

# Consistent ecosystem functional response across precipitation extremes in a sagebrush steppe

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## ABSTRACT

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 drought and deluge are major drivers of ecosystem functioning in water limited grasslands, but how ecosystems respond to precipitation may change as the duration of above and below average periods increases. Changes in ecosystem functional response could reflect compensatory changes in species composition or species reaching physiological thresholds at extreme precipitation levels. Here we report the results of a five-year experiment where we used drought and irrigation treatments (approximately 50% decrease/increase) to investigate whether ecosystem functional response remains consistent at extreme precipitation levels. We also use species-level abundance data to link ecosystem functional response to community dynamics. Ecosystem functional response, defined as the relationship between soil moisture and aboveground net primary productivity, was surprisingly consistent across drought, control, and irrigation treatments. Aboveground net primary productivity (ANPP) responded positively to available soil moisture, but the response was weak and did not vary across treatments. There was also no evidence that treatment effects grew over time. The similarity of ecosystem functional response across treatments was not due to compensatory shifts at the plant community level, where species composition among treatments was similar and remarkably stable over the five years. At least in the short-term, ecosystem functional response and community composition in this sagebrush steppe system is consistent, even at extreme precipitation levels. Such consistency may be due to bet-hedging strategies of constituent species.

## 1 INTRODUCTION

Projected changes in precipitation regimes, associated with global climate change, will affect

Water availability is a strong driver of aboveground net primary productivity (ANPP) in grassland ecosystems. Mean annual precipitation (MAP) is strongly correlated with ANPP across sites (Huxman et al., 2004), and, in water-limited ecosystems, interannual variation in MAP is also correlated with interannual variation in ANPP (Hsu et al., 2012). These relationships suggest that chronic alterations in levels of precipitation, associated with global climate change, will impact ANPP.

At a given site, the functional response of ANPP to water availability (e.g., soil moisture) can be characterized by fitting a model to historical observations of ANPP and soil moisture. However, the fitted functional response may provide an incomplete picture because future conditions are likely to be outside the historical range of variability (Smith, 2011). For example, historical trends may show a linear soil moisture-ANPP relationship, but that relationship could potentially saturate if soil moisture is pushed far beyond typical levels. Saturating relationships are actually common (Hsu et al., 2012; Gherardi and

46 Sala, 2015b), perhaps because other resources, like nitrogen, become more limiting in wet years than dry  
47 years. Knowing the curvature of the soil moisture-ANPP relationship is critical for understanding how  
48 ecosystems will respond to chronic alterations in water availability.

49 Another problem with relying on historical ecosystem functional responses is that they are not static.  
50 Changes in species identities and abundances can alter an ecosystem's functional response to water  
51 availability because different species have different physiological thresholds for producing biomass.  
52 Smith et al. (2009) introduced the 'Hierarchical Response Framework' (HRF) for understanding the  
53 interplay of community composition and ecosystem functioning in response to resource manipulations  
54 over time. In the near term, ecosystem functioning such as annual net primary productivity (ANPP) will  
55 reflect the physiological responses of individual species to the manipulated resource level. For example,  
56 ANPP may decline under simulated drought because the initial community consisted of drought-intolerant  
57 species (Hoover et al., 2014). Over longer time spans, ecosystem functioning may recover as new species  
58 colonize or initial species reorder in relative abundance. For example, ANPP may initially decline,  
59 but eventually rise back to pre-treatment levels once drought-tolerant species become more abundant  
60 and compensate for drought-intolerant species (Hoover et al., 2014). It is also possible that ecosystem  
61 functioning shifts to a new mean state, reflecting the suite of species in the new community (Knapp et al.,  
62 2012).

63 Manipulating potentially limiting resources like precipitation offers a route to understanding how  
64 ecosystems will respond to resource levels that fall outside the historical range of variability (Avolio et al.,  
65 2015; Gherardi and Sala, 2015a; Knapp et al., 2017). Altering the amount of precipitation over many years  
66 should provide insight into the time scales at which water-limited ecosystems respond to chronic resource  
67 alteration. Following the HRF, we propose four alternative predictions for the effect of precipitation  
68 manipulation on the ecosystem functional response to soil moisture, that is, the soil moisture-ANPP  
69 relationship (Figure 1). The four predictions are based on possible outcomes at the community (e.g.,  
70 community composition) and ecosystem (e.g., soil moisture-ANPP regression) levels.

