Ecosystem functional response across precipitation extremes in a sagebrush steppe

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ABSTRACT

Background. Precipitation is predicted to become more variable in the western United States, meaning years of above and below average precipitation will become more common. Periods of extreme precipitation are major drivers of interannual variability in ecosystem functioning in water limited communities, but how ecosystems respond to these extremes over the long-term may shift with precipitation means and variances. Long-term changes in ecosystem functional response could reflect compensatory changes in species composition or species reaching physiological thresholds at extreme precipitation levels.
Methods. We conducted a five year precipitation manipulation experiment in a sagebrush steppe ecosystem in Idaho, United States. We used drought and irrigation treatments (approximately 50% decrease/increase) to investigate whether ecosystem functional response remains consistent under sustained high or low precipitation. We recorded data on aboveground net primary productivity (ANPP), species abundance, and soil moisture. We fit a generalized linear mixed effects model to determine if the relationship between ANPP and soil moisture differed among treatments. We used nonmetric multidimensional scaling to quantify community composition over the five years.
Results. Ecosystem functional response, defined as the relationship between soil moisture and ANPP was similar among drought and control treatments, but the irrigation treatment had a lower slope than the control treatment. However, ANPP response to availabile soil moisture was weak and uncertain regardless of treatment, with all slopes overlapping zero. There was also large spatial variation in ANPP within-years. Plant community composition was remarkably stable over the course of the experiment and did not differ among treatments.
Discussion. Despite some evidence that ecosystem functional response became less sensitive under sustained wet conditions, the response of ANPP to soil moisture was consistently weak and community composition was stable. Differences in ecosystem functional responses across treatments were not related to compensatory shifts at the plant community level, but instead may reflect the insensitivity of the dominant species to soil moisture. These species may be successful precisely because they have evolved life history strategies which buffer them against precipitation variability.

1 INTRODUCTION

At any given site, the relationship between aboveground net primary productivity (ANPP) and water availability (e.g., soil moisture) can be characterized by regressing historical observations of ANPP on observations of soil moisture. The fitted functional response can then be used to project ANPP under future precipitation regimes (give example REF). A problem with this approach is that it requires extrapolation if future precipitation falls outside outside the historical range of variability (Smith, 2011). For example, the soil moisture-ANPP relationship may be linear within the historical range of interannual variation, but could saturate at higher levels of soil moisture. In fact, saturating relationships are actually common (Hsu et al., 2012; Gherardi and Sala, 2015b), perhaps because other resources, like nitrogen, become more limiting in wet years than dry years. Failure to accurately estimate the curvature of the soil moisture-ANPP relationship will lead to over- or underprediction of ANNP under extreme precipitation.

Another problem with relying on historical ecosystem functional responses to predict impacts of altered precipitation regimes is that these relationships themselves might shift over the long-term. Changes in species identities and abundances can alter an ecosystem's functional response to water availability because different species have different physiological thresholds. Smith et al. (2009) introduced the 'Hierarchical Response Framework' for understanding the interplay of community composition and ecosystem functioning in response to long-term shifts in resources. In the near term, ecosystem functioning such as ANPP will reflect the physiological responses of individual species to the manipulated resource level. For example, ANPP may decline under simulated drought because the initial community consisted of drought-intolerant species (Hoover et al., 2014). Ecosystem functioning may recover over longer time spans as new species colonize or initial species reorder in relative abundance. It is also possible that ecosystem functioning shifts to a new mean state, reflecting the suite of species in the new community (Knapp et al., 2012).

Experimental manipulations of limiting resources, like precipitation, offer a route to understanding how ecosystems will respond to resource levels that fall outside the historical range of variability (Avolio et al., 2015; Gherardi and Sala, 2015a; Knapp et al., 2017). Altering the amount of precipitation over many years should provide insight into the time scales at which water-limited ecosystems respond to chronic resource alteration. We propose four alternative predictions for the effect of precipitation manipulation on the ecosystem functional response to soil moisture based on the Hierarchical Response Framework (Fig. 1). We define 'ecosystem functional response' as the relationship between available soil moisture and ANPP. The four predictions are based on possible outcomes at the community (e.g., community composition) and ecosystem (e.g., soil moisture-ANPP regression) levels.

First, altered precipitation might have no effect on either ecosystem functional response or community composition (Fig. 1, top left). In this case, changes in ANPP would be well predicted by the current, observed soil moisture-ANPP relationship. This corresponds to the early phases of the Hierarchical Response Framework, where ecosystem response follows the physiological responses of individual species. Second, the ecosystem functional response might change while community composition remains the same (Fig. 1, top right). A saturating soil moisture-ANPP response fits this scenario, where individual species hit physiological thresholds or are limited by some other resource. Third, the ecosystem functional response might be constant but community composition changes (Fig. 1, bottom left). In this case, changes in species' identities or abundances occur in response to altered precipitation levels and species more suited to the new conditions compensate for reduced function of initial species. Fourth, and last, both ecosystem functional response and community composition could change (Fig. 1, bottom right). New species, or newly abundant species, with different physiological responses completely reshape the ecosystem functional response.

