Ecosystem and community resistance to five years of drought and deluge in a sagebrush steppe

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Abstract

Precipitation is predicted to become more variable in the western U.S., meaning years of above and below average precipitation will become more common. Such periods of drought and deluge could become major drivers of plant community dynamics and ecosystem functioning in water limited grasslands. Here we report the results of a five-year experiment where we used drought and irrigation treatments (50% decrease/increase) to see how a sagebrush steppe plant community in Idaho will respond to future climate changes. The ecosystem was suprisingly resistant to both drought and irrigation. Aboveground net primary productivity (ANPP) responded positively to ambient growing season precipitation, but the response did not vary across treatments. There was also no evidence that treatment effects grew over time. The similarity of ecosystem functioning 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 functioning and community composition in this sagebrush steppe system is resistant to increases and decreases in growing season precipitation.

Key words: aboveground net primary productivity, climate change, community dynamics, drought, ecosystem resistance, sagebrush steppe

Introduction

As the rate of climate change accelerates, ecologists are being pressed to forecast its impacts on ecosystem functions and services. Making such forecasts faces two challenges. First, future conditions are likely to be outside the historical range of variability (Smith 2011), meaning we cannot simply look to the past to predict the future. Second, ecosystems will likely exhibit unique responses to climate change induced resource alterations (e.g., Byrne et al. 2017), meaning we

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cannot simply look across space to predict the future. These two challenges motivate the use of *in situ* experimental manipulations of resource availability (Avolio et al. 2015).

Manipulating potentially limiting resources offers a route to understanding how ecosystems will respond to resource levels that fall outside the historical range of variability (Knapp et al. 2017). Chronic alterations to resource availability should cause community composition to shift over time, the focal ecosystem is sensitive to the manipulated resource. Species' relative abundances are expected to re-order and, eventually, some species will be lost from the local community and new species will be gained (Smith et al. 2009, Avolio et al. 2015). On the heels of changes in community composition, subsequent changes in the level of ecosystem functioning may occur.

Smith et al. (2009) introduced the 'Hierarchical Response Framework' 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, reflective of the suite of species in the new community (Knapp et al. 2012).

Much of the research on ecosystem and community responses to global climate change has focused on grassland systems, where soil water is typically a limiting resource. The sensitivity of ANPP to water availability in grasslands has been characterized spatially (across sites) and temporally (within sites). Across sites, there is a strong positive relationship between the amount of precipitation at a given site and mean ANPP (Sala et al. 1988, Huxman et al. 2004). Within sites, however, the response of ANPP to annual precipitation amount is much weaker (Huxman et al. 2004, Hsu et al. 2012). Furthermore, it is becoming clear that grassland ecosystem response to altered water availability is likely to be idiosyncratic, conforming to neither cross-site nor within-site ANPP-precipitation relationships (Wilcox et al. 2016). This is because within-site relationships do not account for species reordering under chronic resource alterations, while cross-site relationships may overestimate the ability of species compensation. Thus, discovering which ecosystems are most sensitive to chronic alterations of water availability, and the time scales at which ecosystem and community responses occur, is critical to avoid surprises in the face of climate change.

Here we report the results of a five-year precipitation manipulation experiment in a sagebrush steppe grassland. We imposed drought and irrigation treatments (50% decrease/increase) and measured ecosystem (ANPP) and community (species composition) responses. We focus on how the drought and irrigation treatments affect the linear relationship between ANPP and growing season precipitation, and if community dynamics underly the ecosystem responses. In particular, we sought to answer the following questions:

1. Does drought or irrigation impact mean ANPP (i.e., different intercepts)?
2. Does drought or irrigation impact the effect of ambient precipitation on ANPP (i.e., different slopes)?
3. Is the resistance or sensitivity of ANPP to altered precipitation related to underlying community dynamics?

Materials and Methods

Study Area

We conducted our precipitation manipulation experiment at the United States Sheep Experimental Station (USSES) near Dubois, Idaho (44.2° N, 112.1° W), 1500 m above sea level. The vegetation is typical of high elevation sagebrush steppe. 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.

Precipitation Experiment

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 (well, one of us [P. Adler]) relocated 14 of the original quadrats, six of which were inside a large, permanent livestock exclosure. We use these six plots as control plots that have recieved no treatment, just ambient precipitation. In spring 2011, we (well, two of us [A. Kleinhesselink and P. Adler]) established 16 new 1 m^2 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%, respectively. 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 fall and reconnected them, often with difficulty, each spring. The rain-out shelters remained in place throughout the year.