71 First, altered precipitation changes neither ecosystem functional response nor community composition  
72 (Fig. 1, top left). In this case, changes in ANPP simply follow the soil moisture-ANPP relationship under  
73 ambient conditions. This corresponds to the early phases of the HRF, where ecosystem response is due to  
74 the physiological responses of individual species. Second, the ecosystem functional response changes but  
75 community composition remains the same (Fig. 1, top right). A saturating soil moisture-ANPP response  
76 fits this scenario, where individual species hit physiological thresholds or are limited by some other  
77 resource. Third, the ecosystem functional response is consistent but underlying community composition  
78 changes (Fig. 1, bottom left). In this case, changes in species' identities or abundances occur in  
79 response to altered precipitation levels and species more suited to the new conditions compensate for  
80 reduced function of initial species. Fourth, and last, both ecosystem functional response and community  
81 composition change (Fig. 1, bottom right). New species, or newly abundant species, with different  
82 physiological responses completely reshape the ecosystem functional response.

83 All four outcomes are possible in any given ecosystem, but the time scales at which the different  
84 scenarios play out likely differ (Smith et al., 2009; Wilcox et al., 2016; Knapp et al., 2017). Thus, our  
85 task is not to test the validity of the HRF, but rather to amass information on how quickly ecosystem  
86 functional responses change in different ecosystems. Likewise, we need to understand whether changes at  
87 the ecosystem level are driven by community level changes or individual level responses.

88 To that end, here we report the results of a five-year precipitation manipulation experiment in a  
89 sagebrush steppe grassland. We imposed drought and irrigation treatments (approximately  $\pm 50\%$ ) and  
90 measured ecosystem (ANPP) and community (species composition) responses. We focus on how the  
91 drought and irrigation treatments affect the relationship between available soil moisture and ANPP, and if  
92 community dynamics underly the ecosystem responses. In particular, we are interested in the consistency  
93 of the soil moisture-ANPP relationship among treatments. Is the relationship steeper under the drought  
94 treatment, at low soil moisture? Does the relationship saturate under the irrigation treatment, at high soil  
95 moisture? To answer these questions we fit a random intercepts, random slopes model to test whether the  
96 regressions differed among treatments. We also analyzed community composition over time, allowing us  
97 to place our experimental results within the framework of the HRF and our competing predictions (Fig.  
98 1).

## 99 2 METHODS

### 100 2.1 Study Area

101 We conducted our precipitation manipulation experiment in a sagebrush steppe community at the United  
102 States Sheep Experimental Station (USSES) near Dubois, Idaho (44.2° N, 112.1° W), 1500 m above  
103 sea level. The plant community is dominated by the shrub *Artemisia tripartita* and three perennial  
104 bunchgrasses, *Pseudoroegneria spicata*, *Poa secunda*, and *Hesperostipa comata*. During the period of our  
105 experiment (2011 – 2015), average mean annual precipitation was 265 mm year<sup>-1</sup> and mean monthly  
106 temperature ranged from -5.2°C in January to 21.8°C in July.

### 107 2.2 Precipitation Experiment

108 Between 1926 and 1932, range scientists at the USSES established 26 permanent 1 m<sup>2</sup> quadrats to track  
109 vegetation change over time. In 2007, we (well, one of us [P. Adler]) relocated 14 of the original quadrats,  
110 six of which were inside a large, permanent livestock enclosure. We use these six plots as control plots  
111 that have recieved no treatment, just ambient precipitation. In spring 2011, we (well, two of us [A.  
112 Kleinhesselink and P. Adler]) established 16 new 1 m<sup>2</sup> plots located in one of the same enclosures as 6 of  
113 the original vegetation monitoring plots. We avoided areas on steep hill slopes, areas with greater than  
114 20% cover of bare rock, and areas with greater than 10% cover of the shrubs *Purshia tridentata* and/or  
115 *Amelanchier utahensis*. We established the new plots in pairs and randomly assigned each plot in a pair to  
116 receive a “drought” or “irrigation” treatment.

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

126 We monitored soil moisture in four of the drought-irrigation pairs using Decagon Devices (Pulman,  
127 Washington) 5TM and EC-5 soil moisture sensors. We installed four sensors around the edges of each plot,  
128 two at 5 cm soil depth and two at 25 cm soil depth. We also installed four sensors in areas nearby the four  
129 selected plot pairs to measure ambient soil moisture at the same depths. Soil moisture measurements were  
130 automatically logged every four hours. We coupled this temporally intensive soil moisture sampling with  
131 spatially extensive readings taken at six points within all 16 plots and associated ambient measurement  
132 areas. These snapshot data were collected on 06/06/2012, 04/29/2015, 05/07/2015, 06/09/2015, and  
133 05/10/2016 using a handheld EC-5 sensor.

