

## Intra-annual precipitation effects on annual grassland productivity and phenology are moderated by community responses

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**Intra-annual precipitation effects on annual grassland productivity and phenology are moderated by community responses**

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## Abstract

1. Within ecosystems, intra-annual precipitation patterns – the variability and timing of rainfall and drought – may be stronger drivers of productivity than total annual precipitation. In particular, the amount and timing of precipitation directly affects the amount and timing of plant production, but also indirectly affects productivity via changes to plant community composition. Community response patterns may either buffer or amplify productivity responses to precipitation, as different species respond to different conditions.

2. In a semi-arid California grassland, we experimentally tested how plant communities respond to intra-annual precipitation variability using rainout shelters in which we manipulated precipitation amount and timing (early-season fall drought, peak-season spring drought, continuous drought and ambient precipitation) over three years and assessed plant responses: aboveground net primary production (ANPP), phenological timing of plant production and senescence, and plant community composition.

3. Overall, early-season and consistent drought treatments had lower productivity than late-season drought and ambient precipitation treatments, while late-season and consistent drought treatments senesced earlier than early-season drought and ambient precipitation treatments. Plots with functionally diverse communities exhibited shifting community composition and species tradeoffs in response to precipitation treatments, and had a significant ANPP response to precipitation treatments. In contrast, communities dominated by a single resource-acquisitive grass species demonstrated dominant stability with no change in community composition over time and had no ANPP response to precipitation treatments.

4. The timing of production also differed by community, however, where functionally diverse communities remained active longer (particularly under the early-season drought treatment)

36 compared communities dominated by one grass species, which senesced earlier (particularly  
37 under the late-season drought treatment).

38     5. *Synthesis*. Our study demonstrates that intra-annual precipitation patterns – the variability  
39 and timing of precipitation and drought – may indirectly drive productivity via plant community  
40 responses in composition and phenology. This suggests that the combination of species  
41 composition and vegetation phenology could jointly alter ecosystem-level sensitivity to  
42 precipitation seasonality under future climate change. We show that both functional diversity and  
43 dominant stability mechanisms are in operation simultaneously, highlighting the need to  
44 understand both the context and variation in community structure to predict productivity  
45 responses to intra-annual precipitation.

46  
47 **Key words:** California grassland, rangeland, drought, stability mechanisms, dominant species,  
48 functional diversity

## 50 **1. Introduction**

51 Predicting plant productivity is challenging within ecosystems (Adler & Levine, 2007; Lauenroth  
52 & Sala, 1992; Sala et al., 2012). Both the timing and amount of precipitation is key to within-site  
53 productivity patterns due to plant species' differing sensitivity to resource needs throughout the  
54 growing season (Cleland et al., 2013; Hallett et al., 2019; A. K. Knapp et al., 2002; Pitt & Heady,  
55 1978; Zeppel et al., 2014). Thus, intra-annual precipitation patterns – not only how much  
56 precipitation occurs, but when – may predict within-site productivity responses better than total  
57 annual precipitation alone (A. K. Knapp et al., 2002; Alan K. Knapp et al., 2008). While seasonal  
58 swings in the timing and amount of precipitation directly affect the timing of plant production

(e.g. phenology, Zelikova et al., 2015), such swings can also indirectly drive production responses via effects on plant community composition (Suttle et al., 2007). As substantial shifts in precipitation regimes including increased seasonal rainfall variability and the frequency of extreme events such as severe storms and droughts is expected globally (Tebaldi et al 2006; IPCC 2007; Groisman et al. 2012), a better understanding of intra-annual precipitation's effects on phenology, community composition, and consequently, within-site productivity is needed.

Intra-annual precipitation patterns – the variability and timing of rainfall and drought – directly determines soil water availability to plants during key growth stages, affecting ecosystem productivity in ways not reflected by total annual precipitation (Alan K. Knapp et al., 2008). Specifically, water availability during particular windows of time may affect net primary productivity (NPP; Epstein et al., 1999), as well as when peak productivity occurs and how long it lasts (Zelikova et al., 2015). For example, early growing season precipitation impacts annual productivity (Chelli et al., 2016; Craine et al., 2012; Hossain & Beierkuhnlein, 2018) due to the critical need for water to initiate and support early growth. As such, consistent early-season precipitation is often associated with higher plant densities, whereas dry periods following early rains may have disproportionate negative effects on young plants compared to similar-length dry periods later in the growing season (Duncan & Woodmansee, 1975; Jongen et al., 2019; Pitt & Heady, 1978). Consistent precipitation later in the season may extend the growing season, whereas a peak or late-season drought can drive early senescence, cutting the growing season short and limiting biomass production (Chelli et al., 2016; Suttle et al., 2007). Generally, longer growing seasons lead to greater productivity compared to shorter, making precipitation at the end of the growing season of key importance to ecosystem productivity (S. Ma et al., 2007; X. Ma et

al., 2015); however, this effect depends on the species present in the community (Suttle et al., 2007).

Intra-annual precipitation variability also affects productivity indirectly via plant community responses. Because the timing of rainfall or drought periods impacts which species germinate, build biomass, and reproduce via resource availability during early and peak growth, precipitation variability shifts community composition and diversity independent of precipitation amount (Cleland et al., 2013; Gherardi & Sala, 2015, 2019; A. K. Knapp et al., 2002). Species' life history strategies determine how seasonal precipitation patterns affect their survival, growth, and competitive ability (Cleland et al., 2013; Huenneke et al., 2002), and subsequently, community composition. For example, in California annual grasslands, consistent early-season precipitation favors competitive, resource-acquisitive grasses. Conversely, drought following germinating rains favors conservative, stress-tolerant forbs (Duncan & Woodmansee, 1975; Hallett et al., 2017, 2019; Pitt & Heady, 1978). While early-season precipitation driven species compositional shifts may ultimately affect end-of-season annual net primary productivity (ANPP) due to different growth capacities of plant functional groups (Dudney et al. (2017), community changes may potentially moderate production responses to seasonal swings in precipitation.