To make sure the treatments were having the desired effects, we monitored soil moisture in four of the drought-irrigation pairs using Decagon Devices (Pulman, Washington) 5TM and EC-5 soil moisture sensors. We installed four sensors in each 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 using a handheld EC-5 sensor.

[ANDY: paragraph here on SOILWAT. Is this the right thing to show/do? See Fig. 1C.]

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 (xxx and xxx) and two associated with near-infrared reflectance (xxx and xxx). At each plot in each year, we took four readings of ground reflectances at the above wavelengths. We also took readings in ten 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 NDVI using the MODIS and AVHRR algorithms. To convert NDVI to ANPP we regressed NDVI against the dry biomass weight from the ten calibration plots. We fit regressions to MODIS-based NDVI and AVHRR-based NDVI 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 annual census maps for each plot made using a pantograph (Hill 1920). The maps record the spatial location and size of each individual plant. Using those annual maps, we aggregated over individuals to calculate total basal cover for each species in each plot.

Data Analysis

Our main goal was to test whether the relationship between ANPP and growing season precipitation (hereafter, precipiation) differed among the drought, control, and irrigation treatments. To achieve this goal, we fit a multi-level random intercept and random slope regression with log(ANPP) as the response variabile and precipitation as the sole predictor (hereafter, 'ANPP-Precipitation' model). 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 precipitation were standardized to have mean 0 and unit variance before fitting the model [i.e., $(x_i - \bar{x})/\sigma_x$].

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. Formally, our model is defined as follows:

$$\mu_{i(j(k))} = \beta_{0,j(k)} + \beta_{1,j(k)} x_i, \tag{1}$$

$$y_{i(j(k))} \sim \text{Normal}\left(\mu_{i(j(k))}, \sigma_k^2\right), \tag{2}$$

where $\mu_{i(j(k))}$ is the deterministic prediction from the regression model for observation i for plot j associated with treatment k, $\beta_{0,j(k)}$ is the intercept for plot j associated with treatment k, $\beta_{1,j(k)}$ is the slope term for the effect of precipitation for plot j associated with treatment k, and σ_k^2 is the process variance for treatment k. Data include the standardized log(ANPP) observations ($y_{i(j(k))}$) and precipitation (x_i). Although we include observation subscript i on the xs, observations within a year all share the same precipitation values.

The intercept and slope terms are modeled hierarchichally 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-precipitation relationship. As noted above, plot-level coefficients are drawn from treatment-level coeffecients, which are drawn from overall coefficients. We also include a covariance structure among the intercept and slope at each level. Formally, our hierarhical structure is as follows, where we drop the intercept (0) and slope (1) subscripts and instead refer to a vector of coefficients, $\boldsymbol{\beta}$:

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

$$\boldsymbol{\beta}_k \sim \text{MVN}\left(\boldsymbol{\beta}, \boldsymbol{\Sigma}\right), \tag{4}$$

$$\boldsymbol{\beta} \sim \text{Normal}\left(0, 1\right), \tag{5}$$

where $\boldsymbol{\beta}_{j(k)}$ 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 $\mathbf{\Sigma}$. For the plot-level coefficients, each treatment has its own variance-covariance matrix (i.e., $\mathbf{\Sigma}(k)$). The overall coefficients are drawn from a normal prior with mean 0 and standard deviation 1. A full description of model is in Appendix 2.

Unfortunately, we cannot detect whether treatments grow stronger over time in the ANPP-Precipitation model described above because year and precipitation are perfectly colinear. Therefore, we fit simpler model with log(ANPP) as the response and treatment effects for drought and irrigation (hereafter, 'ANPP-Treatment' model). We again use a hierarchical structure, where the treatment effects were allowed to vary by year (i.e., year random effects). This allowed us to test whether treatment effects got stronger over time. We also included a plot random effect to account for non-independence of observations through time in a plot. This model is also fully described in Appendix 2.

We fit both models using a Bayesian approach, obtaining posterior estimates of all unkowns via the No-U-Turn Hamiltonian Monte Carlo sampler in Stan (Stan Development Team 2016a). We used the R package 'rstan' (Stan Development Team 2016b) 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$^{\text{th}}$ 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. We plotted the first two axes of NMDS scores to see if community composition overlapped, or not, among treatments in each year. We used functions in the R package 'vegan' (Oksanen 2016) to calculate Bray-Curtis distances and then to run the NMDS analysis. Lastly, we examined rank clocks of species' abundances through time to assess the stability of community composition over the course of the experiment (Collins et al. 2008). Rank clocks were made using 'ggplot2' (Wickham 2009) and R code from Hallett et al. (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.