All four outcomes are possible in any given ecosystem, but the time scales at which the different scenarios play out likely differ (Smith et al., 2009; Wilcox et al., 2016; Knapp et al., 2017). To determine these time scales, we need to amass information on how quickly ecosystem functional responses change in different ecosystems. We also need to understand whether changes at the ecosystem level are driven by community level changes or individual level responses.

To that end, here we report the results of a five-year precipitation manipulation experiment in a sagebrush steppe grassland. We imposed drought and irrigation treatments (approximately $\pm 50\%$) and measured ecosystem (ANPP) and community (species composition) responses. We focus on how the drought and irrigation treatments affect the relationship between interannual variation in available soil moisture and interannual variation in ANPP, and if community dynamics underlie the ecosystem responses. In particular, we are interested in the consistency of the soil moisture-ANPP relationship among treatments. Is the relationship steeper under the drought treatment, at low soil moisture? Does the relationship saturate under the irrigation treatment, at high soil moisture? To answer these questions we fit a generalized linear mixed effects model to test whether the regressions differed among treatments. We also analyzed community composition over time, allowing us to place our experimental results within the framework our competing predictions (Fig. 1).

2 METHODS

2.1 Study Area

We conducted our precipitation manipulation experiment in a sagebrush steppe community at the USDA-ARS Sheep Experimental Station (USSES) near Dubois, Idaho (44.2° N, 112.1° W), 1500 m above sea level. The plant community is dominated by the shrub *Artemesia tripartita* and three perennial bunchgrasses, *Pseudoroegneria spicata*, *Poa secunda*, and *Hesperostipa comata*. During the period of our experiment (2011 – 2015), average mean annual precipitation was 265 mm year^{-1} and mean monthly temperature ranged from -5.2°C in January to 21.8°C in July. Between 1926 and 1932, range scientists at the USSES established 26 permanent 1 m^2 quadrats to track vegetation change over time. In 2007, we relocated 14 of the original quadrats, six of which were inside a large, permanent livestock exclosure. We use these six plots as control plots (i.e. ambient precipitation) in the experiment described below.

2.2 Precipitation Experiment

In spring 2011, we established 16 new 1 m^2 plots located in the same exclosure as the six control plots. We avoided areas on steep hill slopes, areas with greater than 20% cover of bare rock, and areas with greater than 10% cover of the shrubs *Purshia tridentata* and/or *Amelanchier utahensis*. We established the new plots in pairs and randomly assigned each plot in a pair to receive a "drought" or "irrigation" treatment.

Drought and irrigation treatments were designed to decrease and increase the amount of ambient precipitation by 50%. To achieve this, we used a system of rain-out shelters and automatic irrigation (Gherardi and Sala, 2013). The rain-out shelters consisted of transparent acrylic shingles 1-1.5 m above the ground that covered an area of 2.5 $\times$ 2 m. The shingles intercepted approximately 50% of incoming rainfall, which was channeled into 75 liter containers. Captured rainfall was then pumped out of the containers and sprayed on to the adjacent irrigation plot via two suspended sprinklers. Pumping was triggered by float switches once water levels reached about 20 liters. We disconnected the irrigation pumps each October and reconnected them each April. The rain-out shelters remained in place throughout the year.

We monitored soil moisture in four of the drought-irrigation pairs using Decagon Devices (Pullman, Washington) 5TM and EC-5 soil moisture sensors. We installed four sensors around the edges of each 1x1 m census plot, two at 5 cm soil depth and two at 25 cm soil depth. We also installed four sensors in areas nearby the four selected plot pairs to measure ambient soil moisture at the same depths. Soil moisture measurements were automatically logged every four hours. We coupled this temporally intensive soil moisture sampling with spatially extensive readings taken at six points within all 16 plots and associated ambient measurement areas. These snapshot data were collected on 06-06-2012, 04-29-2015, 05-07-2015, 06-09-2015, and 05-10-2016[1] using a handheld EC-5 sensor.

Analyzing the response to experimental treatments was complicated by the fact that we did not directly monitor soil moisture in each plot on each day of the experiment. Only a subset of plots were equipped with soil moisture sensors, and within those plots, one or more of the sensors frequently failed to collect data. To remedy these problems, and to produce average daily soil moisture values for the ambient, drought, and irrigation treatments, we used a statistical model to predict the average treatment effects on soil moisture during the course of the experiment.