Community responses to precipitation amount and timing might buffer the sensitivity of productivity to precipitation due to biotic stability mechanisms. For example, temporal niche partitioning, in which different species or functional groups vary in their responses to precipitation, can generate a pattern of species trade-offs that enhances the stability of total productivity over time, both within and across years (Gonzalez & Loreau, 2009; Hallett et al., 2014). Alternatively, dominant plant stability (e.g. mass-ratio hypothesis, Grime, 1998) may

determine a site's productivity responsiveness to intra-annual precipitation. If dominant species are relatively unaffected by precipitation variability, they may dampen the overall sensitivity of productivity to precipitation because dominants contribute the largest proportion of the biomass (Grime, 1998; Hillebrand et al., 2008). If species tradeoffs control ecosystem productivity responses to drought, the effect of precipitation variability patterns on plant community composition would buffer their effect on production (Gherardi & Sala, 2015; Hallett et al., 2017). If a stable dominant species determines productivity responses, altered intra-annual precipitation patterns would have little effect on plant community composition, but ANPP would follow the production of the dominant plant (Grman et al., 2010; Roscher et al., 2011; Sasaki & Lauenroth, 2011). Thus, productivity responses to the timing and variability of precipitation may depend on these biotic mechanisms.

California Mediterranean annual grasslands are an ideal model system to test questions about the effects of inter- and intra-annual precipitation variability on plant phenology, community composition, and resultant productivity. Here, species turnover and composition patterns are on an annual timeline and precipitation is highly variable within and between growing seasons. Using a 3-year field experiment in which we partition the effects of early-season, late-season, and continuous drought from a control, we asked: 1) How does precipitation timing affect the quantity and timing of production? We expected that a late-season drought would limit maximum growth and induce earlier senescence, because late-season precipitation affects water availability during peak growth. 2) How does plant community composition respond to precipitation timing? We hypothesized that early season precipitation would determine community composition, where a wet early-season would select for competitive annual grasses, but early-season drought would select for drought tolerant forbs (e.g. species tradeoffs). And 3)

Do plant compositional responses amplify or buffer the response of productivity to precipitation timing, and what biotic mechanisms underlie this effect? If species tradeoffs are in effect, we would expect high community turnover and indirect effects of precipitation timing on plant productivity via these plant community composition changes. Alternatively, if dominant stability is in effect, we would expect low community change but direct effects of precipitation on productivity.

**2. Materials and Methods**

*2.1 Study site*

Our research took place in semi-arid Mediterranean grasslands at the University of California Sierra Foothill Research and Extension Center (SFREC) in Browns Valley, California (39.25 N, -121.31 W). Soils are generally shallow (~50cm), well-drained, silty loams classified as xeric Inceptisols and Alfisols. This site receives 717 mm of mean annual precipitation and has a mean annual temperature of 15.8 °C. Interannual variation in precipitation is high, ranging from < 250 to > 1200 mm (PRISM climate group). The system is characterized by frequent drought. Fall (i.e., early) season begins with germinating rains in October, becoming spring (i.e., late) season in February as plants build biomass. The season generally ends with drying and senescence in May, followed by a hot and dry summer with little to no plant growth from May-September. Annual precipitation during the experiment was 454 mm in 2015, 625 mm in 2016, and 978 in 2017 (Fig S1a, California Irrigation Management Information System). Vegetation at the site is characteristic of California's annual grasslands and includes grasses *Avena barbata*, *Festuca perennis*, and *Bromus hordeaceus* and forbs such as *Erodium botrys* and *Trifolium hirtum*. Annual grasses, such as *A. barbata*, often dominate plant communities.



## 2.2 *Experimental design*

Our field experiment began in October 2014 and continued for 3 growing seasons until May 2017. Precipitation treatments consisted of control (ambient precipitation), consistent drought (50% of rain blocked from October – May), early-season drought (50% of rain blocked from October - January), and late-season drought (50% of rain blocked from February-May) across four replicate blocks (4 precipitation treatments x 4 blocks x 3 years = 48). To create these precipitation treatments, rainout shelters were constructed (5.2 m x 6.4 m) as cold frames with high tunnels with removable covers made of UV resistant polyethylene and metal gutters to carry water away from the rainout shelter. Treatments were implemented following the first germinating rains in the fall. Removable covers allowed us to both implement the seasonal treatments and to minimize solar radiation effects, as we only deployed shelters during rain events (shelters were uncovered ~90% of the time). We monitored soil moisture for all treatments throughout the experiment using five soil moisture sensors (EC-5, Decagon Devices, Pullman, WA USA) in each plot (Fig. S2). Volumetric water content was measured to 10 cm depth and normalized to maximum field capacity and minimum air-dried moisture content. Water year 2015 was the final year of a 6-year drought, among the worst on state record since record keeping began in 1895 in California (California Department of Water Resources, 2017). Conversely, water year 2017 was above the 92<sup>nd</sup> percentile for wettest years since 1895 (California Department of Water Resources, 2017).

## 2.3 *Plant biomass and community measurements*

In 2015, 2016, and 2017 we measured aboveground net primary productivity in April and May by clipping plant biomass from a 0.25 m<sup>2</sup> quadrat. We harvested in both April and May to capture peak forb and grass production, respectively. We sorted samples to functional group (e.g. grass, forb, and N-fixer) and dried them at 60°C for 48 h and weighed them.

For species composition, we visually estimated percent cover of grass, forbs, bare ground, and litter cover and all plant species present within a 1 m<sup>2</sup> quadrat in April and May of each spring. For subsequent analyses, data were integrated and the maximum for each species or functional group was used. Plant senescence (visual estimate of percent cover that is green and brown) was assessed at four time points throughout the season from early April to mid-May each year.