Results

Three of our five treatment years fell in years of below average rainfall (Fig. 1A). 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. 1C). ANPP was slightly higher in irrigation plots and slightly lower in drought plots (Fig. 1C), corresponding to estimated soil volumetric water content (VWC) differences among treatments (Fig. 1B). Such differences in soil VWC indicate our treatment infrastructure was successful.

Growing season precipitation had a positive effect on ANPP (mean of β_1 = 0.67; 80% BCI = 0.24, 1.10; 95% BCI = -0.11, 1.34) (Fig. 1D). Average ANPP was similar among treatments (similar intercepts, Fig. 2A), as was the effect of precipitation (similar slopes, Fig. 2B). In an average precipitation year (i.e., $x = 0$ in Eq. 1), the probability that ANPP in a drought plot is less than ANPP in a control plot was 0.58, and the probability that ANPP in an irrigation plot is higher than in a control plot was 0.57. In other words, the posterior distributions of $\beta_0(\text{control}) - \beta_0(\text{drought})$ and $\beta_0(\text{control}) - \beta_0(\text{drought})$ broadly overlapped zero. There was also no evidence that the treatment effects became more important over time because there was no directional trend in the yearly treatment effects estimated from the ANPP-Treatment model (Fig. 3).

Community composition was similar among treatments, whether looking at basal cover or density (Fig. 4). Likewise, community composition was remarkably stable over time, with no evidence of divergence among treatments (Fig. 4). Species' abundances and ranks showed little deviation over the five-year experiment, regardless of treatment (Fig. 5).

Discussion

We manipulated growing season precipitation for five years in a sagebrush steppe to reach the extremes of the historical distribution of precipitation (Fig. 1A). In so doing, we aimed to understand how this ecosystem might respond to periods of relatively novel precipitation regimes. Our results suggest that ecosystem functioning, as measured by annual net primary productivity, and community composition are not sensitive to the precipitation manipulations we imposed.