We first averaged the observed soil moisture for each day and within each plot. Then we standardized the averages within each plot group by subtracting the average ambient soil moisture in that plot group and dividing by the standard deviation of the ambient soil moisture in that plot group. We then found the difference between the standardized ambient soil moisture and the standardized drought and irrigation soil moisture within each plot group. These transformations ensured that the treatment effects in each plot were appropriately scaled by the local ambient conditions within each plot group.

We then modeled the daily deviation from ambient conditions of the drought and irrigation treatments using a linear mixed effects model with independent variables for treatment, season (winter, spring,

[1] Dates formatted as: mm-dd-yyyy.

summer, fall), rainfall, and all two-way interactions. Rainy days were defined as any day in which precipitation was recorded and average temperature was above 3°C. The day immediately following rainfall was also classified as rainy. We fit the model using the `lme4::lmer()` function (Bates et al., 2015) in R (R Core Team, 2016), with random effects for plot group and date. We weighted observations by the number of unique sensors or spot measurements that were taken in each plot on that day. We then used the model to predict the average daily soil moisture in the treated plots based on the average daily ambient soil moisture. We could only predict soil moisture in the treated plots on days for which we took at least one ambient soil moisture measurement.

2.3 Data Collection

We estimated aboveground net primary productivity (ANPP) using a radiometer to relate ground reflectance to plant biomass (see Byrne et al., 2011, for a review). We recorded ground reflectance at four wavelengths, two associated with red reflectance (626 nm and 652 nm) and two associated with near-infrared reflectance (875 nm and 859 nm). At each plot in each year, we took four readings of ground reflectances at the above wavelengths. We also took readings in 12 (2015), 15 (2012, 2013, 2014), or 16 (2016) calibration plots adjacent to the experimental site, in which we harvested all aboveground biomass produced in the current year (we excluded litter and standing dead material), dried it to a constant weight at 60°C, and weighed it to estimate ANPP. We harvested at peak biomass each year, typically in late June.

For each plot and year, we averaged the four readings for each wavelength and then calculated a greenness index based on the same bands used to calculate NDVI using the MODIS and AVHRR [YOU HAVEN'T DEFINED THESE] bands for NDVI. We regressed the greenness index against the dry biomass weight from the ten calibration plots to convert the greenness index to ANPP. We fit regressions to a MODIS-based index and an AVHRR-based index for each year and retained the regression with the better fit based on R^2 values. We then predicted ANPP using the best regression equation for each year (Appendix 1).

Species composition data came from two sources: yearly census maps for each plot made using a pantograph (Hill, 1920) and yearly counts of annual species in each plot. From these sources, we determined the density of all annuals and perennials forbs, the basal cover of perennial grasses, and the canopy cover of shrubs. We made a large plot-treatment-year by species matrix, where columns were filled with either basal cover or density, depending on the measurement made for the particular species. We standardized the values in each column so we could directly compare species quantified with different metrics (density, basal cover, and canopy cover). This puts all abundance values on the same scale, meaning that common and rare species are weighted equally. Assuming that rare species will respond to treatments more than common ones, our approach is biased towards detecting compositional changes.

2.4 Data Analysis

Our main goal was to test whether the relationship between ANPP and soil moisture differed among the drought, control, and irrigation treatments. Based on our own observations and previous work at our study site (Blaisdell, 1958; Dalgleish et al., 2011; Adler et al., 2012), we chose to use cumulative volumetric water content from March through June as our metric of soil moisture (hereafter referred to as 'VWC'). To achieve this goal, we fit a generalized linear mixed effects regression model with log(ANPP) as the response variable and VWC and treatment as fixed effects. Plot and year of treatment were included as random effects to account for non-independence of observations, as described below. We log-transformed ANPP to account for heteroscedasticity. Both log(ANPP) and VWC were standardized to have mean 0 and unit variance before fitting the model [i.e., $(x_i - \bar{x})/\sigma_x$].

Our model is defined as follows:

$$\mu_i = \boldsymbol{\beta}\mathbf{x}_i + \boldsymbol{\gamma}_{j(i)}\mathbf{z}_i + \eta_t, \tag{1}$$

$$\mathbf{y} \sim \text{Normal}\left(\boldsymbol{\mu}, \sigma^2\right), \tag{2}$$

where μ_i is the deterministic prediction from the regression model for observation i, which is associated with plot j and treatment year t. $\boldsymbol{\beta}$ is the vector of coefficients for the fixed effects in the design matrix $\mathbf{X}$. Each row of the design matrix represents a single observation ($\mathbf{x}_i$) and is a vector with the following elements: 1 for the intercept, a binary 0 or 1 if the treatment is "drought", a binary 0 or 1 if the treatment is "irrigation", the scaled value of VWC, binary "drought" value times VWC, and binary "irrigation" value times VWC. Thus, our model treats "control" observations as the main treatment and then estimates intercept and slope offsets for the "drought" and "irrigation" treatments. We use our model to test the following hypotheses:

H1. The coefficient for drought$\times$VWC is positive and different from zero.