134 Analyzing the response to experimental treatments was complicated by the fact that we did not directly  
135 monitor soil moisture in each plot on each day of the experiment.

136 Only a subset of plots were equipped with soil moisture sensors, and within those plots, one or more of the  
137 sensors frequently failed to collect data. To remedy these problems, and to produce average daily soil  
138 moisture values for the ambient, drought, and irrigation conditions, we used a statistical model to predict  
139 the average treatment effects on soil moisture during the course of the experiment.

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

146 We then modeled the daily deviation from ambient conditions of the drought and irrigation treatments  
147 using a linear mixed effects model with independent variables for treatment, season (winter, spring,  
148 summer, fall), rainfall, and all two-way interactions.

149 Rainy days were defined as any day in which precipitation was recorded and average temperature was  
150 above 3°C. The day immediately following rainfall was also classified as rainy. We fit the model using the

151 ‘lme4::lmer()’ function (Bates et al., 2015) in R (R Core Team, 2016), with random effects for plot group  
 152 and date. We weighted observations by the number of unique sensors or spot measurements that were  
 153 taken in each plot on that day. We then used the model to predict the average daily soil moisture in the  
 154 treated plots based on the average daily ambient soil moisture.  
 155 We could only predict soil moisture in the treated plots on days for which we took at least one ambient  
 156 soil moisture measurement (Fig. 2B).

## 157 2.3 Data Collection

158 We estimated aboveground net primary productivity (ANPP) using a radiometer to relate ground re-  
 159 flectance to plant biomass (see Byrne et al., 2011, for a review). We recorded ground reflectance at  
 160 four wavelengths, two associated with red reflectance (626 nm and 652 nm) and two associated with  
 161 near-infrared reflectance (875 nm and 859 nm). At each plot in each year, we took four readings of ground  
 162 reflectances at the above wavelengths. We also took readings in 12 (2015), 15 (2012, 2013, 2014), or 16  
 163 (2016) calibration plots adjacent to the experimental site, in which we harvested all aboveground biomass,  
 164 dried it to a constant weight at 60°C, and weighed it to estimate ANPP.

165 For each plot and year, we averaged the four readings for each wavelength and then calculated a  
 166 greenness index based on the same bands used to calculate NDVI using the MODIS and AVHRR bands for  
 167 NDVI. To convert the greenness index to ANPP we regressed the greenness index against the dry biomass  
 168 weight from the ten calibration plots. We fit regressions to MODIS-based index and AVHRR-based index  
 169 for each year and retained the regression with the better fit. Using the best regression equation for each  
 170 year, we predicted ANPP (Appendix 1).

171 Species composition data came from two sources: yearly census maps for each plot made using a  
 172 pantograph (Hill, 1920) and yearly counts of annual species in each plot. From those maps, we have  
 173 data on the density of all annuals and perennials forbs, basal cover of perennial grasses, and canopy  
 174 cover of shrubs. We made a large plot-treatment-year by species matrix, where columns were filled with  
 175 either basal cover or density, depending on the measurement made for the particular species. So we  
 176 could analyze the different types of data together, we standardized the values in each column. This puts  
 177 all abundance values on the same scale, meaning that common and rare species are weighted equally.  
 178 Nonetheless, if we assume that rare species will respond more than common ones, then this approach  
 179 is anti-conservative for detecting community change. This means that our approach is biased toward  
 detecting compositional changes.

Did I say this  
right?

## 181 2.4 Data Analysis

182 Our main goal was to test whether the relationship between ANPP and soil moisture differed among the  
 183 drought, control, and irrigation treatments. Based on our own observations and previous work at our study  
 184 site (Blaisdell, 1958; Dalglish et al., 2011; Adler et al., 2012), we chose to use cumulative volumetric  
 185 water content from March through June as our metric of soil moisture (hereafter referred to simply as  
 186 ‘soil moisture’). To achieve this goal, we fit a multi-level random intercept and random slope regression  
 187 with  $\log(\text{ANPP})$  as the response variable and soil moisture as the sole predictor. We log-transformed  
 188 ANPP to account for heteroscedasticity. We fit the model under a Bayesian framework, allowing us to test  
 189 for treatment differences by comparing the posterior distributions of the treatment-level coefficients (e.g.,  
 190 Tredennick et al., 2013). Both  $\log(\text{ANPP})$  and soil moisture were standardized to have mean 0 and unit  
 191 variance before fitting the model [i.e.,  $(x_i - \bar{x})/\sigma_x$ ].