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Figures

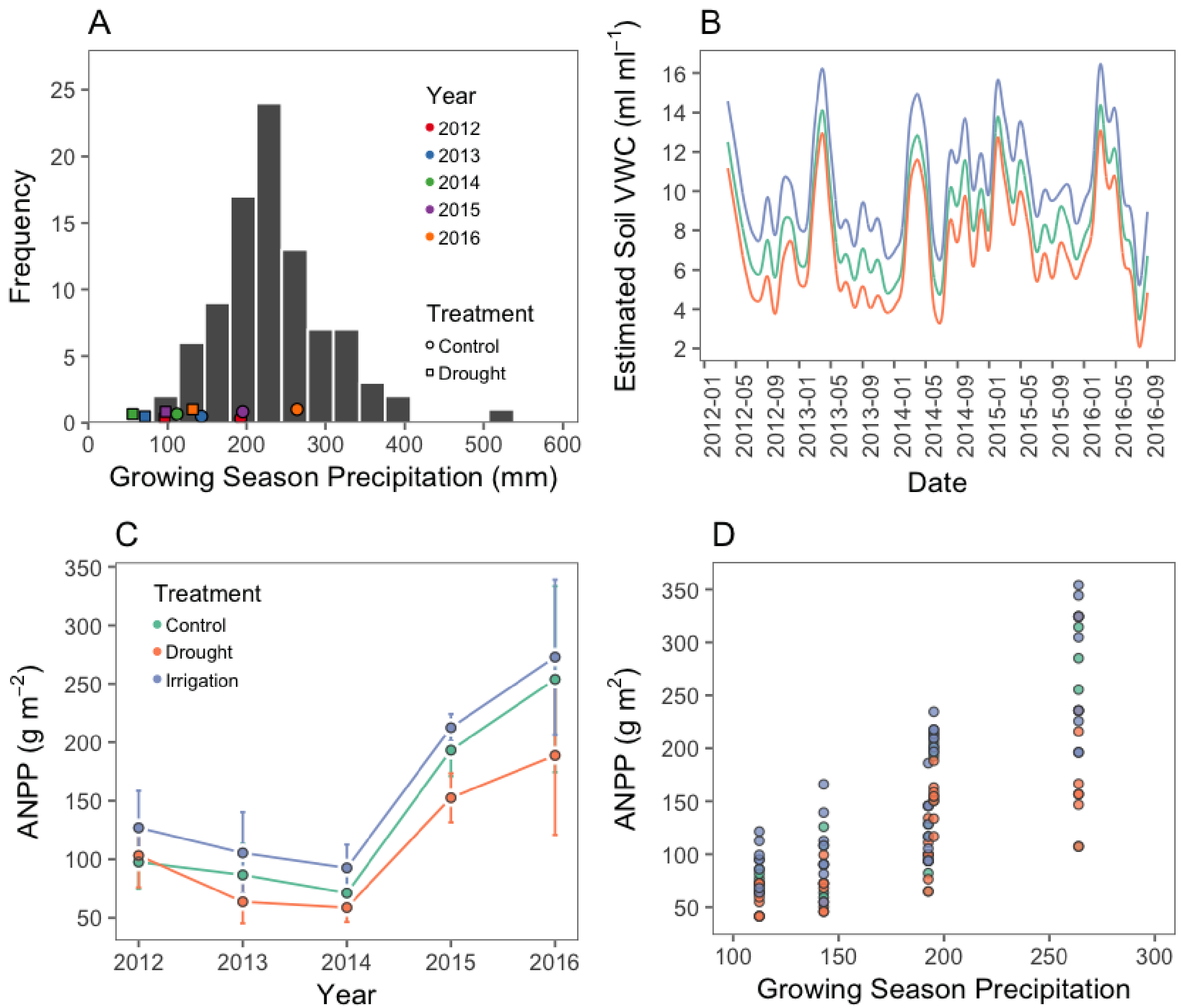

Figure 1: (A) Histogram of historical precipitation from 1926-2016, with the years of the experiment overlaid as colored points. “Drought” treatments (squares) are shown as a 50% reduction from the observed precipitation. “Irrigation” treatment precipitation levels are not shown. (B) Monthly average estimated soil volumetric water content (VWC) from SOILWAT model fit using soil moisture data from experimental plots. (C) Mean (points) ANPP and its standard deviation (error bars) for each year of the experiment. (D) Scatterplot of ANPP versus growing season precipitation.

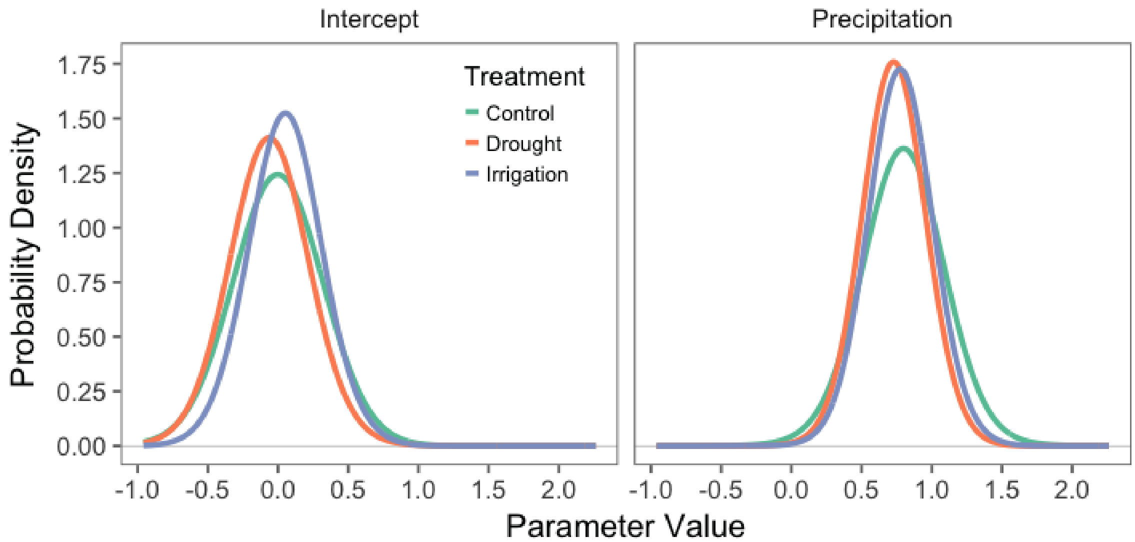

Figure 2: Posterior distributions of treatment-level parameters ('Intercept' and the effect of 'Precipitation') from the ANPP-Precipitation model.

