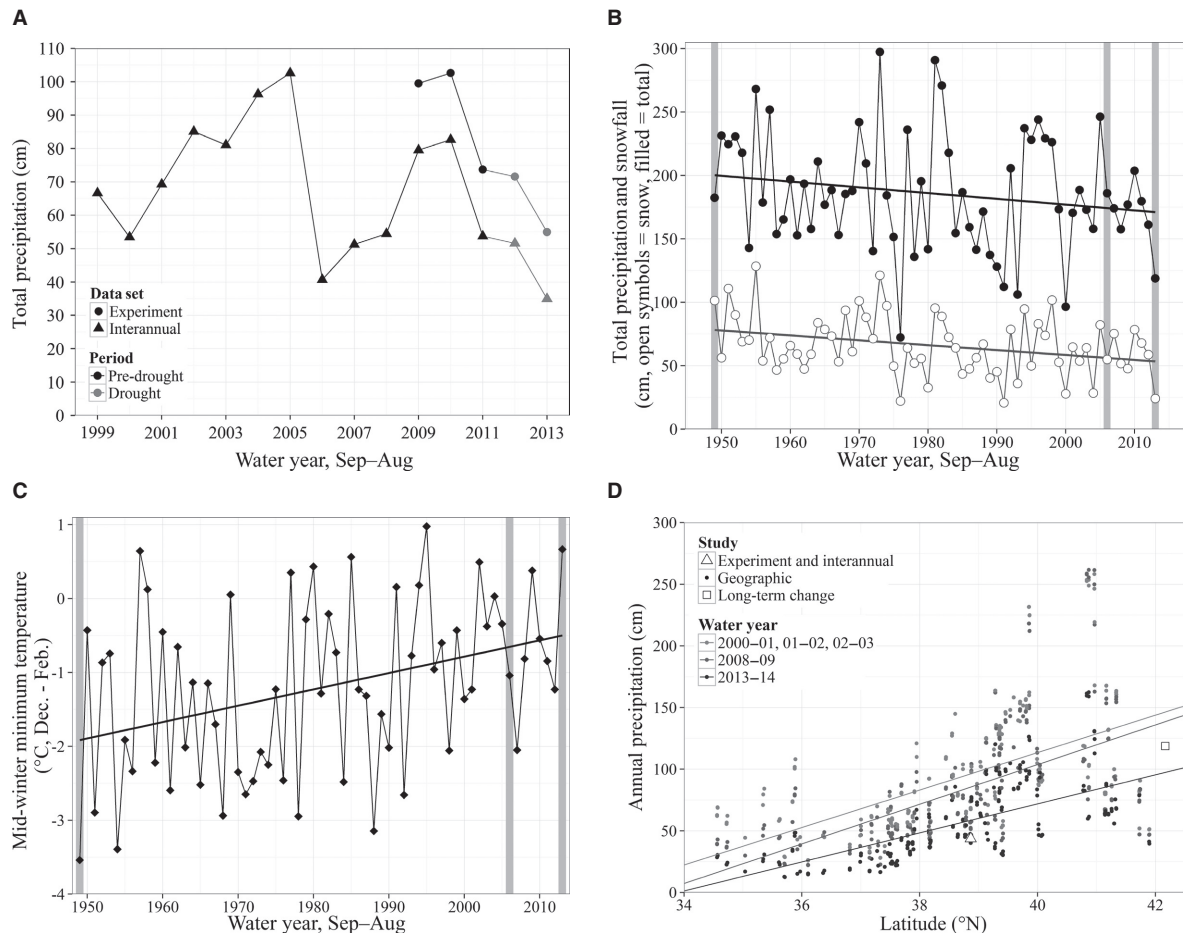


Fig. 2. Water availability gradients. (A) Precipitation by water year for the Watering Experiment (18% of annual precipitation added) and the Interannual Variability Study (UC McLaughlin Reserve, for pre-drought and drought periods). (B) Long-term Directional Change Study: total precipitation (black circles) and snowfall (open circles). Gray bars indicate the sampling periods (1950, 2007, 2014). (C) Long-term Directional Change Study: mid-winter temperatures by water year. Gray bars indicate the sampling periods (1950, 2007, 2014). (D) Geographic Gradient Study: precipitation by latitude for the drought year (2014) and the two pre-drought sampling periods (serpentine: 2001–2003, non-serpentine: 2009), with symbols showing the mean 2014 values for the other three studies for comparison.

closely resembled normal vs. dry than wet vs. normal years, respectively. We note that the 18% difference in water availability imposed by the experiment did not approach the magnitude of a severe drought.

**Interannual variability study.**—In the same landscape where the watering experiment took place, species composition was sampled annually for 15 yr at 80 sites in grasslands on serpentine and non-serpentine soils (Table 1). Each site consisted of five 1-m<sup>2</sup> plots separated by 10 m. Species richness was recorded in April and May–June from 2000 to 2014, and species cover was recorded from 2006 to 2014. Site selection is fully described in Harrison et al. (2003). Species present in dry years were found to be a nested subset of those present in wetter years (Elmendorf and Harrison 2009), and the variation in species richness and composition in response to interannual rainfall variability was lower

on serpentine than on non-serpentine soils (Fernandez-Goñi et al. 2012).

**Long-term directional change study.**—In understory herbaceous communities first studied in 1949–1951 (Whittaker 1960), a resurvey was conducted in 2007–2008 (Damschen et al. 2010, Harrison et al. 2010). The study location is at the northernmost end of the California Floristic Province in southern Oregon (Fig. 1). Over the 57 yr between the two sampling time periods (here termed “1950” and “2007”), average mid-winter temperatures increased and precipitation decreased (Fig. 2B, C; Appendix S1: Figs. S2 and S4). The plots in this study consisted of 50-m transects in undisturbed forests and woodlands, distributed among serpentine and non-serpentine soils at low elevations (500–1300 m), and non-serpentine at higher elevations that receive winter snowpack (1500–2100 m, Table 1). Percent cover of understory herbs was

estimated by summing the number of corner intercepts for each species in 25 1 × 1 m quadrats, following the methods of Whittaker (1960). Previous research demonstrated differential responses at low vs. high elevations. At low elevations, species associated with xeric environments were favored and species richness, community mean specific leaf area, and the prevalence of species of mesic northerly biogeographic origins all decreased (Damschen et al. 2010). At high elevations, however, there were minimal changes to community composition and species with northerly biogeographic origins were actually favored (Harrison et al. 2010). These results suggested that the long-term drying trend may have increased water limitation for communities at low elevations while lengthening the growing season for communities at high elevations. While our analysis of drought effects relies on only two time points, i.e., 2007–2008 and 2014, the sites in this study experienced no fire, logging, grazing, or other obvious land-use changes that might have been comparable in magnitude to the drought and would have been visible to us in 2014.