192 Our model is defined as follows:

$$\mu_{j(k(t))} = \beta_{0,j(k)} + \beta_{1,j(k)}x_{k(t)} + \gamma_t, \quad (1)$$

$$y_{j(k(t))} \sim \text{Normal}(\mu_{j(k(t))}, \sigma_k^2), \quad (2)$$

193 where  $\mu_{j(k(t))}$  is the deterministic prediction from the regression model for plot  $j$  associated with treatment  
 194  $k$  in year  $t$ ,  $\beta_{0,j(k)}$  is the intercept for plot  $j$  associated with treatment  $k$ ,  $\beta_{1,j(k)}$  is the slope term for the  
 195 effect of soil moisture for plot  $j$  associated with treatment  $k$ ,  $\gamma_t$  is the intercept offset for year  $t$ , and  $\sigma_k^2$  is  
 196 the process variance for treatment  $k$ . Data include the standardized  $\log(\text{ANPP})$  observations ( $y_{j(k(t))}$ ) and  
 197 soil moisture ( $x_{k(t)}$ ).

The intercept and slope terms are modeled hierarchically to account for the non-independence of observations across years within plots and to allow us to test the hypothesis that our treatments alter the ANPP-soil moisture relationship. Thus, our multi-level model has three grouping levels for coefficients, representing the nested structure of the data: (i) overall coefficients, (ii) treatment coefficients, and (iii) plot coefficients. Each subsequent level is drawn from the distribution of coefficients at the previous level, meaning plot-level coefficients are drawn from treatment-level coefficients, which are drawn from overall coefficients. We also include a covariance structure among the intercept and slope at each level. Formally, our hierarchical structure is as follows, where we drop the intercept (0) and slope (1) subscripts and instead refer to a vector of coefficients,  $\boldsymbol{\beta}$ :

$$\boldsymbol{\beta}_{j(k)} \sim \text{MVN}(\boldsymbol{\beta}_k, \boldsymbol{\Sigma}(k)), \quad (3)$$

$$\boldsymbol{\beta}_k \sim \text{MVN}(\boldsymbol{\beta}, \boldsymbol{\Sigma}), \quad (4)$$

$$\boldsymbol{\beta} \sim \text{Normal}(0, 1), \quad (5)$$

where  $\boldsymbol{\beta}_{j(k)}$  is the vector of regression coefficients (intercept and slope) for plot  $j$  associated with treatment  $k$ ,  $\boldsymbol{\beta}_k$  is the vector of coefficients for each treatment, and  $\boldsymbol{\beta}$  is the vector of overall coefficients. The plot- and treatment-level coefficients are drawn from multivariate normal distributions with covariance matrix  $\boldsymbol{\Sigma}$ . For the plot-level coefficients, each treatment has its own variance-covariance matrix (i.e.,  $\boldsymbol{\Sigma}(k)$ ). The overall coefficients are drawn from a normal prior with mean 0 and standard deviation 1. The random year effects ( $\boldsymbol{\gamma}$ ) are drawn from a normal prior with mean 0 and standard deviation  $\sigma_{\text{year}}$ , which was drawn from a weibull distribution. A full description of model is in Appendix 2.

We fit the model using a Bayesian approach, obtaining 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<sup>th</sup> sample. Traceplots of all parameters were visually inspected to ensure well-mixed chains and convergence. We also made sure all scale reduction factors ( $\hat{R}$ ) were less than 1.1.

To see if community composition differed among treatments through time, we used non-dimensional multivariate scaling (NMDS) based on Bray-Curtis distances. For each year of the experiment, we first calculated Bray-Curtis distances among all plots, and then extracted those distances for use in the NMDS. Because we standardized species’ abundances, some values 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 ‘metaMDS()’ function in the R package ‘vegan’ (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](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 treatment years fell in years of below average rainfall (Fig. 2A). Thus, those three years represent a lower magnitude of absolute change in precipitation experienced by the treatments. Averaged across treatments, ANPP varied from a minimum of 74.5 g m<sup>-2</sup> in 2014 to a maximum of 237.1 g m<sup>-2</sup> in 2016 (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.