Plant trait values for height, specific leaf area, leaf dry matter content, root density, specific root length of fine and coarse roots, and coarse root diameter had previously been collected on both greenhouse reared (Butterfield & Suding, 2013; Hallett et al., 2017) and field collected plants. To test treatment effects on functional diversity, we paired this species-level trait data with composition data for our plots. We measured functional diversity via Rao's quadratic entropy of plant traits.

#### *2.4 Data analyses*

All statistical analyses were performed in R version 3.5.1 (R Development Core Team 2018).

#### *2.5 The effect of precipitation timing on quantity and timing of productivity*

We tested for effects of precipitation treatments over time on the quantity (e.g. ANPP) and timing of production. To test for treatment effects on ANPP, we first built a linear mixed effect

model using the ‘lme’ function in the nlme package (Pinheiro et al., 2020), where precipitation treatment and year were fixed effects and block was random. We followed this with post-hoc comparisons using Tukey HSD tests in the lsmeans package (Lenth, 2016). To test for effects of precipitation treatment on timing of peak production, we built a linear mixed effect model to test for differences in senescence (% greenness) at different time points during peak season where precipitation treatment and time point were fixed effects and block nested within year were random effects. Hypothesis 1 would be supported if late and consistent drought treatments had earlier senescence and lower productivity compared to early drought treatment and the control.

## *2.6 Plant community composition and functional diversity responses to drought timing*

To test for community composition responses to precipitation timing, we used non-metric multidimensional scaling (NMDS) paired with perMANOVA using the vegan package (Oksanen et al., 2019). We traced shifts in community composition within each treatment by block over time by connecting vectors from 2015 to 2016, and 2016 to 2017. The direction and length of these vectors were then used to identify changes in communities across time points, where shorter vectors represent less change in community composition (e.g., Pucko et al., 2011). We tested for treatment differences in community change (e.g. vector length) using linear mixed models with treatment as a fixed effect and block as a random effect. To identify groups of associated species in our experimental plots, and to test if community clusters form by treatment, year, or block, we performed a cluster analysis (k-means) to assess community associations in the cluster package (Maechler et al., 2019). After identifying community clusters, we measured changes in community composition over time using vector lengths on the NMDS ordination. Indicator species analysis on clusters was performed to reveal which species significantly group

with community clusters (function “multipatt” in package indicpecies; de Caceres & Legendre, 2009). We tested for differences in functional diversity between community clusters using Rao’s quadratic entropy of plant traits (Rao’s Q; Botta-Dukát, 2005). Hypothesis 2 would be supported if greater community change and functional diversity occurred under early and consistent drought treatments compared to the late drought treatment and control, because both early and consistent drought limit water availability when seeds are germinating, favoring stress-tolerant groups.

*2.7 Plant communities and their productivity responses*

To test if communities amplify or buffer the response of productivity to intra-annual precipitation variability, we treated cluster identity as a factor and used a linear mixed effects model to test if community clusters had different ANPP, functional diversity, cover of the dominant grass *A. barbata* , and functional group biomass (grass, forb, N-fixer) responses to treatments. Treatment and cluster were fixed effects and block nested within year was a random effect. We then tested ANPP and functional group biomass (grass, forb, N-fixer) responses to treatments within each cluster individually to identify if community composition determines responses to treatments. We used linear mixed effect models to test precipitation treatment effects by community clusters on plant senescence (visual estimate of percent cover that is green) by time point (four time points throughout the season from early April to mid-May), where year and block were random effects, and precipitation treatment, cluster, and time point were fixed effects. If communities with the greatest functional diversity had the most stable ANPP over time and in response to treatments, especially early drought, the species tradeoff mechanism would be

supported. If communities have low functional diversity, high dominance, and a negative response in ANPP to drought, the dominant stability mechanism would be supported.

### 3. Results

#### 3.1 *The effect of precipitation timing on quantity and timing of productivity*

There were significant main effects of treatment ( $F_{3,33} = 4.59$ ,  $p = 0.001$ ) and year ( $F_{2,33} = 12.36$ ,  $p < 0.001$ ) on total ANPP, while the interaction of treatment and year was not significant (Figure 1a and Figure S1b). Total ANPP was highest when precipitation occurred during the early-season (e.g., control and late drought treatments) and was lowest when precipitation occurred either primarily during the late-season (e.g., early drought) or under continuous drought (Figure 1a). There was greater ANPP in 2016 and 2017 compared to 2015 (Fig S1b). This interannual productivity pattern followed the annual precipitation pattern (Fig S1a), where annual precipitation was lowest for the 2015 growing season, the same year as the lowest ANPP.

There were significant main effects of treatment ( $F_{3,357} = 81.01$ ,  $p < 0.001$ ) and time period ( $F_{3,357} = 145.64$ ,  $p < 0.001$ ), and a significant interaction of treatment and time period ( $F_{9,357} = 3.60$ ,  $p < 0.001$ ) on plant senescence (Figure 1b). Although total ANPP was not affected by late drought, plant senescence occurred earlier in late and consistent drought plots compared to control precipitation and early drought plots, effectively shortening the active growing season for these treatments (Figure 1b).

#### 3.2 *Plant community composition and functional diversity responses to drought timing*

Community composition did not differ by treatment (perMANOVA,  $p = 0.26$ , Table S1).