*Geographic gradient study.*—Vegetation plots were sampled throughout the California Floristic Province to compare responses of communities on serpentine and non-serpentine soils to climatic gradients and other factors (Harrison et al. 2006, Anacker and Harrison 2012, Fernandez-Going et al. 2013). The sampling sites spanned a large range of latitude (34.6° N to 42.9° N; Figs. 1 and 2D), elevation (70–2740 m), and climate (minimum temperatures –10°C to 7°C, maximum temperatures 18°–37°C, annual precipitation 19–162 cm). Sites consisted of sets of two 50 × 10 m subplots chosen within typical regional vegetation types, one on a north slope and one on an adjacent south slope; these two aspect transects were merged for this analysis. Serpentine soil sites were sampled in 2001–2003 while non-serpentine soil sites were sampled in 2009 and selected to match in aspect and elevation with nearby serpentine sites (Table 1). Reanalysis of a subset of serpentine sites in 2010 showed that basic patterns in community composition were robust to the difference in sampling dates of the serpentine and non-serpentine sites. At each north or south slope subplot, presence of all vascular plant

species was recorded, and percent cover by species was measured in seven 1 × 1 m subplots. Sites were visited two to four times to capture the full growing season. On serpentine soils, higher precipitation was associated with a shift toward woody vegetation (Grace et al. 2007), dominance by species with mesic biogeographic origins (Harrison and Grace 2007), and higher regional-scale species richness that filtered down to have a weak effect on local richness (Harrison et al. 2006). Considering both soils, higher precipitation was associated with higher phylogenetic diversity (Anacker and Harrison 2012) and shifts toward stress-intolerant functional traits (Fernandez-Going et al. 2013) in the woody species. Phylogenetic and functional patterns in the herbaceous species were not analyzed prior to the present study.

#### *Resampling to assess drought effects*

In spring and summer 2014, we resampled the sites of the above studies using methods identical to the original ones. We resampled all sites in the experimental, interannual, and long-term directional trend studies, and a subset of those in the geographic gradient study (73 on serpentine and 67 on non-serpentine soils), prioritizing sites that had not burned or been otherwise disturbed and that did not present access or relocation problems. Because we did not expect the drought to immediately affect the abundances of woody species as their response will likely be relatively slow, we resampled and analyzed only herbaceous vascular plants. In the interannual study, unlike the other three studies, we also had data for 2013, and therefore we defined the drought period in this study as 2013–2014 and compared these two years to the pre-drought period (Table 1).

*Climate data.*—For the experimental and interannual studies, we obtained total annual precipitation using daily records from a weather station within the study location (Knoxville Creek, California, weather station, RAWs network; Western Regional Climate Center 2015). For all four studies, we extracted climate data from a hydrologic model that integrates monthly temperature, precipitation, soil characteristics, and drainage to describe water balance at the watershed scale (Flint et al. 2013, Thorne et al. 2015).

TABLE 1. Number of plots and sampling periods (years) for each study by major factors: soil type, watering treatment, and elevation band.

Study	Number of plots by category		Sampling period	
	Serpentine	Non-serpentine	Pre-drought	Drought
Watering experiment	Controls: 24 Watered: 22	Controls: 11 Watered: 11	2012	2014
Interannual variability	38	42	Richness: 2000–2012 Cover: 2006–2012	2013–2014
Long-term directional change	500–1300 m: 49	500–1300 m: 53 1500–2100 m: 68	1949–1951, 2007–2008	2014
Geographic gradient	Pre-drought: 109 Drought: 73	Pre-drought: 90 Drought: 69	Serpentine: 2001–2003 Non-serpentine: 2009	2014

*Community metrics.*—We classified species into the following four functional groups: native annual forbs, native perennials, exotic annual grasses, and exotic forbs and perennial grasses (Calflora 2014, USDA NRCS 2014). We note that in the long-term directional change study, exotic species were virtually absent, and grasses were not identified to species in the original 1950 data set, resulting in a slightly different set of functional groups (native annual forbs, native perennials excluding grasses, and all native grasses). Similarly, the exotic forb group in the watering experiment does not include any exotic perennial grasses because these did not occur in any of the plots.

Functional trait data were collected primarily in 2009–2010 (see Anacker and Harrison 2012, Fernandez-Going et al. 2013), and were supplemented by additional collections made in the present study. We measured specific leaf area (SLA), foliar C:N, leaf water content (LWC), and plant height for 10 individuals per species using standard protocols (Cornelissen et al. 2003, Perez-Harguindeguy et al. 2013). We selected these traits because of their well-documented relationships to water use efficiency and climatic gradients (Reich et al. 1999, Wright et al. 2004). For each community sample in our studies, we then calculated two complementary metrics of functional diversity: community-weighted mean trait values (Garnier et al. 2004) and multivariate functional dispersion (FD<sub>Dis</sub>; Laliberté and Legendre 2010). Mean trait values were calculated for each trait as the sum of species-level traits weighted by the species relative abundances (Garnier et al. 2004). Because of our hypothesis that annual species would be highly responsive to drought, we also calculated mean trait values for native annuals in studies and on soil types where annual species reached high abundance (interannual variability, geographic gradient, and serpentine soils in the experimental study). Functional dispersion 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 (Laliberté and Legendre 2010). Both metrics were calculated using the FD package in R (Laliberté and Shipley 2011).

