

Consistent ecosystem functional response across precipitation extremes in a sagebrush steppe

Andrew T. Tredennick¹, Andrew R. Kleinbasselink², Bret Taylor³, and Peter B. Adler¹

¹Department of Wildland Resources and the Ecology Center, Utah State University, Logan, Utah 84322

²Department of Ecology and Evolutionary Biology, University of California, Los Angeles, Los Angeles, California 90095

³United States Department of Agriculture, Agriculture Research Station, U.S. Sheep Experiment Station, Dubois, Idaho 83423

Corresponding author:

Andrew T. Tredennick¹

Email address: atredenn@gmail.com

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

Ecosystems worldwide are projected to experience either wetter or drier conditions in the future (Zhang et al., 2007; Greve et al., 2014). This has important implications for ecosystem functioning because mean annual net primary productivity (ANPP) positively covaries with mean annual precipitation across ecosystems (Sala et al., 1988; Huxman et al., 2004) and interannual responses of ANPP are linked to interannual variability in precipitation within ecosystems (Lauenroth and Sala, 1992; Hsu et al., 2012; Gherardi and Sala, 2015b). To predict how ecosystems might respond to extreme precipitation levels, we need to understand whether ecosystems tend to follow temporal trends, which assume relatively constant plant community composition, or spatial trends, which allow community composition to shift (Wilcox et al., 2016).

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 underestimate the potential for the soil moisture-ANPP relationship to saturate if soil moisture is pushed far beyond typical levels. 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. Knowing the curvature of the soil moisture-ANPP relationship at extreme precipitation levels is critical for understanding how ecosystems will respond to chronic alterations in water availability.

Another problem with relying on historical ecosystem functional responses is that they are not static. Changes in species identities and abundances can alter an ecosystem's functional response to water availability because different species have different physiological thresholds for producing biomass. Smith et al. (2009) introduced the 'Hierarchical Response Framework' (HRF) for understanding the interplay of community composition and ecosystem functioning in response to resource manipulations over time. In the near term, ecosystem functioning such as annual net primary productivity (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). Over longer time spans, ecosystem functioning may recover as new species colonize or initial species reorder in relative abundance. For example, ANPP may initially decline, but eventually rise back to pre-treatment levels once drought-tolerant species become more abundant and compensate for drought-intolerant species (Hoover et al., 2014). 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).

Manipulating potentially limiting resources, like precipitation, offers 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. Following the HRF, we propose four alternative predictions for the effect of precipitation manipulation on the ecosystem functional response to soil moisture, that is, the soil moisture-ANPP relationship (Fig. 1). 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 changes neither ecosystem functional response nor community composition (Fig. 1, top left). In this case, changes in ANPP simply follow the soil moisture-ANPP relationship under ambient conditions. This corresponds to the early phases of the HRF, where ecosystem response is due to the physiological responses of individual species. Second, the ecosystem functional response changes but 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 is consistent but underlying 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 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). Thus, our task is not to test the validity of the HRF, but rather to amass information on how quickly ecosystem functional responses change in different ecosystems. Likewise, we 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 available soil moisture and ANPP, and if community dynamics underly 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 random intercepts, random slopes model to test whether the regressions differed among treatments. We also analyzed community composition over time, allowing us

101 to place our experimental results within the framework of the HRF and our competing predictions (Fig.
102 1).

103 2 METHODS

104 2.1 Study Area

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

111 2.2 Precipitation Experiment

112 Between 1926 and 1932, range scientists at the USSES established 26 permanent 1 m² quadrats to track
113 vegetation change over time. In 2007, we (well, one of us [P. Adler]) relocated 14 of the original quadrats,
114 six of which were inside a large, permanent livestock enclosure. We use these six plots as control plots
115 that have received no treatment, just ambient precipitation. In spring 2011, we (well, two of us [A.
116 Kleinhesselink and P. Adler]) established 16 new 1 m² plots located in the same enclosure as the six
117 control plots. We avoided areas on steep hill slopes, areas with greater than 20% cover of bare rock, and
118 areas with greater than 10% cover of the shrubs *Purshia tridentata* and/or *Amelanchier utahensis*. We
119 established the new plots in pairs and randomly assigned each plot in a pair to receive a “drought” or
120 “irrigation” treatment.