Although communities shifted over time (Figure 2a), there was not a significant effect of year on

these patterns (perMANOVA,  $p = 0.19$ , Table S1). The greatest changes in community composition occurred in consistent drought plots, while the least change occurred in late-season drought plots (Figure 2b). Cluster analysis of communities revealed two distinct clusters that did not group with treatments, blocks, or years (Figure 2a). Community composition significantly differed by cluster membership (perMANOVA,  $p < 0.05$ , Table S1). Annual grasses *Festuca perennis*, *Festuca bromoides*, perennial grass *Cynodon dactylon*, forb *Centaurea solstitialis*, and N-fixers *Vicia sativa* and *Trifolium glomeratum* were indicator species for Cluster 1, while only the annual grass *Avena barbata* was an indicator species for Cluster 2 (Figure 2a). Functional diversity ( $F_{1,29} = 26.09$ ,  $p < 0.001$ , Table S2), forb production ( $F_{1,29} = 9.86$ ,  $p = 0.004$ , Table S2), and N-fixer production ( $F_{1,29} = 6.90$ ,  $p = 0.01$ , Table S2) differed by cluster. Cluster 1 had significantly greater functional diversity (Figure 3a) and greater productivity of forbs and N-fixers (Figure 3c) compared to Cluster 2, which was composed of a mean 80% *A. barbata* cover (Figure 3b). While the functionally diverse community (Cluster 1) shifted community composition over time in response to treatments, the *A. barbata* dominated community (Cluster 2) remained stable through time (Figure 2d).

There was no overall change in functional group abundance (% cover) by treatment or year (Fig. S3). However, there were shifts in functional group abundance within the functionally diverse community, where forb abundance was greater under late drought (Fig. S4).

### 3.3 Plant communities moderate productivity responses to drought timing

The functionally diverse plant communities (Cluster 1) responded differently to drought timing than *A. barbata* dominated communities (Cluster 2). Functionally diverse communities' ANPP differed by precipitation treatments and was significantly lower in early and consistent drought

treatments compared to the control (Fig. 4a). There were no differences in *A. barbata* dominated communities' ANPP across precipitation treatments (Fig. 4b). Additionally, the diverse communities were less stable, with greater variation in ANPP over time compared to the dominated communities (Fig. S5). There were significant main effects of precipitation treatment on grass ( $F_{3,29} = 3.86$ ,  $p = 0.02$ , Table S2) and N-fixer ( $F_{3,29} = 8.40$ ,  $p < 0.01$ , Table S2), but not forb production ( $F_{3,29} = 0.39$ ,  $p = 0.78$ , Table S2). Forb and N-fixer ANPP was significantly affected by cluster membership ( $F_{1,29} = 9.86$  and  $6.90$ ,  $p = 0.004$  and  $0.01$ , respectively, Table S2), and both were overall more productive in the functionally diverse cluster (Figure 3c).

The effects on plant senescence differed by community, where early drought plots remained active longer and consistent drought plots senesced earlier for functionally diverse communities (Fig. 4c). For *A. barbata* dominated communities, late-drought treatments senesced earlier than all other treatments (Fig. 4d).

#### 4. Discussion

Intra-annual precipitation variability is an important driver of ANPP, but predicting its effects is difficult because the timing of this precipitation may both directly and indirectly influence ANPP via community phenology and composition responses. Here we experimentally partitioned the effects of early versus late-season precipitation in a Mediterranean ecosystem. Overall, we found that early precipitation increased peak ANPP, whereas late-season precipitation extended the time period of peak ANPP. Critically, the sensitivity of ANPP to intra-annual precipitation timing depended on the underlying community and its dynamics. We observed two distinct communities, one dominated by a single, productive grass, *Avena barbata*, and another characterized by a functionally diverse and dynamic set of species. The stability of the dominant

grass *A. barbata* buffered the sensitivity of ANPP to precipitation variability, but also curtailed the maximum potential ANPP relative to functionally diverse communities. In contrast, functionally diverse communities were more dynamic in their response to precipitation timing, resulting in greater swings in peak ANPP but also a consistently longer growing season than the dominant-driven communities. As both amount and timing of precipitation is predicted to become more variable in future (IPCC 2013), our results highlight that predicting ANPP responses will require characterizing the biotic community and understanding the mechanisms that govern its response to precipitation.

We hypothesized that late-season precipitation would be the primary driver of total ANPP in California grasslands, because the majority of plant growth occurs in the spring. However, we found that early-season precipitation was most strongly associated with biomass growth, whereas late-season precipitation was key to growing season length. The strong relationship between early-season precipitation and peak ANPP suggests that growth investments early in the season allow species to reach high levels of ANPP coming out of winter (Chelli et al., 2016; Jongen et al., 2019; Murphy, 1970), but that a subsequent spring drought causes them to peak early and then senesce. Our results mirror other studies in Mediterranean ecosystems that have found that early precipitation is key to green-up (Esch et al., 2019) and that early drought decreases total potential biomass by inhibiting germination and seedling establishment, and subsequent stem density (Jongen et al., 2019; Murphy, 1970; Pitt & Heady, 1978). Moreover, the importance of early-season precipitation for peak ANPP may be amplified by its effect on community composition, as early-season precipitation is commonly associated with productive species (Duncan & Woodmansee, 1975; Hallett et al., 2017, 2019; Pitt & Heady, 1978). These results provide a base for a predictive framework linking intra-annual precipitation and ANPP,



such that total amount of ANPP may be predictable in advance based on early-season precipitation, whereas the timing of peak productivity depends on precipitation received in late-season.

We expected that precipitation timing – in particular early-season precipitation – would drive shifts in community composition. Specifically, we expected that a wet early-season would select for competitive annual grasses and early-season drought would select for drought-tolerant forbs, as is typical in this system (Pitt and Heady 1978, Hallett et al. 2017, 2019). Instead, we found two distinct communities present at our site that persisted regardless of precipitation treatment: 1) a functionally diverse community, which supported a greater abundance of forbs and N-fixers and 2) an *A. barbata* dominated community, which supported ~80% *A. barbata* cover. While community composition was measured after treatments had been applied for one growing season, we expect that the two community clusters are not a product of the precipitation treatment, but rather, appear to reflect community starting conditions as clusters were distributed across all treatments. The two community types differed in their precipitation sensitivity, such that the functionally diverse community shifted in community composition by precipitation treatment, whereas the *A. barbata* dominated community did not change over time or in response to treatments.