To calculate the phylogenetic diversity of each community sample, we constructed a phylogeny for our communities in Phylomatic (Webb and Donoghue 2005) using the R20100428 tree (Bremer et al. 2009) with scaled branch lengths based on inferred node ages with the BLADJ procedure (Wikstrom et al. 2001) in Phylocom vs. 4.2 (Webb et al. 2008). We calculated Faith's phylogenetic diversity (PD) and the net relatedness index (NRI) for each plot in each study. Phylogenetic diversity was calculated as the sum of all branch lengths among species within a plot (Faith 1992). Net relatedness was calculated by comparing the observed mean pairwise distance (MPD) among co-occurring species, the sum of the branch lengths that connect all co-occurring taxa in each plot (Webb et al. 2002), to a null MPD derived from randomizing species co-occurrences 999 times while maintaining sample richness and species occurrence frequencies and multiplying by  $-1$ . These two metrics

describe different aspects of phylogenetic relationships among species. Net relatedness indicates the degree of phylogenetic dispersion or phylogenetic distance between species. An increase in NRI suggests a change toward phylogenetic underdispersion (clustering) while a decrease suggests phylogenetic overdispersion. A decrease in PD may not be accompanied by an increase in NRI if the loss of species is even across clades represented in a plot.

### Statistical analysis

In all analyses, we compared effects of the drought and effects of the pre-drought water gradient for each community metric (species cover, richness, community-weighted mean trait values, functional dispersion, phylogenetic diversity, and net relatedness index) separately for each soil (serpentine and non-serpentine and low-elevation non-serpentine, high-elevation non-serpentine, and low-elevation serpentine in the Long-term Directional Change study). All analyses were conducted in R version 3.0.2 (R Core Team 2013). We adjusted *P* values for the number of tests in our analyses by using the false discovery rate method for each data set and time period (Benjamini and Hochberg 1995).

For the watering experiment, we tested for effects of the watering treatment in the final year (2014) with a random effect for the irrigation line ( $N = 9$ ) in the lme4 package (Bates et al. 2013). We used linear mixed models for all variables except species richness, which we modeled with a generalized linear mixed model assuming a Poisson distribution of the species counts. Significance of variables was assessed with the Wald  $\chi^2$  tests in the package (Fox and Weisberg 2011). We tested for drought effects on the community metrics by comparing their values in the control plots in 2014 vs. 2012 using paired *t* tests with plots as replicates. Non-serpentine plots were excluded from the native perennial analyses because of extremely low cover of that functional group (mean <1%).

For the interannual variability study, we analyzed the effects of annual precipitation using mixed models with site as the random factor. Species richness was modeled as described in the last paragraph (generalized mixed model, Poisson distribution) and significance of precipitation assessed with Wald  $\chi^2$  tests (see above). Species richness was analyzed for 2000–2014, while cover, functional diversity, and phylogenetic diversity metrics were only available for 2006–2014. We compared mean values of the variables between the drought (2013–2014) and the pre-drought period (2000–2012 or 2006–2012) using a paired *t* test with sites as replicates.

For the long-term directional change study, we used two sets of *t* tests, one comparing the beginning and end of the pre-drought period (2007 vs. 1950), and the other assessing the drought period itself (2014 vs. 2007). We conducted separate analyses for low (no spring snowpack) and high (spring snowpack) elevations on non-serpentine soils. As described in the functional group section, grasses were not identified to species in the 1950 data set, therefore grass

species are not included in total community metrics (e.g., species richness and traits) but are included in total cover.

For the geographic gradient study, we tested for relationships between mean annual precipitation and community metrics using an asymptotic permutation test for significant correlations in the R perm package (perMTREND function; Fay and Shaw 2010). We used a correlative permutation approach because most of the models for different response variables did not meet parametric assumptions with or without standard transformations, and we wanted to assess the direction (positive or negative) of significant relationships between water availability and community metrics. We tested whether these metrics differed between 2014 and the pre-drought sampling (2001–2003 for serpentine, 2009 for non-serpentine) using paired *t* tests with the Welch approximation for unequal variance.

For any community metric that responded significantly and in the same direction to both the drought and the pre-drought gradient, as was the case for some metrics in the interannual variability and watering experiment studies, we asked whether the drought response equaled, exceeded, or was less than, the expected response based on linear extrapolation from the pre-drought gradient. For the interannual variability study, we derived the mean expected values for community metrics in the drought years (2013 and 2014) with the precipitation values for those years, and the estimated values for the intercept, annual precipitation coefficient, and the random effects for site. For the watering experiment study, we calculated the mean expected change with drought, defined as the difference between controls from pre-drought and drought years (2012 and 2014), by subtracting the estimated watering treatment coefficient from the control values in the pre-drought year (2012). We bootstrapped 95% confidence intervals for the intercept and the coefficient of annual precipitation for the interannual variability study and for the coefficient for the water addition treatment for the watering experiment using function `confint.merMod` in the `lme4` package ( $N = 500$ , random effects held at estimated values). Confidence intervals for mean predictions for the interannual variability study were constructed with the bootstrapped confidence intervals for the intercept and annual precipitation coefficients. Confidence intervals for the watering experiment were constructed by subtracting the bootstrapped confidence intervals for the watering coefficient from the mean control values in the pre-drought data.

## RESULTS

### *Watering experiment*

*Watering effects.*—Watering increased total cover on both soils, and led to higher cover of exotic annual grasses on serpentine soils and higher cover of exotic forbs on non-serpentine soils. Watering did not significantly affect total species richness on either soil. Community weighted mean SLA and LWC increased while mean C:N decreased with watering on non-serpentine soils. Community weighted

mean SLA and C:N of native annuals both decreased on serpentine soils in response to watering. Multivariate functional dispersion was not significantly affected by watering on either soil type. Net relatedness index decreased with watering on serpentine soils while phylogenetic dispersion was unaffected (Appendix S1: Table S1, Table 2).

*Drought effects.*—Total cover and species richness of exotic forbs decreased only on non-serpentine soils, while cover of exotic annual grasses decreased on both soil types. Community weighted mean C:N and height increased with the drought on non-serpentine soils, while mean SLA decreased on serpentine soils. Drought caused multivariate functional dispersion to increase on serpentine and decrease on non-serpentine soils. Phylogenetic dispersion decreased with drought on serpentine soils while net relatedness index was unaffected (Table 2, Fig. 4).

*Match between watering and drought effects.*—As expected, total cover on non-serpentine and of exotic annual grasses on serpentine increased with watering and decreased in response to the drought (Table 2). The effects of the drought on cover variables were within confidence levels for total cover and for exotic annual grasses on serpentine, but led to lower than predicted values for exotic annual grasses on non-serpentine based on the inverse of the effect of the watering treatment (Fig. 3A).