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

130 We monitored soil moisture in four of the drought-irrigation pairs using Decagon Devices (Pulman,
131 Washington) 5TM and EC-5 soil moisture sensors. We installed four sensors around the edges of each plot,
132 two at 5 cm soil depth and two at 25 cm soil depth. We also installed four sensors in areas nearby the four
133 selected plot pairs to measure ambient soil moisture at the same depths. Soil moisture measurements were
134 automatically logged every four hours. We coupled this temporally intensive soil moisture sampling with
135 spatially extensive readings taken at six points within all 16 plots and associated ambient measurement
136 areas. These snapshot data were collected on 06/06/2012, 04/29/2015, 05/07/2015, 06/09/2015, and
137 05/10/2016 using a handheld EC-5 sensor.

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

144 We first averaged the observed soil moisture for each day and within each plot. Then we standardized
145 the averages within each plot group by subtracting the average ambient soil moisture in that plot group
146 and dividing by the standard deviation of the ambient soil moisture in that plot group. We then found the
147 difference between the standardized ambient soil moisture and the standardized drought and irrigation
148 soil moisture within each plot group. These transformations ensured that the treatment effects in each plot
149 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, 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 (Fig. 2B).

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, dried it to a constant weight at 60°C, and weighed it to estimate ANPP.

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 bands for NDVI. To convert the greenness index to ANPP we regressed the greenness index against the dry biomass weight from the ten calibration plots. We fit regressions to MODIS-based index and AVHRR-based index for each year and retained the regression with the better fit. Using the best regression equation for each year, we predicted ANPP (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 those maps, we have data on the density of all annuals and perennials forbs, basal cover of perennial grasses, and 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. So we could analyze the different types of data together, we standardized the values in each column. This puts all abundance values on the same scale, meaning that common and rare species are weighted equally. Nonetheless, if we assume that rare species will respond more than common ones, then this approach is anti-conservative for detecting community change. This means that our approach is biased toward detecting compositional changes.

Did I say this
right?

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; Dalglish 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 simply as 'soil moisture'). To achieve this goal, we fit a multi-level random intercept and random slope regression with log(ANPP) as the response variable and soil moisture as the sole predictor. We log-transformed ANPP to account for heteroscedasticity. We fit the model under a Bayesian framework, allowing us to test for treatment differences by comparing the posterior distributions of the treatment-level coefficients (e.g., Tredennick et al., 2013). Both log(ANPP) and soil moisture 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:

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

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

where $\mu_{j(k(t))}$ is the deterministic prediction from the regression model for plot j associated with treatment 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

effect of soil moisture for plot j associated with treatment k , γ_t is the intercept offset for year t , and σ_k^2 is the process variance for treatment k . Data include the standardized log(ANPP) observations ($y_{j(k(t))}$) and 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, β :

$$\beta_{j(k)} \sim \text{MVN}(\beta_k, \Sigma(k)), \quad (3)$$

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

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

where $\beta_{j(k)}$ is the vector of regression coefficients (intercept and slope) for plot j associated with treatment k , β_k is the vector of coefficients for each treatment, and β is the vector of overall coefficients. The plot- and treatment-level coefficients are drawn from multivariate normal distributions with covariance matrix Σ . For the plot-level coefficients, each treatment has its own variance-covariance matrix (i.e., $\Sigma(k)$). The overall coefficients are drawn from a normal prior with mean 0 and standard deviation 1. The random year effects (γ) are drawn from a normal prior with mean 0 and standard deviation σ_{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 10th 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). 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⁻² in 2014 to a maximum of 237.1 g m⁻² 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 $\beta_1 = 0.41$; Fig. 3), but the effect is associated with high uncertainty, with credible intervals that overlap zero (80% BCI =

246 -0.08, 0.86; 95% BCI = -0.45, 1.13). Ecosystem functional response was similar among treatments, with
247 treatment level regressions between soil moisture and log(ANPP) having similar intercepts and slopes
248 (Fig. 3A). There was also no evidence that the treatment effects became more important over time because
249 there was no directional trend in the random year effects (Fig. 4).