The sensitivity of ANPP to precipitation variability may be buffered either by tradeoffs among species or the presence of a stable dominant species. We expected that species tradeoffs would be a particularly important stabilizing mechanism in functionally diverse communities, especially under early drought (Hallett et al. 2017). We found that the underlying plant community, and its respective dynamics, determined the sensitivity of ANPP to intra-annual precipitation timing. Despite changes in composition in response to precipitation, however, the

functionally diverse community was dynamic in its ANPP response to precipitation, with significantly lower ANPP under consistent and early drought. In contrast, we found that *A. barbata* dominated communities had no response to precipitation treatments and produced consistent ANPP regardless of precipitation amount or timing. Other studies have similarly found that dominant annual grasses have little response to changes in precipitation amount once established (Suttle et al., 2007). One explanation could be functional compensation where many dense, short individuals produce equivalent biomass to fewer large, tall individuals due to a tradeoff in plant size and density, where individual plants are smaller under high density conditions (Goldberg et al., 2001), or simply, that the dominant species is drought resistant (Chelli et al., 2016; Sasaki & Lauenroth, 2011). There is a growing recognition that the biotic mechanisms of stability can differ by the environmental context (Grman et al. 2010, Hallett et al. 2014); our results highlight that different mechanisms can operate (and to a different effect) within the same site in relation to variation in the local community.

Precipitation timing was important for growing season length, where late drought induced earlier senescence overall. This effect was particularly accentuated under the *A. barbata* dominated community, where a late drought caused early senescence (approximately 2-3 weeks earlier than other treatments) despite no differences in peak ANPP by treatment. Late-season water stress causes phenological changes and is linked to early maturity and senescence in many Mediterranean grass species (Aronson et al., 1992; Berger & Ludwig, 2014; Esch et al., 2019; Sherrard & Maherali, 2006). In the functionally diverse community, however, late drought had a much lower effect on senescence, which may be due to species differences in drought tolerance. Phenological timing does differ by species, where some experience rapid growth early and mature earlier than others, such that sequences of maturity are predictable in annual grasslands

(Ratliff and Heady 1962). As such, while we did not see strong species tradeoffs across precipitation regimes, our results indicate that functionally diverse communities were composed of species with varied phenological responses to any given precipitation scenario. Consequently, species phenological tradeoffs within a growing season in the diverse communities consistently extended growing season length relative to the *A. barbata* dominated communities. Taken together, our results indicate that the importance and effect of different biotic stabilizing mechanisms can differ in relation to what aspect of productivity is considered, with dominant stability important for buffering peak ANPP and species tradeoffs important for buffering the duration of productivity.

While annual precipitation directly affects primary productivity across and within ecosystems worldwide (Huxman et al., 2004; Alan K. Knapp & Smith, 2001), temporal models of ANPP responses to precipitation within an ecosystem explain less variability than the spatial precipitation-ANPP relationship across ecosystems (Adler & Levine, 2007; Lauenroth & Sala, 1992; Sala et al., 2012). This might be due to an emphasis on total annual precipitation. Our study demonstrates that intra-annual precipitation patterns – the variability and timing of precipitation and drought – may indirectly drive productivity via community responses in composition and phenology. This suggests that the combination of species composition and vegetation phenology could jointly alter ecosystem-level sensitivity to seasonality of precipitation under future climate change. We show that both functional diversity and dominant stability mechanisms are in operation simultaneously, highlighting the need to understand both the context and variation in community structure in order to predict productivity responses to intra-annual precipitation.

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**6. Author Contributions**

KNS, WLS, and LMH conceived the ideas and designed methodology; CTW and LMH collected the data; EAS analyzed the data and led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

**7. Data accessibility**

The authors intend to archive data and R scripts on github.

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**Figure legends**

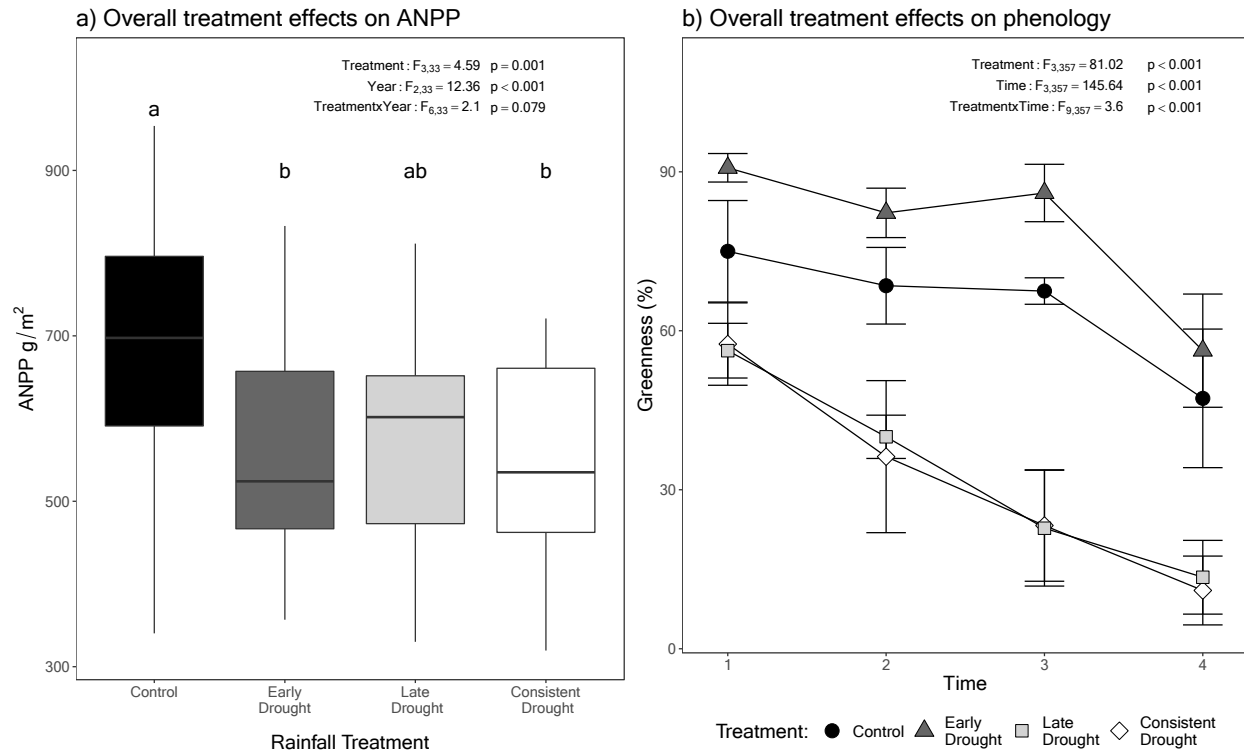
Figure 1. Effects of precipitation treatment on a) ANPP. Results of a two-way analysis of variance for ANPP by treatment and year are shown in text on the figure. Different letters denote significant differences by treatment, differences in ANPP by year are shown in Figure S1b; and effects of precipitation on b) phenology of plant senescence, measured as percent greenness as plants senesce at the end of the growing season. Time refers to 4 timepoints approximately 1 week apart beginning in early April. Results of a two-way analysis of variance in percent greenness by treatment and time point are shown in text on the figure.