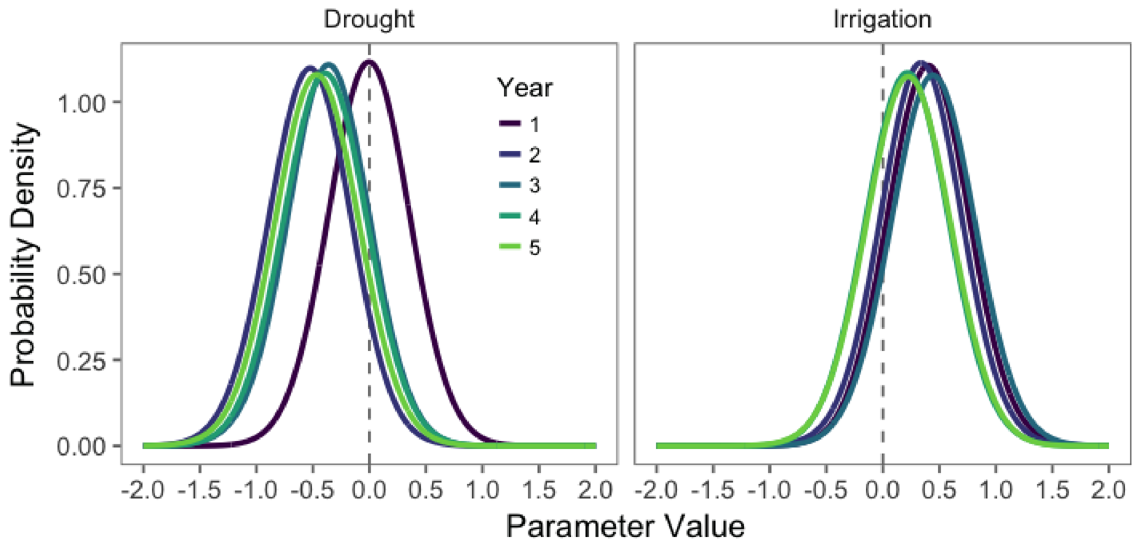

Figure 3: Posterior distributions of yearly treatment effects from the ANPP-Treatment model.