H2. The coefficient for irrigation$\times$VWC is negative and different from zero.

These hypotheses are based on evidence that precipitation-ANPP relationships often saturate with increasing precipitation (REFERENCES).

We include two random effects to account for the fact that observations within plots and years are not independent. Specifically, we include plot-specific offsets ($\boldsymbol{\gamma}$) for the intercept and slope terms and year-specific intercept offsets (η_t). The covariate vector $\mathbf{z}_i$ for each observation i has two elements: a 1 for the intercept and the scaled value of VWC for that plot and year. The plot-specific coefficients are modeled hierarchically, where plot level coefficients are drawn from a multivariate normal distribution with mean 0 and a variance-covariance structure that allows the intercept and slope terms to be correlated:

$$\boldsymbol{\gamma}_{j(i)} \sim \text{MVN}(0, \Sigma), \tag{3}$$

where Σ is the variance-covariance matrix and *j(i)* reads as "plot *j* associated with observation *i*". The random year effects ($\boldsymbol{\eta}$) are drawn from a normal prior with mean 0 and standard deviation σ_{year}, which was drawn from a half-Cauchy distribution. A full description of our model is in Appendix 2.

We fit the model using a Bayesian approach and obtained posterior estimates of all unknowns via the No-U-Turn Hamiltonian Monte Carlo sampler in Stan (Stan Development Team, 2016b). We used the R package 'rstan' (Stan Development Team, 2016a) to link R (R Core Team, 2016) to Stan. We obtained samples from the posterior distribution for all model parameters from four parallel MCMC chains run for 10,000 iterations, saving every 10^{th} sample. Trace plots of all parameters were visually inspected to ensure well-mixed chains and convergence. We also made sure all scale reduction factors ($\hat{R}$ values) were less than 1.1 (Gelman and Hill, 2009).

We used nonmetric multidimensional scaling (NMDS) based on Bray-Curtis distances to identify temporal changes in community composition among treatments. We first calculated Bray-Curtis distances among all plots for each year of the experiment and then extracted those distances for use in the NMDS. Some values of standardized species' abundances were negative, which is not allowed for calculating Bray-Curtis distances. We simply added '2' to each abundance value to ensure all values were greater than zero. We plotted the first two axes of NMDS scores to see if community composition overlapped, or not, among treatments in each year. We used the `vegan::metaMDS()` function (Oksanen, 2016) to calculate Bray-Curtis distances and then to run the NMDS analysis. We used the `vegan::adonis()` function (Oksanen, 2016) to perform permutational multivariate analysis of variance to test whether treatment plots formed distinct groupings. To test whether treatment plots were equally dispersed, or not, we used the `vegan::betadisper()` function (Oksanen, 2016).

All R code and data necessary to reproduce our analysis has been archived on Figshare (*link here after acceptance*) and released on GitHub (`https://github.com/atredennick/usses_water/releases/v0.1`). We also include annotated Stan code in our model description in Appendix 2.

3 RESULTS

Three of our five study years received below average precipitation (Fig. 2A). Because our treatments are proportional changes in ambient precipitation, those three years represent a lower magnitude of absolute difference in precipitation among the treatments. ANPP varied from a minimum of 74.5 g m^{-2} in 2014 to a maximum of 237.1 g m^{-2} in 2016 when averaged across treatments (Fig. 2C). ANPP was slightly higher in irrigation plots and slightly lower in drought plots (Fig. 2C), corresponding to estimated soil volumetric water content (VWC) differences among treatments (Fig. 2B). Such differences in soil VWC indicate our treatment infrastructure was successful. ANPP was highly variable across plots within years (Fig. 2C).

Cumulative March-June soil moisture had a weak positive effect on ANPP (Table 1; Fig. 3). The effect of soil moisture for each treatment is associated with high uncertainty, however, with 95% Bayesian credible intervals that overlap zero (Table 1). Although the parameter estimates for the effect of soil moisture overlap zero, the posterior distributions of the slopes all shrank and shifted to more positive values relative to the prior distributions (Fig. A2-2), which indicates the data did influence parameter estimates beyond the information from the uninformative priors. Ecosystem functional response was similar among treatments (Table 1; Fig. 3B), but there is evidence that the slope for the irrigation treatment is less than the slope for the control treatment. This evidence comes from interpreting the posterior distribution of the slope offset for the irrigation treatment, from which we calculate a 99% one-tailed probability that the estimate is less than zero (Fig. 3A, right panel). There was no evidence that the treatment effects became more important over time because there was no directional trend in the random year effects (Fig. A2-3).