Figure 2. Panel showing a) NMDS ordination of communities by treatment with directional vectors for change in community composition for each plot from 2015-2017. The results of cluster analysis of these communities identified two clusters, which are indicated by a hull plotted around each cluster. Indicator species that significantly group with each cluster are overlaid on the NMDS plot. The distance of community change measured as the distance from 2015 to 2017 points, or the length of the vectors on the NMDS ordination, by b) treatment, and c) cluster membership. Different letters denote significant differences.

Figure 3. Community characteristics of each cluster: a) Functional diversity, measured as Rao's quadratic entropy, of communities within each cluster; b) the percent cover of *A. barbata* within each cluster; and c) the productivity of forb and N-fixers by cluster. Different letters denote significant differences between clusters.

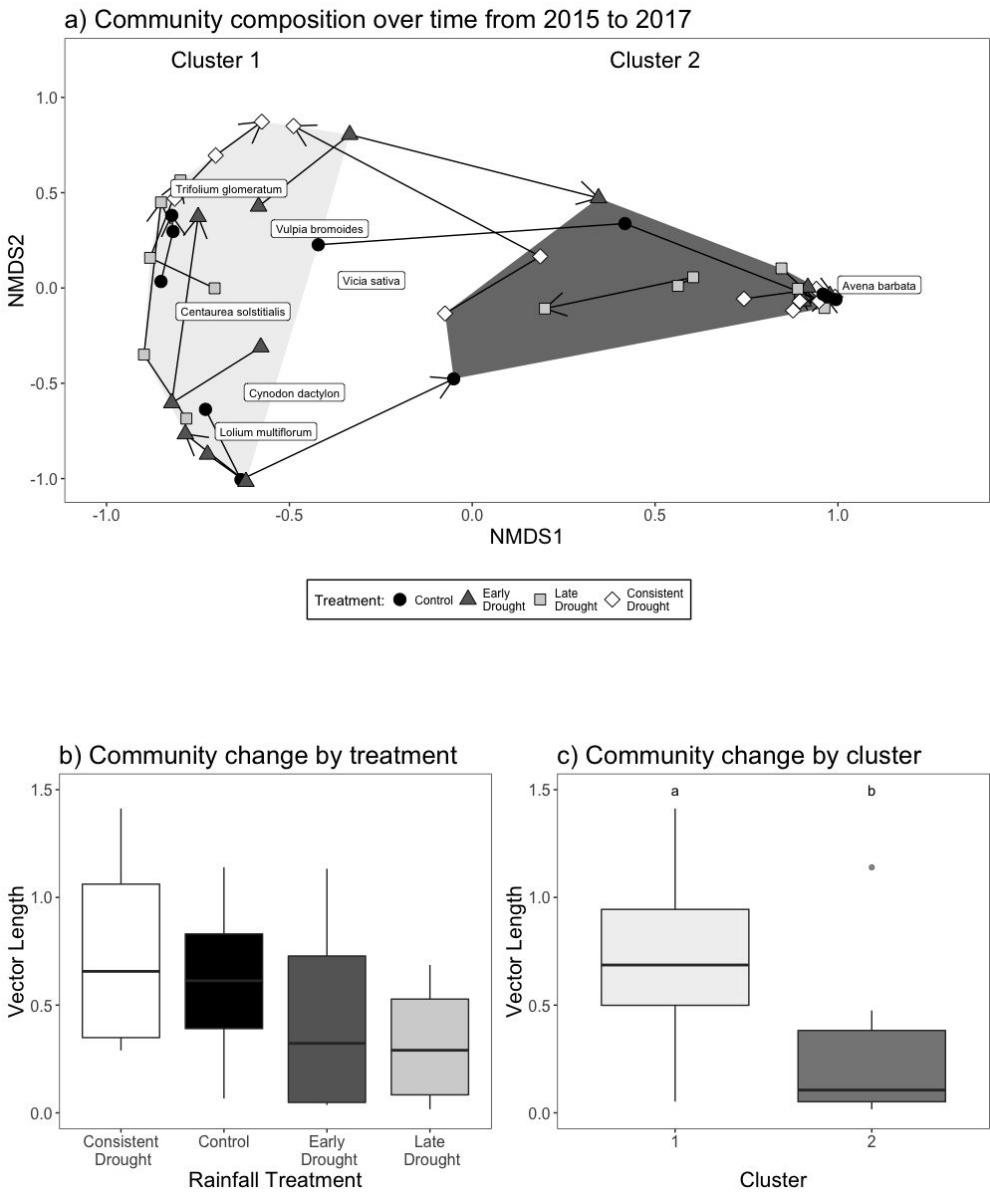
Figure 4. Effects of precipitation treatments on ANPP across all years within community clusters for (a) the functionally diverse community, and (b) the *A. barbata* dominated community, significant differences between treatments are denoted with different letters within each cluster. Effects of precipitation treatments on phenology of plant senescence within community clusters for (c) the functionally diverse community, and (d) the *A. barbata* dominated community, where time refers to 4 timepoints approximately 1 week apart beginning in early April (data shown are mean and standard errors, responses are averaged across years).