Cumulative March-June soil moisture had a weak positive effect on ANPP (mean of  $\beta_1 = 0.41$ ), but the effect is associated with high uncertainty, with credible intervals that overlap zero (80% BCI = -0.08, 0.86; 95% BCI = -0.45, 1.13) (Fig. 3). Ecosystem functional response was similar among treatments, with treatment level regressions between soil moisture and log(ANPP) having similar intercepts and slopes

(Fig. 3A). There was also no evidence that the treatment effects became more important over time because there was no directional trend in the random year effects (Fig. 4).

Community composition was similar among treatments. In no year did community composition among treatments not overlap, and they were equally dispersed in all years (Table 1; Fig. 5). Likewise, community composition was remarkably stable over time, with no evidence of divergence among treatments (Table 1; Fig. 5).

## 4 DISCUSSION

Ecosystem response to chronic resource alteration is expected to follow a temporal trend. Initially, ecosystem response will be modest and reflect the physiological responses of constituent species. Over longer time periods, species reordering will cause greater responses as species better able to take advantage of, or cope with, new resource levels become more abundant. This temporal trend is formalized by the 'Hierarchical Response Framework' (HRF, Smith et al., 2009), and has been empirically supported (Knapp et al., 2012; Wilcox et al., 2016). A lingering question is not whether the HRF is a reasonable model of ecosystem dynamics, but rather how the time scales of ecosystem response and community change differ among ecosystems. Indeed, 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). To add to this growing body of knowledge, we performed a precipitation manipulation experiment in a sagebrush steppe ecosystem.

Ecosystem functional response (i.e., the relationship between soil moisture and ANPP) and community composition in this sagebrush steppe ecosystem was consistent across drought, control, and irrigation treatments (Fig. 2D, Fig. 3). In other words, functional responses estimated from any precipitation level sampled apply to any other level of precipitation, and the consistent functional response was not due to species reordering and compensation. Thus, our results conform to the first of our four predictions: neither ecosystem functional response nor community composition changed with chronic alteration in water availability (Fig. 1, top left).

This is surprising because grasslands generally, and sagebrush steppe specifically, are considered water-limited systems. Thus, our naive expectations were that either (i) ecosystem functional response would differ among treatments as species reach physiological thresholds and resource limitations (Fig. 1, top right), or (ii) ecosystem functional response stays the same due to species reordering and compensation (Fig. 1, bottom left).

In the absence of community composition data, an obvious hypothesis to explain the consistent ecosystem functional response is that species reordered rapidly. In so doing, newly abundant species could compensate for the loss of ecosystem functioning of previously abundant species. We did not find this to be the case, as species composition was remarkably stable over the course of the experiment (Fig. 5).

In combination, the lack of ecosystem and community response to drought or irrigation shows that this sagebrush steppe ecosystem is resistant to chronic alterations in water availability. There are three possible explanations for the resistance we found. First, it could be that our experiment simply was not long enough to induce responses. This may be true for community responses, which can take decades (Wilcox et al., 2016).

Second, it could be that our manipulations were not large enough to induce a response. That is, maybe a 50% decrease/increase in any given year is not abnormal given our sites historical range of variability (Knapp et al., 2017). We cannot definitively rule out this possibility, but we have reason to believe our manipulations *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. 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 have been too small, however.

Third, the ecosystem and community resistance to drought and deluge we observed could be a real phenomenon in this system, at least over the five year time span we observed. The perennial plants in this cold desert ecosystem are tolerant to drought conditions (Bazzaz, 1979; Franks, 2011; A.R. Kleinheselink,

unpublished data), meaning a consistent ecosystem functional response at low soil moisture is perfectly reasonable. 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). Likewise, the dominant shrub in our focal ecosystem, *Artemisia tripartita*, has access to water deep in the soil profile thanks to a deep root system (CITATION). As for the irrigation treatments, the lack of a saturating response (e.g., a lower regression slope) suggests water availability remained a limiting factor at the levels of precipitation we were able to manipulate.