Community composition was similar among treatments. Community composition among treatments overlapped in all years and was equally dispersed in all years (Table 2; Fig. 5). Community composition was also remarkably stable over time, with no evidence of divergence among treatments (Table 2; Fig. 5).

4 DISCUSSION

Ecosystem response to precipitation extremes depends on the physiological responses of constituent species and the rate at which community composition shifts to favor species better able to take advantage of, or cope with, new resource levels (Smith et al., 2009). Previous work has shown that community compositional shifts can be both rapid, on the order of years (Hoover et al., 2014), and slow, on order of decades (Knapp et al., 2012; Wilcox et al., 2016). A lingering question is how the time scales of ecosystem response and community change vary among ecosystems. Precipitation manipulation experiments can help answer this question, especially if they push water availability outside the historical range of variability for long periods.

The results of our five year experiment in a sagebrush steppe conform to two of our four predictions, depending on treatment. Neither ecosystem functional response nor community composition changed under chronic drought (Fig. 3A, Fig. 4), representin the top left SCENARIO in Fig. 1. Ecosystem functional response under chronic irrigation was different from the control treatment, but community composition remained unchanged (Fig. 3A, Fig. 4), representing the top right SCENARIO in Fig. 1. The altered ecosystem functional response under irrigation matched our expectations because we found evidence for a saturating response for the irrigation treatment (Fig. 3). However, the response of ANPP to soil moisture in all treatments was consistently weak (Table 1, Fig. A2-2) and within-year variation of ANPP was large (Fig. 3B).

The similarity of ecosystem functional response (Fig. 3) and community composition (Fig. 5) between drought and control treatments is surprising because grasslands generally, and sagebrush steppe specifically, are considered water-limited systems. Indeed, we expected ecosystem functional response, community composition, or both to change under the drought treatment, landing us in any box of Fig. 1 *except* the top left. Why did our drought treatment fail to induce ecosystem or community responses? We can think of three reasons; two are limitations of our study, and one is the life history traits of the species in our focal communities. We first discuss the potential limitations of our study, and then discuss the biological explanation.

First, it could be that our drought manipulation was not large enough to induce a response. That is, a 50% decrease in any given year may not be abnormal given our site's historical range of variability (Knapp et al., 2017). We cannot definitively rule out this possibility, but we have reason to believe our drought treatment *should* have been large enough. Using the methods described by Lemoine et al. (2016), we calculated the percent reduction and increase of mean growing season precipitation necessary to reach the 1% and 99% extremes of the historical precipitation regime at our site (Fig. A3-3). The 1% quantile of precipitation at our site is 110 mm, a 47% reduction from the mean, and the 99% quantile is 414 mm, a 77% increase from mean growing season precipitation (Appendix 3). Thus, our drought treatment represented extreme precipitation amounts, especially in years where ambient precipitation was below average (Fig. 2A). The irrigation treatment may not qualify as extreme, yet that is the treatment where we did observe an effect (Fig. 3).

Second, ANPP at our site may be influenced by additional factors, not only the cumulative March-June soil moisture covariate we included in our statistical model. For example, temperature can impact ANPP directly (Epstein et al., 1997) and by exacerbating the effects of soil moisture (De Boeck et al., 2011). Measurements of soil moisture likely contain a signal of temperature, through its impact on evaporation and infiltration, but the measurements will not capture the direct effect of temperature on metabolic and physiological processes. We also did not redistribute snow across our treatments in the winter, and snow melt may spur early spring growth. Failure to account for potentially important covariates could explain the within-year spread of ANPP (Fig 2C, Fig. 3B) and the resulting uncertain relationship we observed between soil moisture and ANPP across all treatments (Table 1, Fig. A2-2).

Third, the life history traits of the dominant species in our study ecosystem may explain the consistently positive, but weak and uncertain, effect of soil moisture on ANPP (Fig. 3). Species that live in variable environments, such as cold deserts, must have strategies to ensure long-term success as conditions vary. One strategy is bet hedging, where species forego short-term gains to reduce the variance of long-term success (Seger, 1987). In other words, species follow the same conservative strategy every year, designed to minimize response to environmental conditions. The dry and variable environment of the sagebrush steppe has likely selected for bet hedging species that can maintain function at low water availability and have weak responses to high water availability. In so doing, the dominant species in our ecosystem avoid "boom and bust" cycles, which corresponds to the weak effect of soil moisture on ANPP (i.e., the Bayesian credible intervals for the slopes in $\boldsymbol{\beta}$ in Eq. 1 overlapping zero).