603 Figure 1



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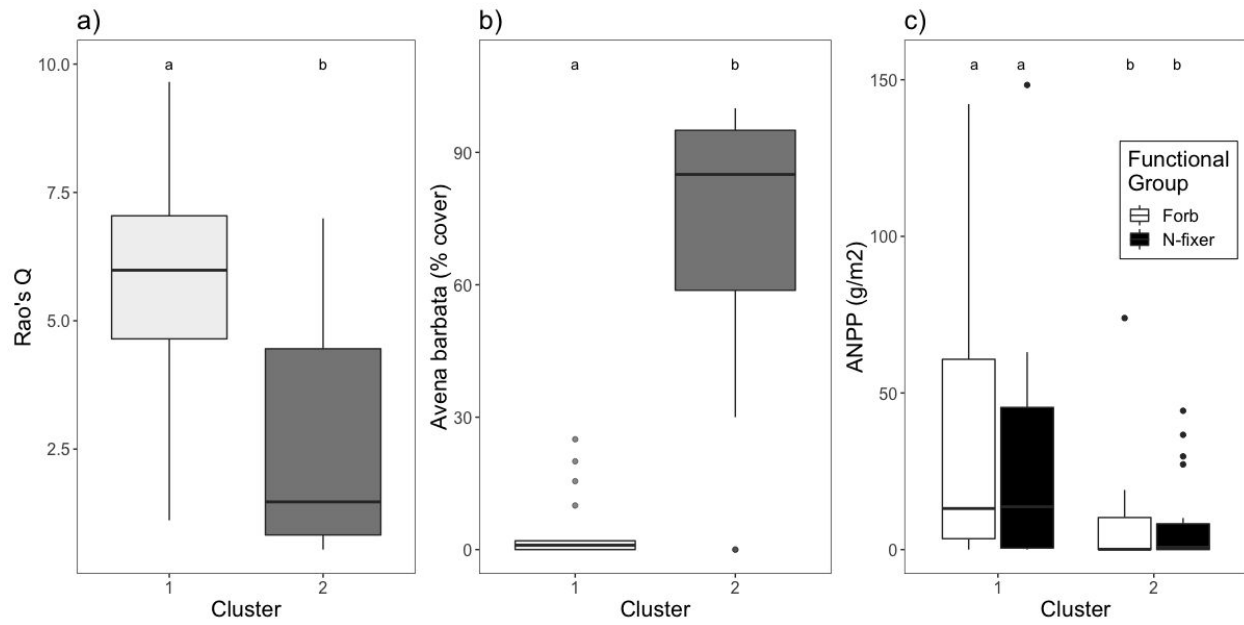
605 Figure 2



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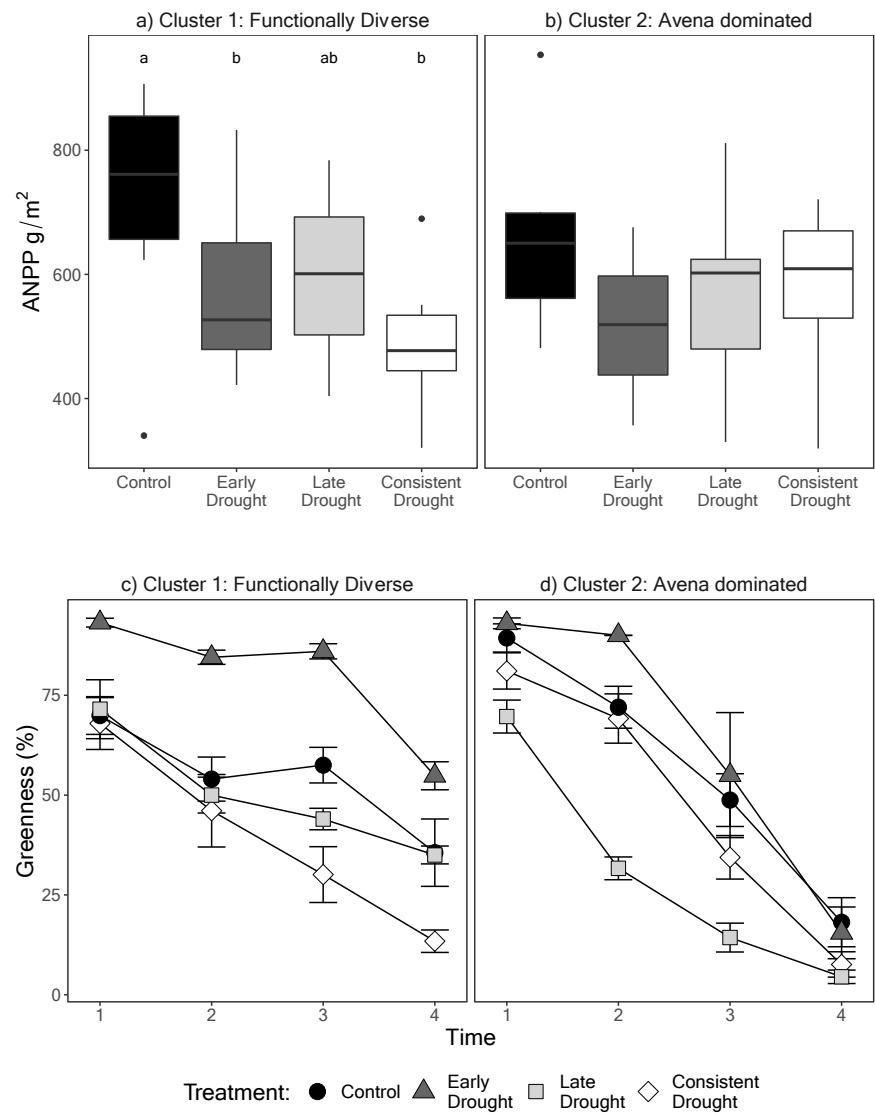
608 Figure 3