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

254 4 DISCUSSION

255 Ecosystem response to precipitation extremes depends on the physiological responses of constituent
256 species and the rate at which community composition shifts to favor species better able to take advantage
257 of, or cope with, new resource levels (Smith et al., 2009). Previous work has shown that community
258 compositional shifts can be both rapid, on the order of years (Hoover et al., 2014), and slow, on order
259 of decades (Knapp et al., 2012; Wilcox et al., 2016). Thus, a lingering question is how the time scales
260 of ecosystem response and community change differ among ecosystems, which can be answered by
261 manipulating precipitation to reach extreme levels. The results of our five year experiment in a sagebrush
262 steppe conform to the first of our four predictions: neither ecosystem functional response nor community
263 composition changed with chronic alteration in water availability (Fig. 1, top left).

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

271 First, it could be that our manipulations were not large enough to induce a response. That is, maybe a
272 50% decrease/increase in any given year is not abnormal given our site's historical range of variability
273 (Knapp et al., 2017). We cannot definitively rule out this possibility, but we have reason to believe our
274 manipulations *should* have been large enough. Using the methods described by Lemoine et al. (2016), we
275 calculated the percent reduction and increase of mean growing season precipitation necessary to reach the
276 1% and 99% extremes of the historical precipitation regime at our site. The 1% quantile of precipitation
277 at our site is 110 mm, a 47% reduction from the mean, and the 99% quantile is 414 mm, a 77% increase
278 from mean growing season precipitation (Appendix 3). Thus, our drought treatment represented extreme
279 precipitation amounts, especially in years where ambient precipitation was below average (Fig. 2A). The
280 irrigation treatment may have been too small, however.

281 Second, ANPP at our site may be influenced by factors beyond the window of soil moisture we
282 included in our statistical model. For example, temperature can impact ANPP directly (Epstein et al.,
283 1997) and by exacerbating the effects of soil moisture (De Boeck et al., 2011). Measurements of soil
284 moisture likely contain a signal of temperature, through its impact on evaporation and infiltration, but the
285 measurements will not capture the direct effect of temperature on metabolic and physiological processes.
286 Likewise, we did not redistribute snow across our treatments in the winter, and snowmelt may spur early
287 spring growth. These statistical issues of missing potentially important covariates could explain the weak
288 and uncertain relationship we observed between soil moisture and ANPP.

289 Third, the life history traits of the dominant species in our study ecosystem may explain the consistent
290 but weak and uncertain effect of soil moisture on ANPP (Fig. 3). Species that live in variable environments,
291 such as cold deserts, must have strategies to ensure long-term success as conditions vary. One strategy is
292 bet hedging, where species forego short-term gains to reduce the variance of long-term success (Seger,
293 1987). In other words, species do the same thing every year, with only minimal response to environmental
294 conditions. The dry and variable environment of the sagebrush steppe has likely selected for bet hedging
295 species that can maintain function at low water availability and have weak responses to high water
296 availability. In so doing, the dominant species in our ecosystem avoid “boom and bust” cycles, which
297 corresponds to the weak effect of soil moisture on ANPP (i.e., the credible intervals for β_1 overlapping
298 zero), even at precipitation extremes.

299 Another strategy to deal with variable environmental conditions is avoidance, which would result
300 in a consistent ecosystem functional response at low soil moisture. The perennial plants in this cold
301 desert ecosystem are tolerant to drought conditions (Bazzaz, 1979; Franks, 2011, A.R. Kleinhesselink,
302 unpublished data). For example, many of the perennial grasses in our focal ecosystem avoid drought stress
303 by growing early in the growing season (Blaisdell, 1958, A.R. Kleinhesselink, personal observation).
304 Likewise, the dominant shrub in our focal ecosystem, *Artemisia tripartita*, has access to water deep in the
305 soil profile thanks to a deep root system (Kulmatiski et al., 2017).