### *Interannual variability study*

*Annual precipitation effects.*—Lower precipitation was associated with decreased total species richness and cover and richness of all functional groups on non-serpentine soils. On serpentine soils, lower precipitation was associated with lower total cover and richness, and with lower cover and richness of native annuals and exotic annual grasses. Lower annual precipitation was also associated with lower community-weighted mean SLA and LWC on both soils and lower mean SLA for native annuals on serpentine soils. For both the entire community and native annuals, lower annual precipitation was associated with increased mean C:N and greater mean height on non-serpentine soils. In drier years, multivariate functional dispersion decreased while net relatedness index increased on non-serpentine, while the opposite was observed on serpentine (Appendix S1: Table S2, Table 3).

*Drought effects.*—Total cover and cover of exotic annuals grasses were lower in the 2013–2014 drought years than in previous years on both soils, as were native annual cover on non-serpentine and native perennial cover on serpentine. Species richness was also lower in drought years on both soils, as were richness of all functional groups except native perennials on non-serpentine soils, and the richness of native annuals and exotic annual grasses on serpentine. However, the richness of exotic forbs and perennial grasses on serpentine soils increased. Community-weighted mean



TABLE 2. Watering experiment study: significant effects ( $P \leq 0.05$ ) of drought on community metrics by soil type compared to effects of experimental water addition.

Category and variable	Water addition		Drought		
	$\chi^2$	Water coefficient	df	$t$	Change (%)
Non-serpentine soil					
Species richness					
Exotics	4.5	0.6	10	-4.2*	-46.7
Cover					
<b>Total</b>	<b>11.8**</b>	<b>38.3</b>	<b>10</b>	<b>-6.0**</b>	<b>-54.3</b>
Exotic annual grasses	3.3	-10.5	10	-5.5**	-56.7
Traits and phylogenetic and functional diversity					
C:N	6.0*	-9.4	10	-3.3*	-26.6
Height	1.9	-4.5	10	3.3*	27.3
Dispersion (RaoQ)	0.4	<-0.1	10	-3.3*	-36.9
Serpentine soil					
Cover					
<b>Exotic annual grasses</b>	<b>7.5*</b>	<b>12.8</b>	<b>23</b>	<b>-4.4**</b>	<b>-54.4</b>
Traits and phylogenetic and functional diversity					
Specific leaf area (SLA)	0.8	7.2	23	-3.1*	-4.69
Dispersion (RaoQ)	1.8	<0.1	22	2.8*	48.7
Phylogenetic diversity	<0.1	<-0.1	23	-2.7*	-93.5

Notes: Water coefficient indicates the strength and direction of the watering treatment (linear mixed models, except a Poisson term for species richness models,  $\chi^2$  statistic). The remaining columns describe the change in control plots between pre-drought (2012) and drought (2014) periods (paired  $t$  statistics and percent change for the difference). Boldface type indicates where the pre-drought and drought results match with a priori expectations. \* $P \leq 0.05$ ; \*\* $P \leq 0.01$ .

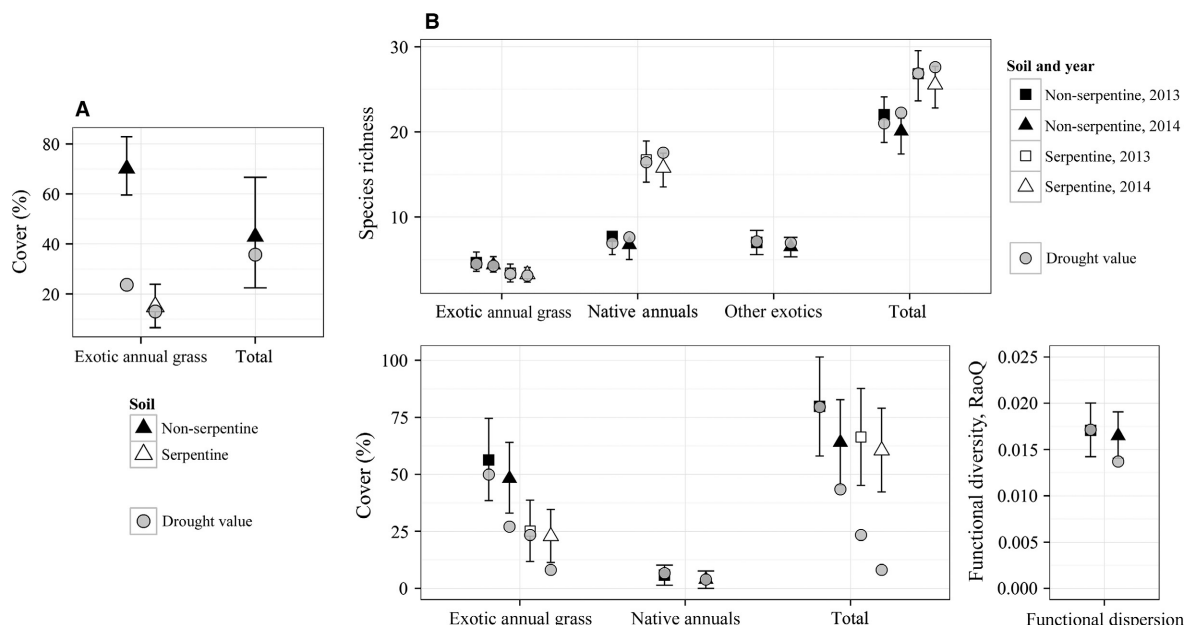


Fig. 3. Comparison of predicted values (triangles, 2013; squares, 2014; non-serpentine, black; serpentine, white, with 95% confidence intervals) made by pre-drought water availability gradients to drought means (gray circles). (A) Watering Experiment, cover. (B) Interannual Variability Study, richness, cover, and functional dispersion, estimated by drought years (2013 and 2014).

LWC increased on serpentine, while mean SLA, LWC, C:N, and height increased on non-serpentine soils. When native annuals were considered alone, the drought was associated with lower community-weighted mean SLA on both soil types and lower mean LWC on serpentine soils. Multivariate functional dispersion decreased significantly while net relatedness decreased on non-serpentine soils (Table 3, Fig. 4).

*Match between annual precipitation and drought effects.*—Total cover and richness, as well as the cover and richness

of most functional groups, declined in response to drought and covaried positively with “normal” interannual precipitation, leading to overall high correspondence between pre-drought and drought effects (Table 3). Drought-year values agreed quantitatively with predictions based on the pre-drought relationships for many of these metrics; however, total cover, cover of exotic annual grasses, and multivariate functional dispersion were lower than predicted in 2014, whereas total species richness and richness of native annuals on non-serpentine were higher than predicted in 2014 (Fig. 3B).