In conclusion, our results suggest that five years of  $\pm 50\%$  ambient precipitation is not enough to induce a shift in ecosystem functional response in a sagebrush steppe. This is likely because component species are tolerant to drought conditions and water remains co-limiting at higher precipitation levels. Longer time series of chronic precipitation alteration may reveal plant community shifts that we did not observe (e.g., Wilcox et al., 2016). 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

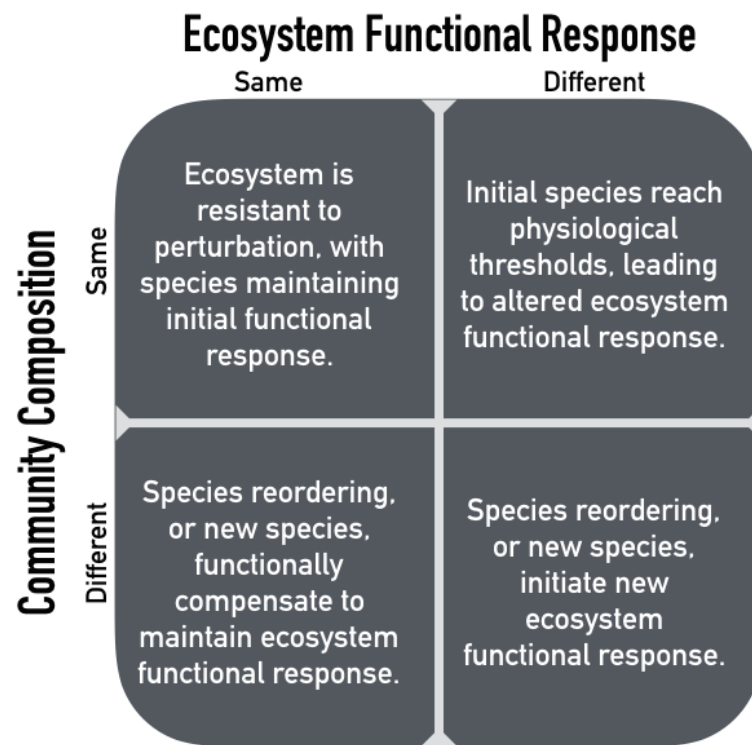
- Andrew T. Tredennick collected data, analyzed the data, wrote the paper, prepared figures and/or tables, reviewed drafts of the paper.
- Andrew R. Kleinhesselink conceived and designed the experiments, performed the experiments, collected data, reviewed drafts of the paper.
- Peter B. Adler conceived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

## 8 TABLES

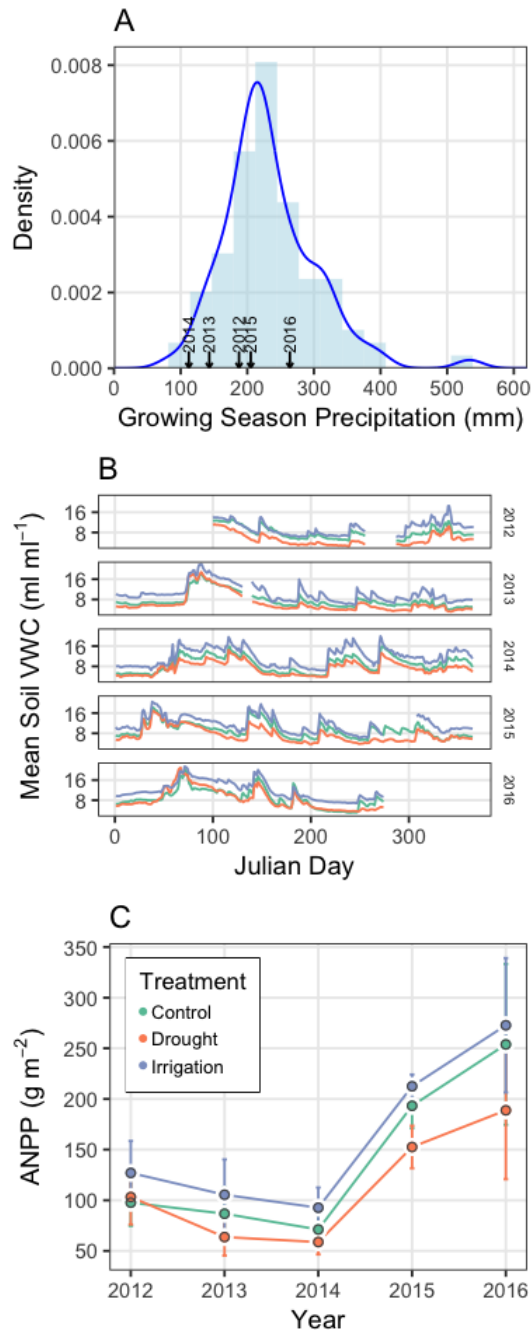
**Table 1.** Results from statistical tests for clustering and dispersion of community composition among precipitation treatments. ‘adonis’ tests whether treatments form unique clusters in multidimensional space; ‘betadisper’ tests whether treatments have similar dispersion. For both tests,  $P$  values 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	0.45
2011	betadisper	21	2	2.23	0.14
2012	adonis	22	2	1.10	0.29
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	0.58
2014	betadisper	22	2	0.35	0.71
2015	adonis	21	2	1.05	0.37
2015	betadisper	21	2	3.01	0.07
2016	adonis	21	2	1.07	0.35
2016	betadisper	21	2	0.50	0.62