306 In conclusion, our results suggest that five years of $\pm 50\%$ ambient precipitation is not enough
307 to induce a shift in ecosystem functional response in a sagebrush steppe. This is likely because the
308 species in our focal plant community are tolerant of drought conditions and bet hedgers in wet conditions,
309 maintaining relatively consistent responses to interannual variation in precipitation to avoid booms and
310 busts. Longer time series of chronic precipitation alteration may reveal plant community shifts that we did
311 not observe (e.g., Wilcox et al., 2016), in which case species that do not bet hedge may gain prominence
312 and dominate the ecosystem functional response. Our results suggest compositional shifts would have the
313 largest impact at high rainfall because the current community maintained consistent ecosystem functional
314 response at very low water availability.

315 **5 ACKNOWLEDGEMENTS**

316 We gratefully acknowledge the support of the Utah Agricultural Experiment Station (journal paper xxxx).
317 We thank the many summer research technicians who collected the data reported in this paper and the
318 US Experimental Sheep Station for facilitating work on their property. We also thank Susan Durham for
319 clarifying our thinking on the statistical analyses and Kevin Wilcox for helpful discussions on analyzing
320 community composition data.

321 **6 FUNDING**

322 NSF DBI-1400370 to Andrew T. Tredennick.
323 NSF Graduate Research Fellowship to Andrew R. Kleinhesselink.
324 NSF DEB-1353078 and DEB-1054040 to Peter B. Adler.

325 **7 AUTHOR CONTRIBUTIONS**

- 326 • Andrew T. Tredennick collected data, analyzed the data, wrote the paper, prepared figures and/or
327 tables, reviewed drafts of the paper.
- 328 • Andrew R. Kleinhesselink conceived and designed the experiments, performed the experiments,
329 collected data, reviewed drafts of the paper.
- 330 • Bret Taylor...
- 331 • Peter B. Adler conceived and designed the experiments, performed the experiments, collected data,
332 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

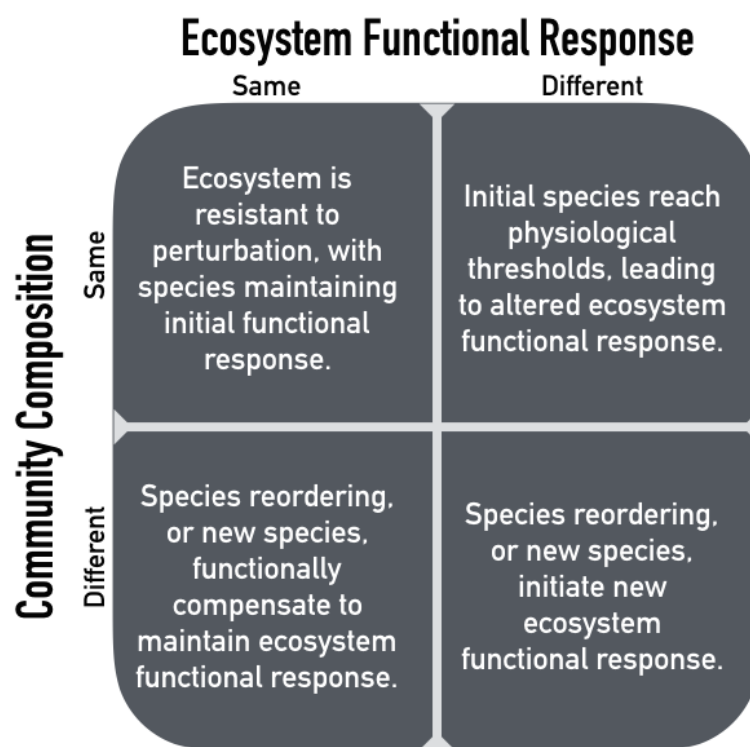


Figure 1. Possible outcomes of chronic resource alteration.