TABLE 3. Interannual variability study: significant effects ( $P \leq 0.05$ ) of drought on community metrics by soil type compared to the effects of annual precipitation.

Category and variable	Precipitation		df	Drought	
	$\chi^2$	Precipitation coefficient		$t$	Change (%)
Non-serpentine soil					
Species richness					
<b>Total</b>	<b>137.8**</b>	<b>0.0006</b>	<b>41</b>	<b>-6.3**</b>	<b>-13.2</b>
<b>Native annuals</b>	<b>106.7**</b>	<b>0.0008</b>	<b>41</b>	<b>-6.2**</b>	<b>-23.9</b>
<b>Exotics</b>	<b>28.2**</b>	<b>0.0004</b>	<b>41</b>	<b>-2.5*</b>	<b>-8.1</b>
<b>Exotic annual grasses</b>	<b>12.7**</b>	<b>0.0004</b>	<b>41</b>	<b>-5.5**</b>	<b>-11.4</b>
Cover					
<b>Total</b>	<b>105.9**</b>	<b>0.0952</b>	<b>41</b>	<b>-14.6**</b>	<b>-33.8</b>
<b>Native annuals</b>	<b>40.3**</b>	<b>0.0115</b>	<b>41</b>	<b>-2.5*</b>	<b>-30.9</b>
<b>Exotic annual grasses</b>	<b>36.7**</b>	<b>0.0487</b>	<b>41</b>	<b>-7.9**</b>	<b>-31.9</b>
Traits and phylogenetic and functional diversity					
Specific leaf area (SLA)	13.7**	0.0320	41	3.8**	17.1
Leaf water content (LWC)	11.0**	0.0001	41	5.3**	19.4
C:N	6.4*	0.0029	41	3.0**	16.9
Height	12.2**	-0.0080	41	8.1**	34.6
SLA: native annuals	1.4	0.0155	41	-2.4*	-5.9
<b>Dispersion (RaoQ)</b>	<b>8.0**</b>	<b>&lt;0.0001</b>	<b>41</b>	<b>-3.1**</b>	<b>-12.1</b>
<b>Net relatedness index</b>	<b>6.7**</b>	<b>-0.0006</b>	<b>41</b>	<b>-2.4*</b>	<b>-55.9</b>
Serpentine soil					
Species richness					
<b>Total</b>	<b>42.4**</b>	<b>0.0003</b>	<b>37</b>	<b>-3.0**</b>	<b>-4.7</b>
<b>Native annuals</b>	<b>36.5**</b>	<b>0.0004</b>	<b>37</b>	<b>-2.8*</b>	<b>-5.8</b>
Exotics	2.9	0.0003	37	2.3*	44.2
<b>Exotic annual grasses</b>	<b>5.1*</b>	<b>0.0003</b>	<b>37</b>	<b>-2.3*</b>	<b>-8.6</b>
Cover					
<b>Total</b>	<b>17.1**</b>	<b>0.0355</b>	<b>37</b>	<b>-6.0**</b>	<b>-21.4</b>
Native perennials	0.1	0.0003	36	-3.9**	-20.8
<b>Exotic annual grasses</b>	<b>5.8*</b>	<b>0.0138</b>	<b>37</b>	<b>-6.1**</b>	<b>-42.7</b>
Traits and phylogenetic and functional diversity					
Leaf water content (LWC)	7.0**	0.0001	37	2.4*	3.2
<b>SLA: native annuals</b>	<b>58.6**</b>	<b>0.0379</b>	<b>37</b>	<b>-3.4**</b>	<b>-3.7</b>
LWC: native annuals	1.8	<-0.0001	37	-2.5*	-1.1

*Notes:* Precipitation coefficient indicates the strength and direction of the effect of precipitation (linear mixed models except for a Poisson term for species richness,  $\chi^2$  statistic). The remaining columns describe the change in control plots between pre-drought (2000–2012 richness, 2006–2012 other variables, mean values) and drought (2013–2014 mean values; paired  $t$  statistics and percent change for the difference). Boldface type indicates where the pre-drought and drought results match with a priori expectations. \* $P \leq 0.05$ ; \*\* $P \leq 0.01$ .