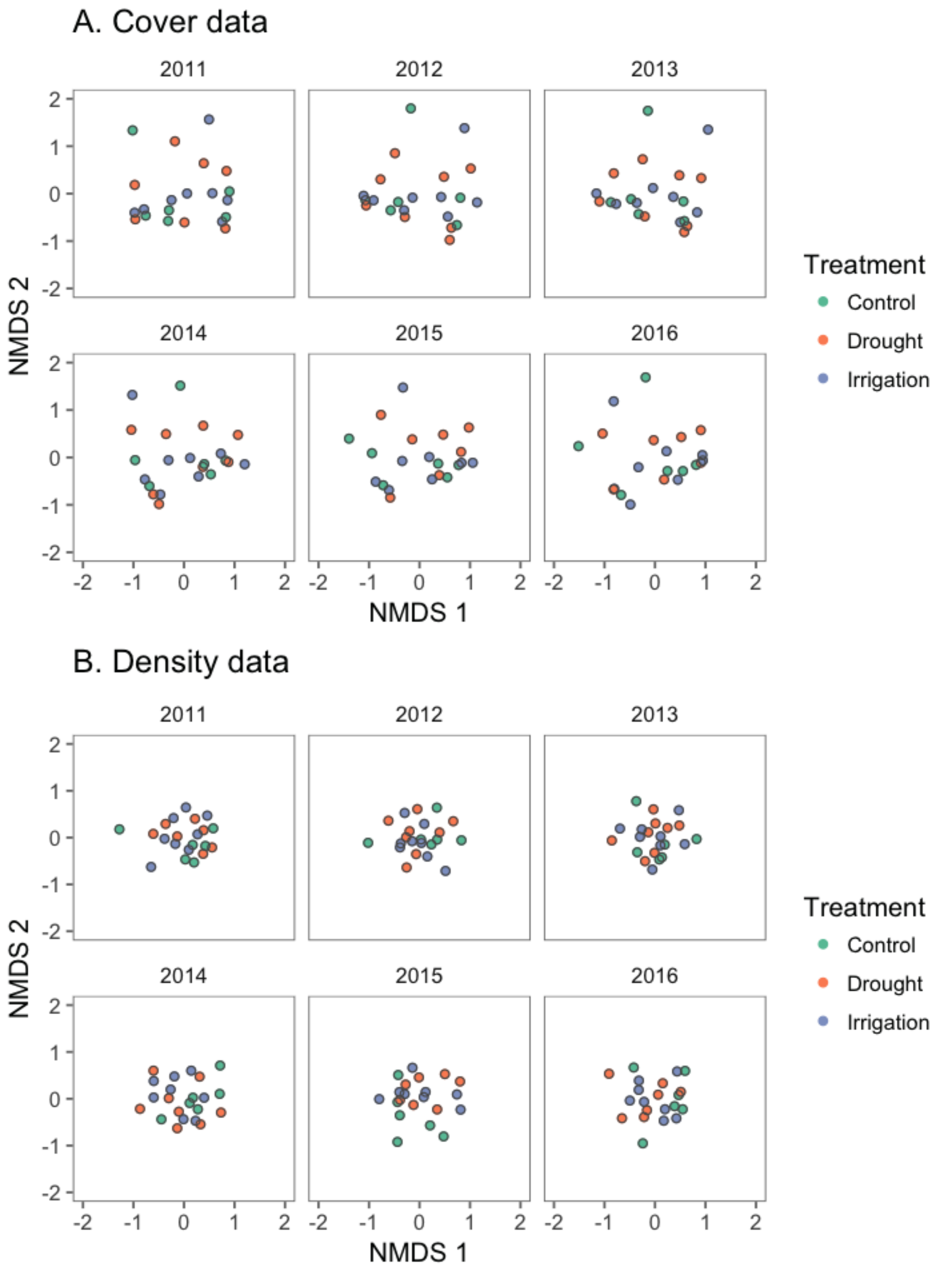

Figure 4: Nonmetric multidimensional scaling scores representing plant communities in each plot, colored by treatment. (A) NMDS results using basal cover data; (B) NMDS results using individual density data. 2011 is a pre-treatment year.

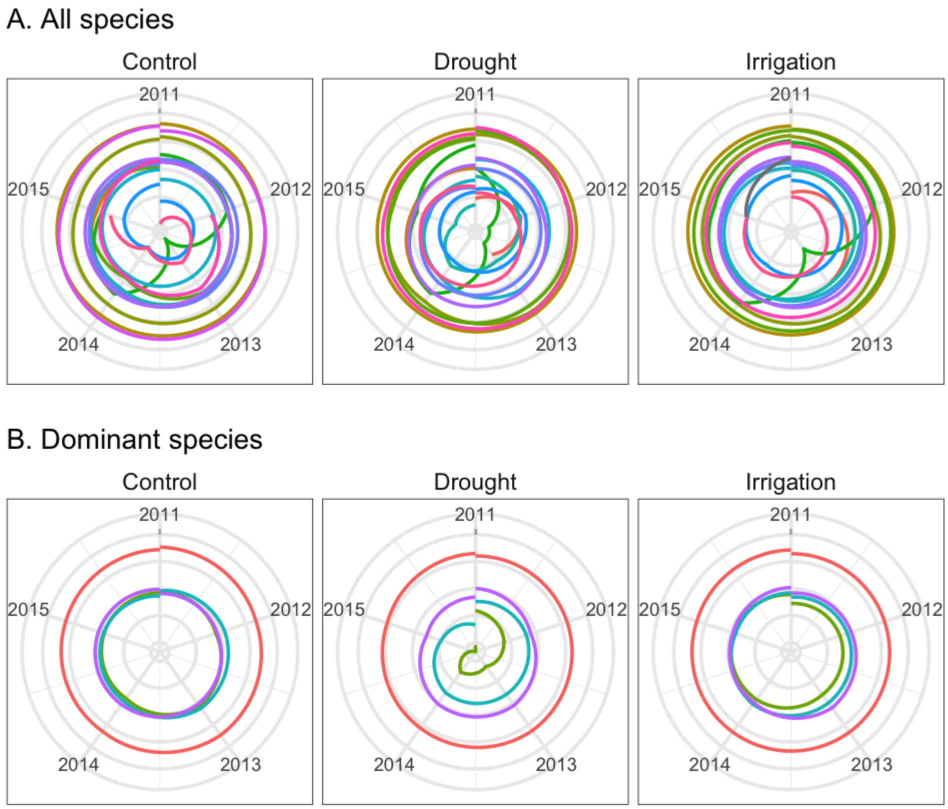

Figure 5: Rank clocks of average species' basal cover by treatment. (A) All species. (B) Dominant species. Cover is log-transformed to improve visualization of species with low cover.

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