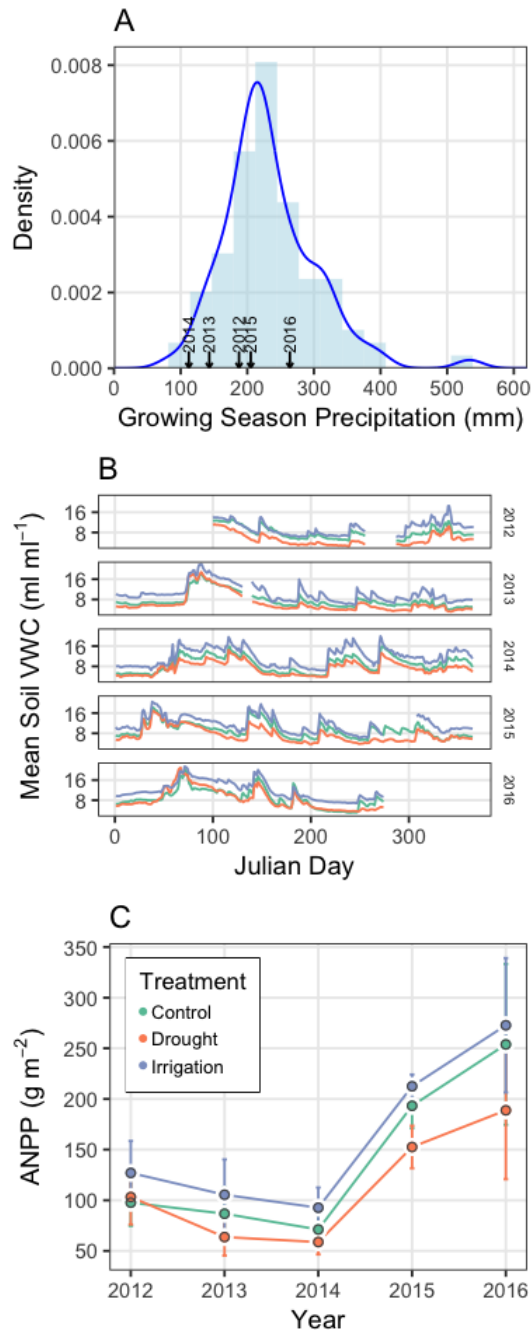


Figure 2. (A) Probability density of historical precipitation from 1926-2016, with the years of the experiment shown with arrows on the x -axis. (B) Observed soil volumetric water content (VWC) over the course of the experiment. (C) Mean (points) ANPP and its standard deviation (error bars) for each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