Another strategy to deal with variable environmental conditions is avoidance, which would also result in a consistent ecosystem functional response between drought and control treatments. For example, many of the perennial grasses in our focal ecosystem avoid drought stress by growing early in the growing season (Blaisdell, 1958, A.R. Kleinhesselink, personal observation). Furthermore, the dominant shrub in our focal ecosystem, *Artemisia tripartita*, has access to water deep in the soil profile thanks to a deep root system (Kulmatiski et al., 2017).

The weaker soil moisture-ANPP relationship we observed for the irrigation treatment has three non-exclusive explanations. First, species' biomass production may have hit physiological thresholds and/or become limited by other factors, such as nitrogen availability (LeBauer and Treseder, 2008). PETER: DO WE KNOW ANYTHING ABOUT NITROGEN AT USSES? WANT TO ADD A SENTENCE HERE ABOUT HOW LIKELY OR UNLIKEL THIS IS...NUTNET SHOWS POSITIVE EFFECTS OF N*P ON PRODUCTION, EFFECT OF N ALONE NOT AS CLEAR. YOU COULD CITE THIS AS UNPUBLISHED DATA

Second, the less positive slope could be an indicator of bet hedging in this community. Avoiding high biomass and seed production in wet years could benefit species in the long run if climate conditions are variable. but why would this have cause a change relative to controls? this should also be true for controls... Third, the less positive slope may be a statistical artifact due the variability of ANPP within years and our low sample size.

In conclusion, our results suggest the species in our focal plant community are tolerant of drought conditions and unresponsive to wet conditions. no, you can't be a bet hedger in wet years but not in dry years... Longer, chronic precipitation alteration might reveal plant community shifts that we did not observe (e.g., Wilcox et al., 2016). For example, a long-term increase in water availability could allow species that do not bet hedge to gain prominence and dominate the ecosystem functional response. Our results suggest compositional shifts would have the largest impact at high rainfall because the current community maintained consistent ecosystem functional response at very low water availability.

5 ACKNOWLEDGEMENTS

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7 AUTHOR CONTRIBUTIONS

- Andrew T. Tredennick collected data, analyzed the data, wrote the paper, prepared figures and/or tables, reviewed drafts of the paper.
- Andrew R. Kleinhesselink conceived and designed the experiments, performed the experiments, collected data, analyzed the data, reviewed drafts of the paper.
- Bret Taylor contributed reagents/materials/analysis tools, reviewed drafts of the paper.
- Peter B. Adler conceived and designed the experiments, performed the experiments, collected data, analyzed the data, reviewed drafts of the paper.

8 SUPPLEMENTAL INFORMATION

Appendix 1. Additional methods and information on estimating aboveground net primary productivity.

Appendix 2. Details of the hierarchical Bayesian model, Fig. A2-1, Fig. A2-2, and Fig. A2-3.

Appendix 3. Details on analysis of precipitation historical range of variability and Fig. A3-1.

9 TABLES

Table 1. Summary statistics from the posterior distributions of coefficients for each treatment.

Coefficient	Treatment	Posterior Mean	Posterior Median	Lower 95% BCI	Upper 95% BCI
Intercept	Control	0.22	0.16	-1.25	2.16
Intercept	Drought	0.64	0.44	-1.37	3.79
Intercept	Irrigation	-0.51	-0.37	-2.99	1.26
Slope	Control	1.31	1.14	-0.30	3.83
Slope	Drought	1.18	1.00	-0.62	4.12
Slope	Irrigation	0.83	0.68	-0.61	3.12

Table 2. Results from statistical tests for clustering and dispersion of community composition among precipitation treatments. 'adonis' tests whether treatments form unique clusters in multidimensial space; 'betadisper' tests whether treatments have similar dispersion. For both tests, *P* values greater than 0.05 indicate there is no support that the treatments differ.

Year	Test	n	d.f.	*F*	*P*
2011	adonis	21	2	1.02	0.42
2011	betadisper	21	2	2.23	0.14
2012	adonis	22	2	1.10	0.34
2012	betadisper	22	2	0.21	0.81
2013	adonis	22	2	1.23	0.14
2013	betadisper	22	2	0.28	0.76
2014	adonis	22	2	0.95	0.54
2014	betadisper	22	2	0.35	0.71
2015	adonis	21	2	1.05	0.40
2015	betadisper	21	2	3.01	0.07
2016	adonis	21	2	1.07	0.33
2016	betadisper	21	2	0.50	0.62