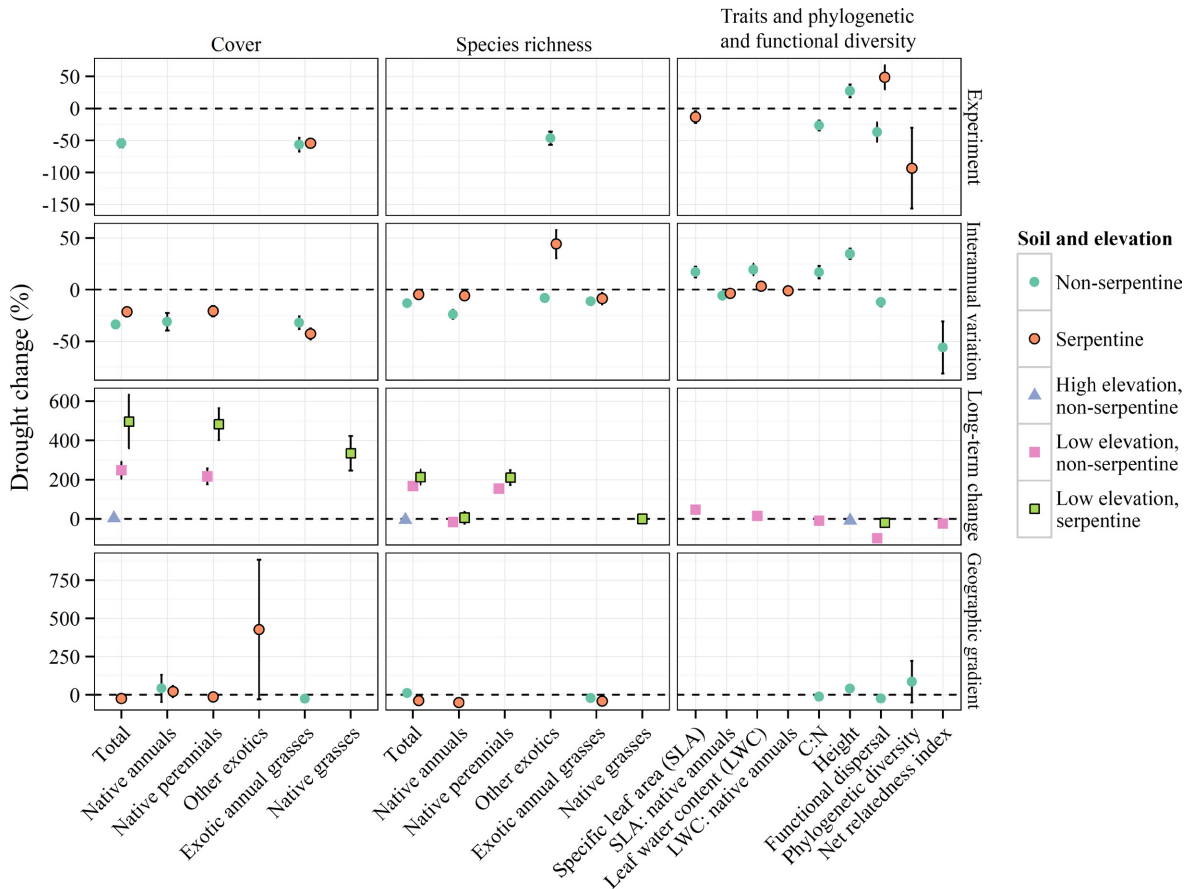


Fig. 4. Percent change relative to pre-drought values for variables significantly affected by the drought ( $P \leq 0.05$  level) in all studies.

#### Long-term directional change study

*Effects of long-term warming and drying trend.*—Total cover as well as cover of native annuals and native perennials decreased from 1950 to 2007 on both soils and across elevation bands, while grass cover increased in low-elevation serpentine and high-elevation non-serpentine sites. Declines were also seen in total and native perennial species richness on both soils and native annual forb richness on non-serpentine soils. Community weighted mean height increased consistently and mean C:N increased at low elevations. Mean SLA and LWC declined on non-serpentine soils at low elevations, and increased at high elevations. Net relatedness decreased while multivariate functional dispersion increased on non-serpentine soils at both elevation bands. Phylogenetic diversity increased at low elevations on both soils (Appendix S1: Table S3, Table 4).

*Drought effects.*—Compared to 2007, cover of total and native perennial forbs was higher in 2014 at low elevations, and did not change at high elevations. Grass cover significantly increased on low-elevation serpentine soils. Total species richness increased at low elevations on both soils with the drought, but decreased at higher elevations; annual

and perennial forb richness increased at low elevations, while native grass richness increased at low elevations on serpentine. Mean SLA and LWC increased on non-serpentine soils at low elevations; mean height significantly decreased at low elevations on both soil types. Multivariate functional dispersion significantly decreased at low-elevations on both soil types. The net relatedness index increased on low elevation non-serpentine (Table 4, Fig. 4).

*Match between long-term trend and drought effects.*—Pre-drought and drought changes were not consistent for most community metrics considered. For example, at low elevations, species richness and cover were higher in 2014 than in 2007, although they had declined from 1950 to 2007. However, at high elevations species richness declined in both time periods, leading to a match between the pre-drought warming trend (1950–2007) and observations made in the drought year (documenting the period 2007–2014; Table 4).

#### Geographic gradient study

*Effects of geographic gradient.*—Mean precipitation (1980–2014) was negatively related to total cover and

functional group cover (native annuals, exotic annual grasses, and exotic forbs and perennial grasses) on both soils. Mean precipitation was also negatively associated with total richness and species richness of native annuals, exotic forb and perennial grasses, and exotic annual grasses on both soil types. Precipitation was positively related to native perennial richness on serpentine soils. Precipitation was negatively related to community-weighted mean SLA on serpentine and positively related to mean SLA on non-serpentine soils. Precipitation was associated with higher phylogenetic diversity on both soil types and lower net relatedness on serpentine (Appendix S1: Table S4, Table 5).

*Drought effects.*—Total cover and cover of native annuals were negatively affected by drought and thus were significantly lower in 2014 on both soils (Table 5). Native perennial and exotic forb and perennial grass cover were significantly lower on serpentine soils. Exotic annual grass cover declined on non-serpentine, but not on serpentine soils. Total species richness and richness of all functional groups declined on serpentine soils. However, on fertile soils, declines were observed only in richness of exotic annual grasses. Considering traits, community-weighted mean C:N declined while mean height increased on non-serpentine soils. Multivariate functional trait dis-

TABLE 4. Long-term directional change study: significant effects ( $P \leq 0.05$ ) of drought on community metrics by soil type and elevation band compared to change due to the long-term warming trend.

Category and variable	Warming trend			Drought		
	df	<i>t</i>	Change, 2007–1950 (%)	df	<i>t</i>	Change, 2014–2007 (%)
High elevation non-serpentine soil						
Species richness						
<b>Total</b>	<b>66</b>	<b>-8.8**</b>	<b>-45.0</b>	<b>66</b>	<b>-2.4*</b>	<b>-4.6</b>
Low elevation non-serpentine soil						
Species richness						
Total	52	-15.5**	-74.6	52	8.6**	167.3
Native annuals	52	-4.2**	-100	52	3.1*	-16.7
Native perennials	52	-15.9**	-74.7	52	9.1**	153.7
Cover						
Total	52	-11.4**	-74.6	52	3.6**	247.7
Native perennials	52	-12.9**	-77.4	52	6.9**	215.9
Traits and phylogenetic and functional diversity						
Specific leaf area	36	-6.2**	-33.3	36	2.7*	46.2
Leaf water content	36	-5.6**	-15.7	36	2.7*	14.9
Height	36	2.3*	67.8	36	-2.4*	-9.9
Dispersion (RaoQ)	10	10.4**	>1000	10	-10.4**	-99.2
Net relatedness index	29	-4.7**	<-1000	28	3.0*	-24.5
Low elevation serpentine soil						
Species richness						
Total	48	-13.9**	-66.5	48	12.5**	212.1
Grass	not measured	48	2.7*	-0.28		
Native annuals	48	-0.4	-66.7	48	2.5*	5.6
Native perennials	48	-14.4**	-67.6	48	12.1**	210.2
Cover						
Total	48	-3.3**	-32.8	48	8.1**	495.7
Grass	48	4.4**	-20.8	48	6.5**	334.1
Native perennials	48	-15.9**	-82.4	48	11.2**	481.9
Traits and phylogenetic and functional diversity						
Height	28	3.4**	104.6	28	-3.1**	-14.8
Dispersion (RaoQ)	14	0.9	94.0	14	-2.8*	-19.8

Notes: Results for change over the period of long-term warming and due to the drought (warming, 2007–1950, and drought, 2014–2007, paired *t* statistics and percent change for the difference). Boldface type indicates where the pre-drought and drought results match with a priori expectations. \* $P \leq 0.05$ ; \*\* $P \leq 0.01$ .

persion significantly decreased on non-serpentine soils. Phylogenetic dispersion increased on serpentine soils (Table 5, Fig. 4).