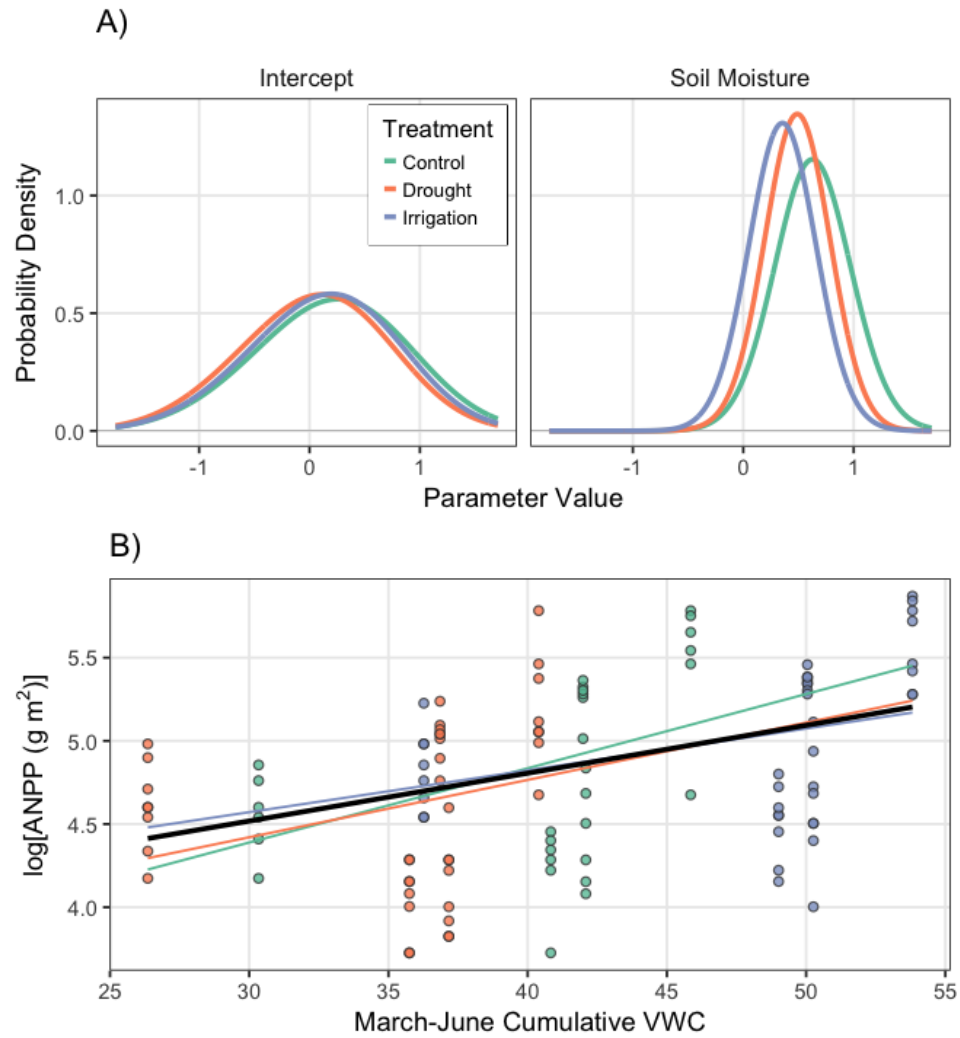




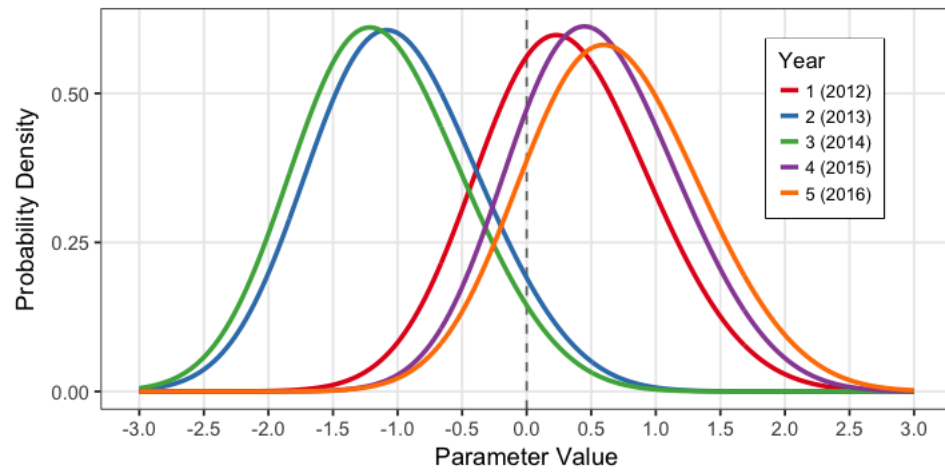
**Figure 1.** Possible outcomes of chronic resource alteration.



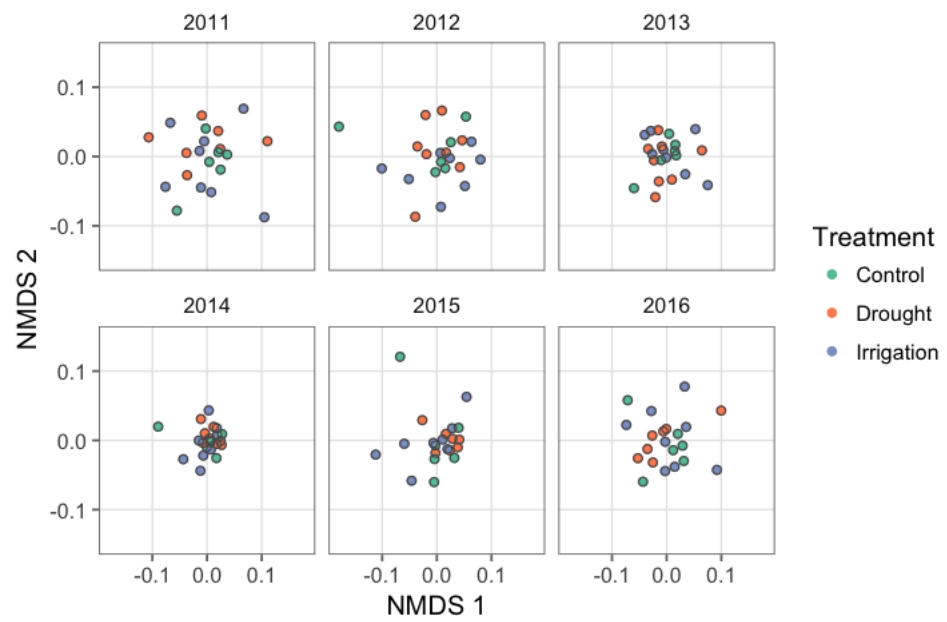
**Figure 2.** (A) Probability density of historical precipitation from 1926-2016, with the years of the experiment shown with arrows on the  $x$ -axis. (B) Observed soil volumetric water content (VWC) over the course of the experiment. (C) Mean (points) ANPP and its standard deviation (error bars) for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



**Figure 3.** Results from the generalized linear mixed effects model. (A) Posterior distributions of treatment-level parameters ('Intercept' and the effect of 'Soil Moisture'). Kernel bandwidths of posterior densities were adjusted by a factor of 5 for visual clarity. (B) Scatterplot of the data and model estimates shown a solid lines. Model estimates come from treatment level coefficients (colored lines) and the overall mean coefficients (heavy black line). Note that we show  $\log(\text{ANPP})$  on the y-axis of panel B; this same plot can be seen on the arithmetic scale in supporting material Fig. S2-1.



**Figure 4.** Posterior distributions of random year effects (intercept offsets). Kernel bandwidths of posterior densities were adjusted by a factor of 5 for visual clarity.



**Figure 5.** Nonmetric multidimensional scaling scores representing plant communities in each plot, colored by treatment.

## 331 References

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