10 FIGURES

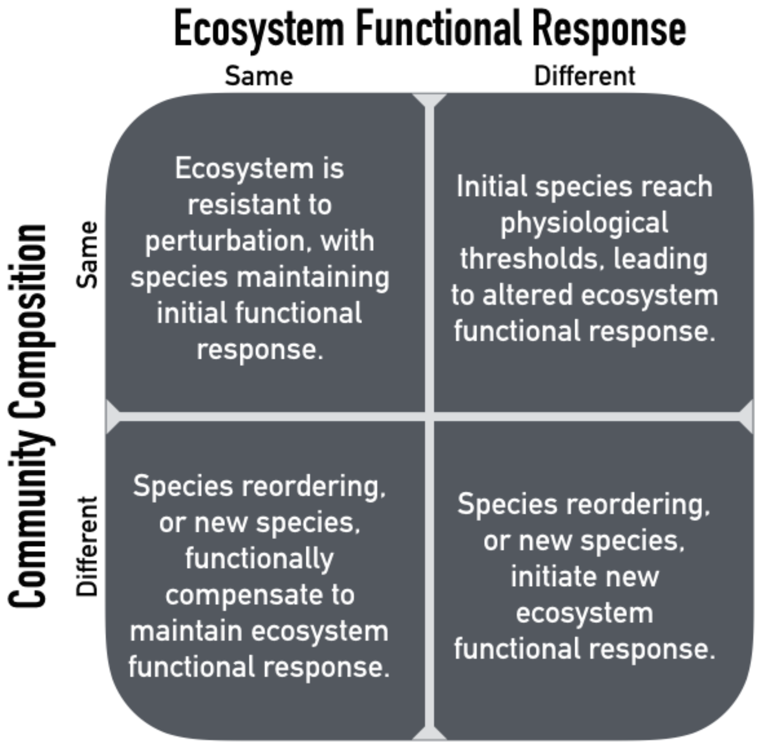

Figure 1. Possible outcomes of chronic resource alteration based on the 'Hierarchical Response Framework' (Smith et al. 2009).

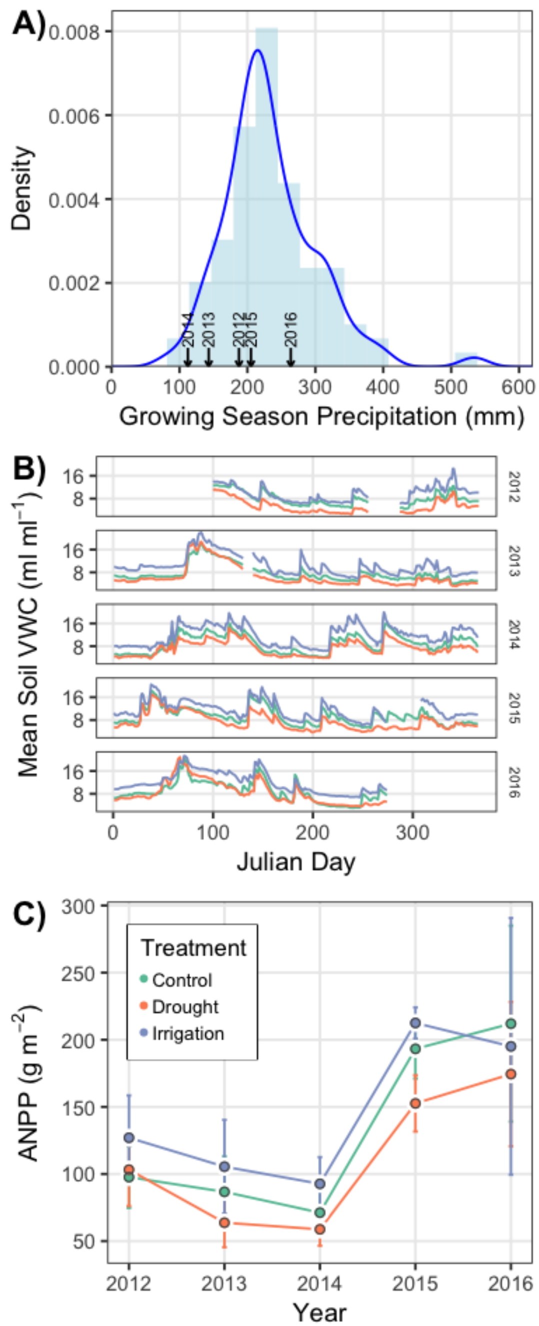

Figure 2. (A) Probability density of historical precipitation from 1926-2016, with the years of the experiment shown with arrows on the *x*-axis. (B) Observed soil volumetric water content (VWC) over the course of the experiment. (C) Mean (points) ANPP and its standard deviation (error bars) for each year of the experiment.