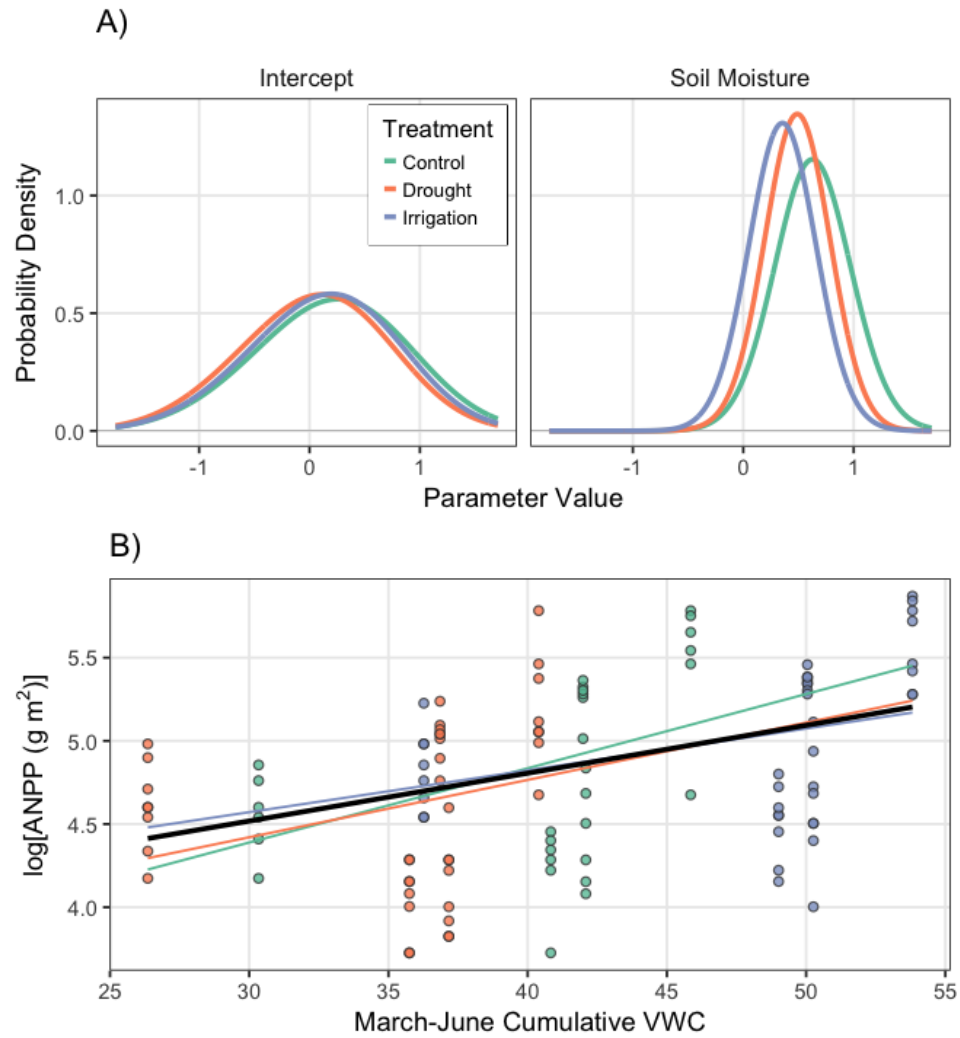


Figure 3. Results from the generalized linear mixed effects model. (A) Posterior distributions of treatment-level parameters ('Intercept' and the effect of 'Soil Moisture'). Kernel bandwidths of posterior densities were adjusted by a factor of 5 for visual clarity. (B) Scatterplot of the data and model 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.

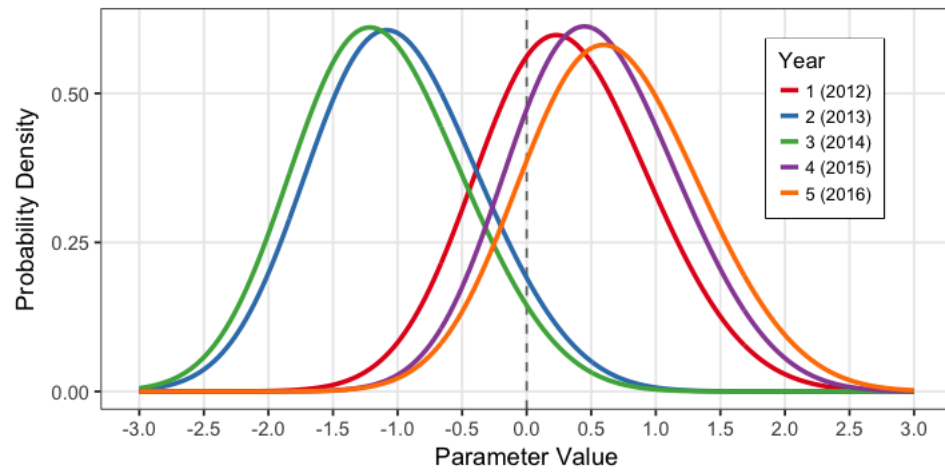


Figure 4. Posterior distributions of random year effects (intercept offsets). Kernel bandwidths of posterior densities were adjusted by a factor of 5 for visual clarity.