*Match between geographic gradient and drought effects.*—Many community properties, such as cover and richness, declined as expected with extreme drought in 2014. However, the only correspondence between the drought effects and the pre-drought water availability gradient was the positive relationship between species richness of native perennials with precipitation and decline of the richness of that functional group with drought (Table 5).

#### DISCUSSION

The most consistent community-level effects of the drought, across our four studies, were reductions in total herbaceous cover and species richness. These results support other drought studies documenting decreases

in species richness (Tilman and El Haddi 1992, Penuelas et al. 2007), plant biomass (Knapp et al. 2015), and/or primary productivity (Ciais et al. 2005) with drought, as well as with the strongest and most consistent patterns seen in studies of plant communities along geographic, experimental, and interannual water gradients (see *Introduction*). Although most functional groups were negatively affected by the drought, annual species were particularly strongly affected, also in agreement with previous studies (Adler and Levine 2007, Cleland et al. 2013, Harrison et al. 2015). Previous evidence suggests that plant communities on infertile soils may be resistant to climate warming and precipitation variability compared to communities fertile soils due to their stress tolerant traits (Damschen et al. 2012, Fernandez-Going et al. 2012, Harrison et al. 2014) while additional studies suggest that they can be vulnerable to long-term drying trends (Damschen et al. 2010, Harrison et al. 2015) and may be more exposed to climate warming in forested

TABLE 5. Geographic gradient study: significant effects ( $P \leq 0.05$ ) of drought on community metrics by soil type compared to effects associated with mean annual precipitation.

Category and variable	Precipitation		Drought		
	Z	Precipitation correlation coefficient	df	t	Change (%)
Non-serpentine soil					
Species richness					
Exotic annual grasses	-5.3**	-0.65	66	-3.6**	-21.3
Cover					
Total	-5.0**	-0.62	66	-2.8*	-2.3
Native annuals	-4.5**	-0.55	66	-4.9**	41.6
Exotic Annual grasses	-4.1**	-0.51	66	-3.1**	-25.7
Traits and phylogenetic and functional diversity					
C:N	-2.0	-0.36	32	-2.8*	-12.2
Height	-1.2	-0.21	32	2.4*	40.0
Dispersion (RaoQ)	1.1	0.22	27	-5.2**	-23.8
Phylogenetic diversity	2.1	0.27	61	4.0**	85.6
Serpentine soil					
Species richness					
Total	-3.1**	-0.37	72	-11.2**	-38.0
Native annuals	-4.8**	-0.56	72	-9.4**	-50.6
<b>Native perennials</b>	<b>3.4**</b>	<b>0.40</b>	<b>72</b>	<b>-7.6**</b>	<b>-24.3</b>
Other exotics	-3.8**	-0.45	72	-3.8**	-47.7
Exotic annual grasses	-4.6**	-0.54	72	-4.7**	-41.7
Cover					
Total	-3.8**	-0.44	72	-3.7**	-24.2
Native annuals	-3.2**	-0.37	72	-3.4**	22.1
Native perennials	0.9	0.11	72	-2.9**	-13.3
Other exotics	-2.6*	-0.30	72	-2.5*	427.3

*Notes:* Precipitation correlation coefficient indicates the strength and direction of association with mean precipitation (permutation correlation test). The remaining columns indicate change between pre-drought (2001-2003 for serpentine, 2009 for non-serpentine) and drought (2014) sampling periods (paired  $t$  statistics and percent change for difference). Boldface type indicates where the pre-drought and drought results match with a priori expectations. \* $P \leq 0.05$ ; \*\* $P \leq 0.01$ .

communities due to low overstory cover (Harrison et al. 2014). We found negative effects of the drought in communities on both infertile serpentine and fertile non-serpentine soils, and little evidence for higher resistance to drought on serpentine soils. This effect could be a result of the extreme conditions created by the drought, which may have exceeded tolerance thresholds for even relatively stress-tolerant species on serpentine. The details of the effects on specific functional groups differed between soils however, likely due to differences in pre-drought community composition. Surprisingly, we did not find consistent declines in either the functional or phylogenetic diversity of plant communities, which we had expected to follow from the selective declines of species having drought-intolerant traits and belonging to ancient mesic-adapted lineages (Anacker and Harrison 2012, Spasojevic et al. 2014, Harrison et al. 2015).

In cases where we found that drought effects matched those of pre-drought water availability gradients, the majority of drought effects were not significantly different in magnitude from the predictions of models based on the pre-drought effects (19/29 cases). However, pre-drought water availability gradients underestimated drought impacts for about a quarter of the community properties, mostly cover variables, and overestimated impacts for a handful of species richness metrics (seven models with values  $\leq$  lower 95% CI, three variables with values  $\geq$ 95% CI). The greater-than-expected changes in cover and less-than-expected shifts for some species richness variables reinforce the general finding that ecosystem productivity is among the community properties most sensitive to drought (Tilman and El Haddi 1992, Ciais et al. 2005, Zhao and Running 2010, Hoover et al. 2014). Overall, our findings suggest that only with respect to cover was the drought an extreme ecological event, in the sense of causing plant community consequences exceeding the normal range of variability (Smith 2011).

The best match between drought effects and pre-drought responses emerged from our observational study of interannual rainfall variability over the past 15 yr. Interannual and drought effects consisted of similar declines in cover and richness of the entire plant community as well as of most individual functional groups. This relatively close matching of effects may be reflective of the high variability in precipitation in this system, as observed over the 13 yr preceding the drought (Fig. 2A). This high precipitation variability may explain why few of the ecological responses to drought that we observed appeared to be extreme, in the sense of falling outside of the predicted confidence limits or indicating the crossing of a response threshold (Smith 2011). The strongest exception to this relatively high consistency was the decline in cover of exotic annual grasses, a response that was underpredicted by the pre-drought data and that suggests that this functional group is highly drought sensitive relative to the rest of the community (see Zavaleta et al. 2003, Baez et al. 2013, Hoover et al. 2014 for other comparisons of grass and forb responses).