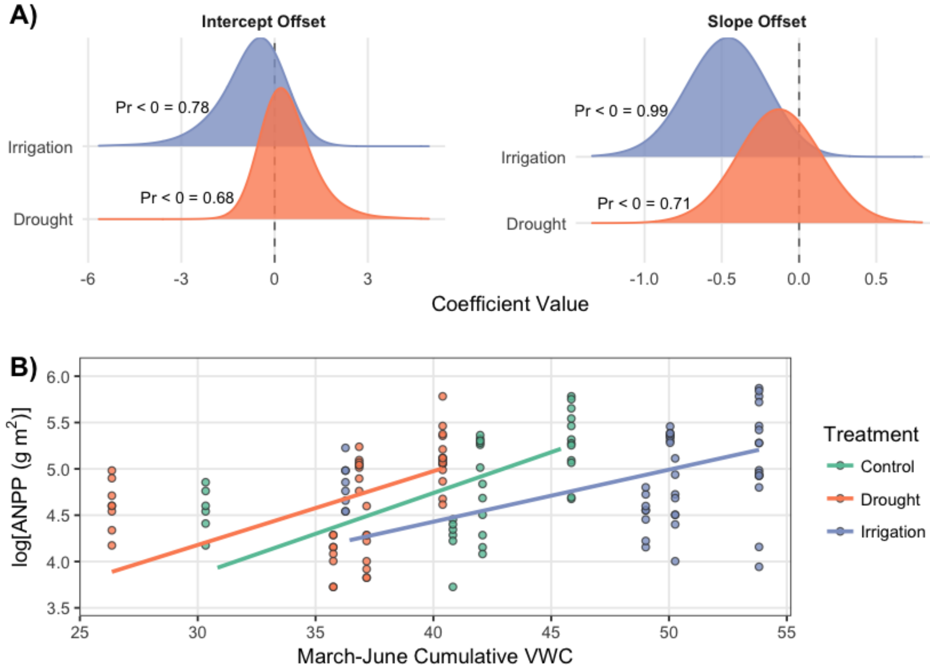

Figure 3. Results from the generalized linear mixed effects model. (A) Posterior distributions of the intercept and slope offsets for the drought and irrigation treatments. Offsets indicate the amount to which the coefficients for drought or irrigation treatments differ from the control treatment estimates. Probabilities ("Pr $<$ 0 =") for each distribution indicate the probability that coefficient is less than zero. Probabilities greater than 0.95 indicate strong support for the coefficient being less than zero. We only show the one-tailed probability for the value being less than zero because the median of each distribution is less than zero. Kernel bandwidths of posterior densities were adjusted by a factor of 5 to smooth the distribution for visual clarity. (B) Scatterplot of the data and model estimates shown a solid lines. Model estimates come from treatment level coefficients (colored lines). Note that we show log(ANPP) on the *y*-axis of panel B; this same plot can be seen on the arithmetic scale in supporting material Fig. A2-1.

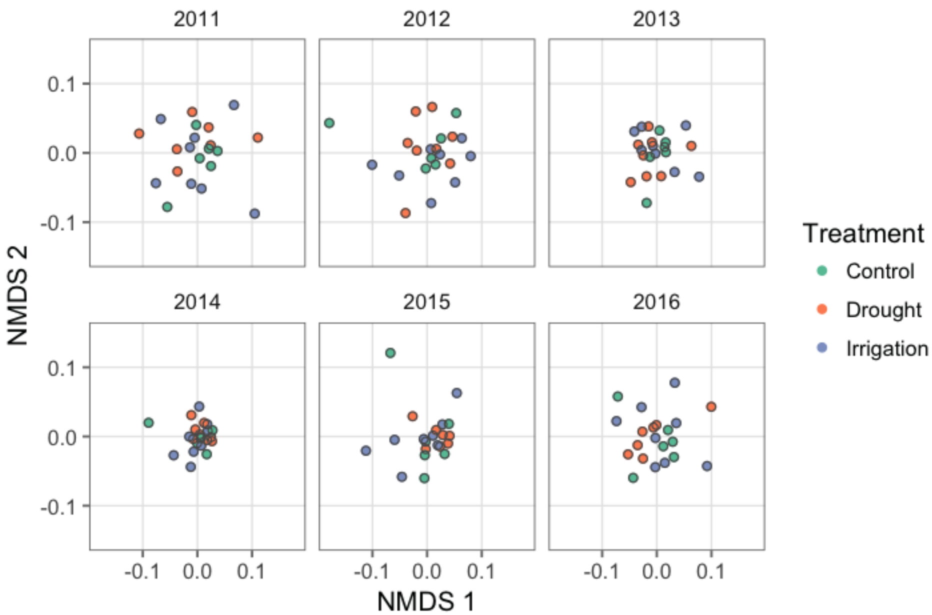

Figure 4. Nonmetric multidimensional scaling scores representing plant communities in each plot, colored by treatment.

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