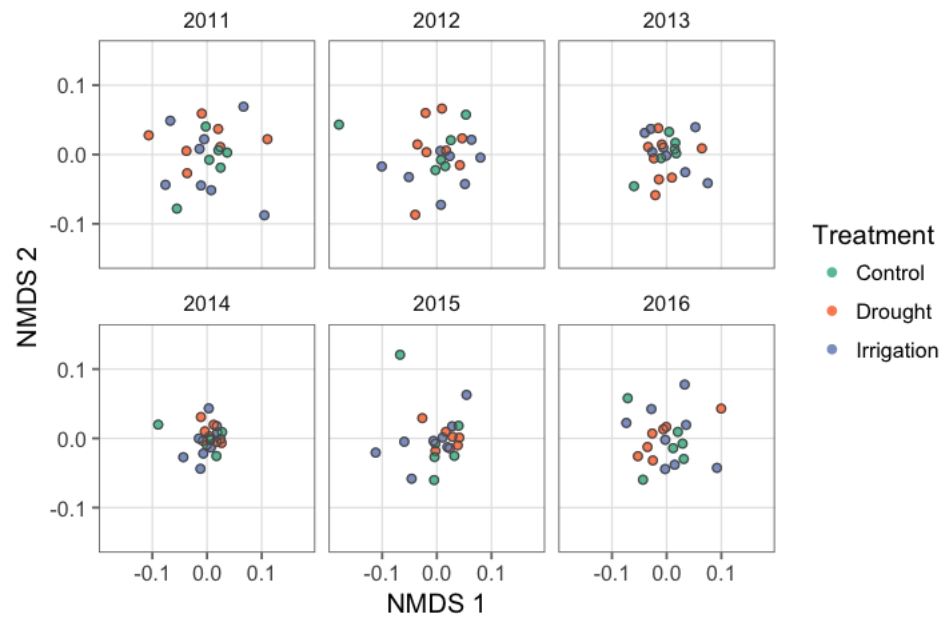


Figure 5. Nonmetric multidimensional scaling scores representing plant communities in each plot, colored by treatment.

References

- Adler, P. B., Dalgleish, H. J., and Ellner, S. P. (2012). Forecasting plant community impacts of climate variability and change: when do competitive interactions matter? *Journal of Ecology*, 100:478–487.
- Avolio, M. L., Pierre, K. J. L., Houseman, G. R., Koerner, S. E., Grman, E., Isbell, F., Johnson, D. S., and Wilcox, K. R. (2015). A framework for quantifying the magnitude and variability of community responses to global change drivers. *Ecosphere*, 6(12):1–14.
- Bates, D., Maechler, M., Bolker, B., and Walker, S. (2015). Fitting linear mixed-effects models using lme4.
- Bazzaz, F. (1979). The Physiological Ecology of Plant Succession. *Annual Review of Ecology and Systematics*, 10:351–371.
- Blaisdell, J. P. (1958). Seasonal development and yield of native plants on the upper snake river plains and their relation to certain climate factors. *United States Department of Agriculture Technical Bulletin No. 1190*.
- Byrne, K. M., Lauenroth, W. K., Adler, P. B., and Byrne, C. M. (2011). Estimating Aboveground Net Primary Production in Grasslands: A Comparison of Nondestructive Methods. *Rangeland Ecology and Management*, 64(5):498–505.
- Dalgleish, H. J., Koons, D. N., Hooten, M. B., Moffet, C. A., and Adler, P. B. (2011). Climate influences the demography of three dominant sagebrush steppe plants. *Ecology*, 92(1):75–85.
- De Boeck, H. J., Dreesen, F. E., Janssens, I. A., and Nijs, I. (2011). Whole-system responses of experimental plant communities to climate extremes imposed in different seasons. *New Phytologist*, 189(3):806–817.
- Epstein, H. E., Lauenroth, W. K., and Burke, I. C. (1997). Effects of temperature and soil texture on ANPP in the U.S. Great plains. *Ecology*, 78(8):2628–2631.
- Franks, S. J. (2011). Plasticity and evolution in drought avoidance and escape in the annual plant *Brassica rapa*. *New Phytologist*, 190(1):249–257.
- Gherardi, L. A. and Sala, O. E. (2013). Automated rainfall manipulation system: a reliable and inexpensive tool for ecologists. *Ecosphere*, 4(2):1–10.
- Gherardi, L. A. and Sala, O. E. (2015a). Enhanced interannual precipitation variability increases plant functional diversity that in turn ameliorates negative impact on productivity. *Ecology Letters*, 18(12):1293–1300.
- Gherardi, L. A. and Sala, O. E. (2015b). Enhanced precipitation variability decreases grass- and increases shrub-productivity. *Proceedings of the National Academy of Sciences*, 112(41):12735–12740.
- Greve, P., Orlowsky, B., Mueller, B., Sheffield, J., Reichstein, M., and Seneviratne, S. I. (2014). Global assessment of trends in wetting and drying over land. *Nature Geoscience*, 7(10):716–721.
- Hill, R. R. (1920). Charting Quadrats with a Pantograph. *Ecology*, 1(4):270–273.
- Hoover, D. L., Knapp, A. K., and Smith, M. D. (2014). Resistance and resilience of a grassland ecosystem to climate extremes. *Ecology*, 95(9):2646–2656.
- Hsu, J. S., Powell, J., and Adler, P. B. (2012). Sensitivity of mean annual primary production to precipitation. *Global Change Biology*, 18(7):2246–2255.
- Huxman, T. E., Smith, M. D., Fay, P. A., Knapp, A. K., Shaw, M. R., Loik, M. E., Smith, S. D., Tissue, D. T., Zak, J. C., Weltzin, J. F., Pockman, W. T., Sala, O. E., Haddad, B. M., Harte, J., Koch, G. W., Schwinning, S., Small, E. E., and Williams, D. G. (2004). Convergence across biomes to a common rain-use efficiency. *Nature*, 429(6992):651–654.
- Knapp, A. K., Avolio, M. L., Beier, C., Carroll, C. J. W., Collins, S. L., Dukes, J. S., Fraser, L. H., Griffin-Nolan, R. J., Hoover, D. L., Jentsch, A., Loik, M. E., Phillips, R. P., Post, A. K., Sala, O. E., Slette, I. J., Yahdjian, L., and Smith, M. D. (2017). Pushing precipitation to the extremes in distributed experiments: recommendations for simulating wet and dry years. *Global Change Biology*, 23(5):1774–1782.
- Knapp, A. K., Briggs, J. M., and Smith, M. D. (2012). Community stability does not preclude ecosystem sensitivity to chronic resource alteration. *Functional Ecology*, 26(6):1231–1233.
- Kulmatiski, A., Adler, P. B., Stark, J. M., and Tredennick, A. T. (2017). Water and nitrogen uptake are better associated with resource availability than root biomass. *Ecosphere*, 8(3).
- Lauenroth, W. and Sala, O. (1992). Long-term forage production of North-American shortgrass steppe. *Ecological Applications*, 2(4):397–403.
- Lemoine, N. P., Sheffield, J., Dukes, J. S., Knapp, A. K., and Smith, M. D. (2016). Terrestrial Precipitation