In contrast to the interannual variability study, effects of the experimental study resembled the effects of the drought only with respect to ecosystem productivity and exotic dominance. As noted previously, the final 3 yr of the 5-yr watering experiment were years of below-average rainfall (Fig. 2A), so that the watered vs. control treatments more closely resembled normal vs. dry than wet vs. normal years, respectively. Nonetheless, the only qualitative and quantitative match we found between the experimental and drought effects were the declines in total community cover and exotic annual grass cover (on serpentine) under drier conditions. One possible reason for this limited match may be the modest magnitude of the water addition (an average of +18% per year), which reflected that the original study (Eskelinen and Harrison 2015b) was not aimed at predicting the effects of an extreme drought. However, our aim in the present study was to ask what aspects of drought effects could be extrapolated linearly from such non-extreme experimental or natural variation. Overall, our results are in broad agreement with other studies that have found experiments to only weakly predict responses to spatial or temporal climatic gradients (e.g., Penuelas et al. 2007, Sandel et al. 2010, Wolkovich et al. 2012).

Drought-induced changes were not always in the expected direction in our study of long-term directional change at the very northern end of the California Floristic Province, where we observed increases in species richness at low elevation in the drought (2014) compared to the pre-drought (2007) year. In 2013–2014, lower annual rainfall was accompanied by mild temperatures and near-normal precipitation in the late spring (Appendix S1: Figs. S1, S2, and S4). In this northerly latitude, most species are dormant through fall and winter, and warming temperatures in the spring are generally associated with emergence, growth, and flowering. As a result, the combination of mild temperatures and moisture in the late spring may have been relatively favorable to growth for many species at low elevations. At high elevations in this study, where snowpack dictates the timing and water supply of the growing season, we did observe drought-associated reductions in species richness, consistent both with general expectations and with the pre-drought study of long-term climatic drying in this region. The strong reduction in snowpack in 2014 (Fig. 2B and Appendix S1: Fig. S3) likely produced a sharply diminished growing-season water supply and may possibly also have caused freezing damage (Inouye 2008). It is possible that the effects of the drought event crossed an ecological threshold at higher elevations that was not met or exceeded at lower elevations. Divergent responses to climate warming between snowpack-free and snowpack-influenced elevations were also observed in the original study (Harrison et al. 2010), and the environmentally-contingent nature of climate change impacts has been highlighted in other studies (e.g., Burkett et al. 2005).

We found little qualitative congruence between drought effects and the effects of the large-scale geographic gradient in precipitation, consistent with a number of

previous studies that have comparatively examined space-for-time substitutions (Adler and Levine 2007, Sandel et al. 2010), although inconsistent with other such studies (Blois et al. 2013, Elmendorf et al. 2015). Feedbacks between the biotic and abiotic environment, taking place over decades to millennia, may create ecological patterns along precipitation gradients that are not reproduced by short-term temporal changes in climate. Reflecting these long-term feedbacks, our precipitation gradient encompassed a shift in dominant life-forms from herbs to shrubs to trees (Grace et al. 2007), so that the herb assemblages in the wetter sites were affected by overstory shading, while those in the driest sites were more open communities. This created considerably more complex patterns in cover, species richness, and functional traits along the precipitation gradient than those previously identified by focusing on the woody species alone (Anacker and Harrison 2012, Fernandez-Going et al. 2013). For comparison, some evidence exists that longer-term (multi-decadal) climatic drying in California has produced shifts in dominant vegetation that are roughly consistent with the climatic limits of vegetation types inferred from their broader geographic patterns (McIntyre et al. 2015).

Unexpectedly, we found few consistent effects of drought on community weighted mean values, or on either functional or phylogenetic diversity, which were expected to change due to selective declines of drought-intolerant species (since we measured only interspecific variation in traits). Among the pre-drought aridity gradients, we detected multiple instances of more drought-tolerant mean values of traits (lower SLA, lower LWC, higher C:N, and/or shorter height) at the drier ends of the gradients. However, these variables did not respond as expected to the drought in most cases, even in cases where pre-drought data showed significant relationships to water availability. We know of no previous studies examining mean functional traits as indicators of drought impacts in communities, and we speculate that the effects of climatic shifts on functional trait means may take longer, perhaps a decade or more, to become consistent enough to be detectable in functionally complex plant communities (e.g., Harrison et al. 2010, 2015). Given the modest responses of community weighted mean functional trait values to drought, and relatively few declines in species richness parallel to those observed along pre-drought water availability gradients, it is not surprising that we did not detect reductions in either functional trait diversity or phylogenetic diversity, which were only expected to decline if species with particular traits, possibly associated with particular lineages, declined disproportionately. Other recent studies have also noted climate-driven community changes that were strong yet lacked phylogenetic signal (CaraDonna and Inouye 2014).

Our analysis is confined to the short-term, immediate effects of the drought, which could be mediated by dormancy, mortality, or both. Longer-term effects will depend on the duration of the drought and the persistence of belowground life stages, as well as on potential feedbacks and indirect effects operating through soil processes, com-

petition, herbivores, and pollinators. While we found that short-term effects of drought most closely resembled those of interannual variability, it is possible that responses to longer-term trends of increasing drought intensity and duration may more closely resemble responses to geographical and multi-decadal decreases in precipitation. Subject to these caveats, our results suggest that drought disproportionately affects annual species abundance and richness, on infertile as well as fertile soils, in spite of the relative stress-tolerance of species occurring on infertile soils. The California Floristic Province is a global hotspot for plant species, many of which are endemic to the region and many of which are restricted to infertile soils such as serpentine. Our results suggest the vulnerability of this exceptional flora to droughts, which are expected to increase in intensity and frequency due to rising temperatures and increasingly variable precipitation (Thorne et al. 2009, Cook et al. 2015, Duffenbaugh et al. 2015, Williams et al. 2015). Interestingly, however, some of the greatest effects of the drought were on the non-native element of the flora, which originated largely in the Mediterranean Basin and has only been present for the past two centuries (Barbour and Major 1977). For today's exotic-dominated Californian vegetation, then, the 2012–2014 drought was a truly unprecedented event.

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