389 Analysis (TPA): A resource for characterizing long-term precipitation regimes and extremes. *Methods*
390 *in Ecology and Evolution*, 7(11):1396–1401.

391 Oksanen, J. (2016). *Vegan: ecological diversity*.

392 R Core Team (2016). *R: A Language and Environment for Statistical Computing*. Vienna, Austria.

393 Sala, O. E., Parton, W. J., Joyce, L. A., and Lauenroth, W. K. (1988). Primary production of the central
394 grassland region of the United States.

395 Seger, J. (1987). What is bet-hedging? In Harvey, P. and Partridge, L., editors, *Oxford surveys in*
396 *evolutionary biology*, pages 182–211. Oxford University Press, Oxford.

397 Smith, M. (2011). An ecological perspective on extreme climatic events: A synthetic definition and
398 framework to guide future research. *Journal of Ecology*, 99(3):656–663.

399 Smith, M. D., Knapp, A. K., and Collins, S. L. (2009). A framework for assessing ecosystem dynamics in
400 response to chronic resource alterations induced by global change. *Ecology*, 90(12):3279–3289.

401 Stan Development Team (2016a). Rstan: the R interface to Stan, Version 2.14.1.

402 Stan Development Team (2016b). Stan: A C++ Library for Probability and Sampling, Version 2.14.1.

403 Tredennick, A. T., Bentley, L. P., and Hanan, N. P. (2013). Allometric convergence in savanna trees and
404 implications for the use of plant scaling models in variable ecosystems. *PLoS One*, 8(3):e58241.

405 Wilcox, K. R., Blair, J. M., Smith, M. D., and Knapp, A. K. (2016). Does ecosystem sensitivity to
406 precipitation at the site-level conform to regional-scale predictions? *Ecology*, 97(3):561–568.

407 Zhang, X., Zwiers, F. W., Hegerl, G. C., Lambert, F. H., Gillett, N. P., Solomon, S., Stott, P. A., and
408 Nozawa, T. (2007). Detection of human influence on twentieth-century precipitation trends. *Nature*,
409 448(7152):461–5.