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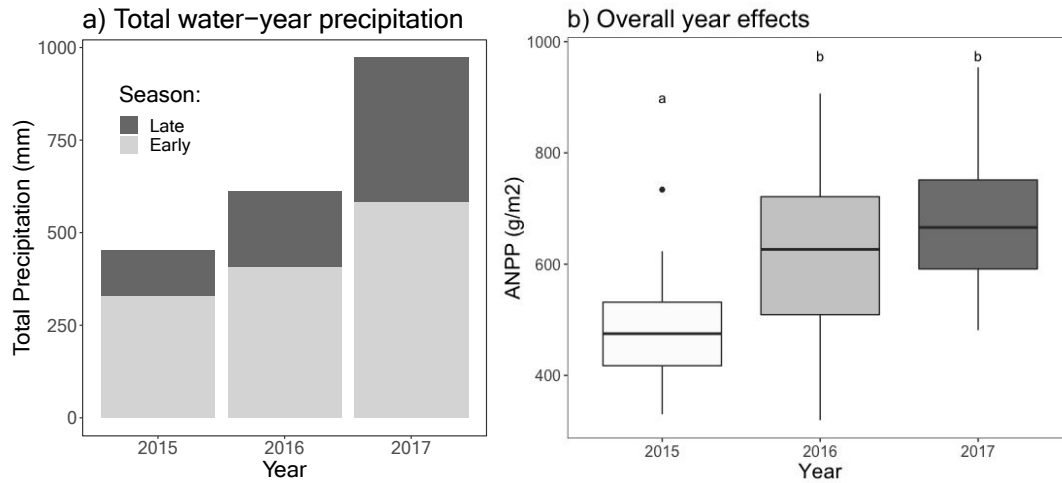
611 Figure 4



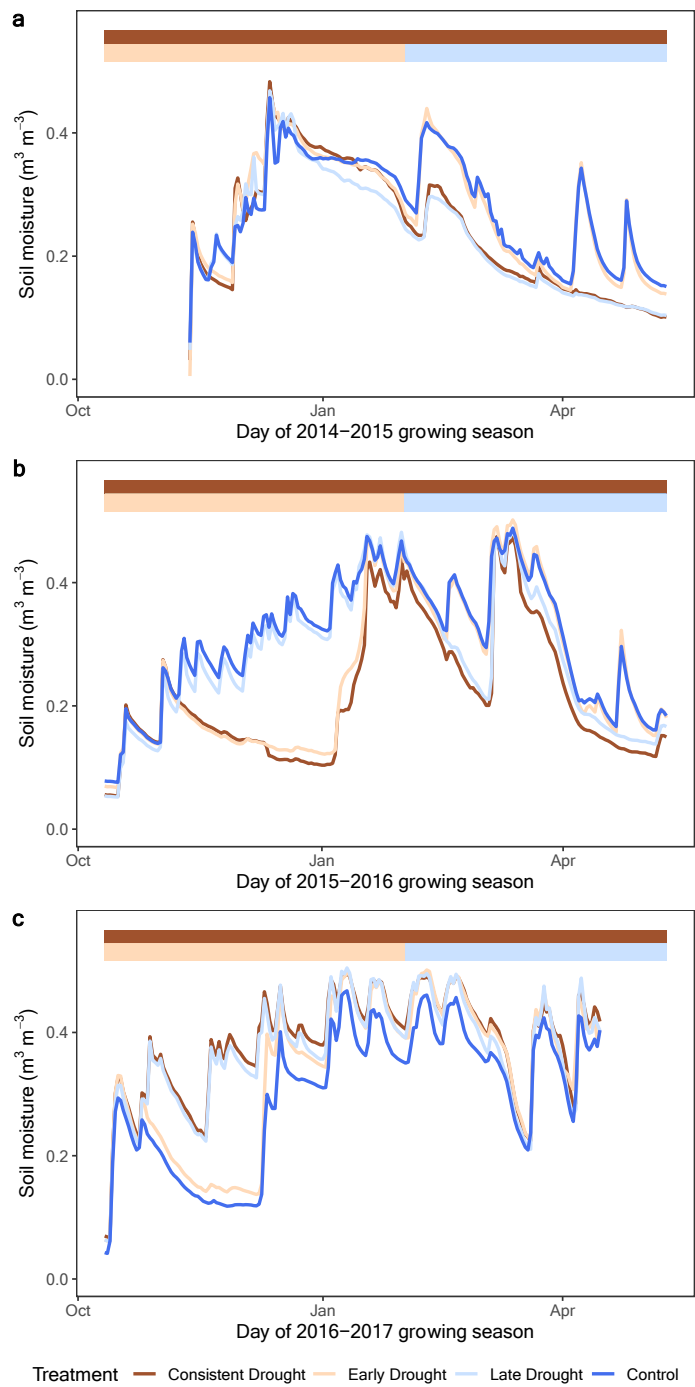
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## 1 Supplementary Tables and Figures

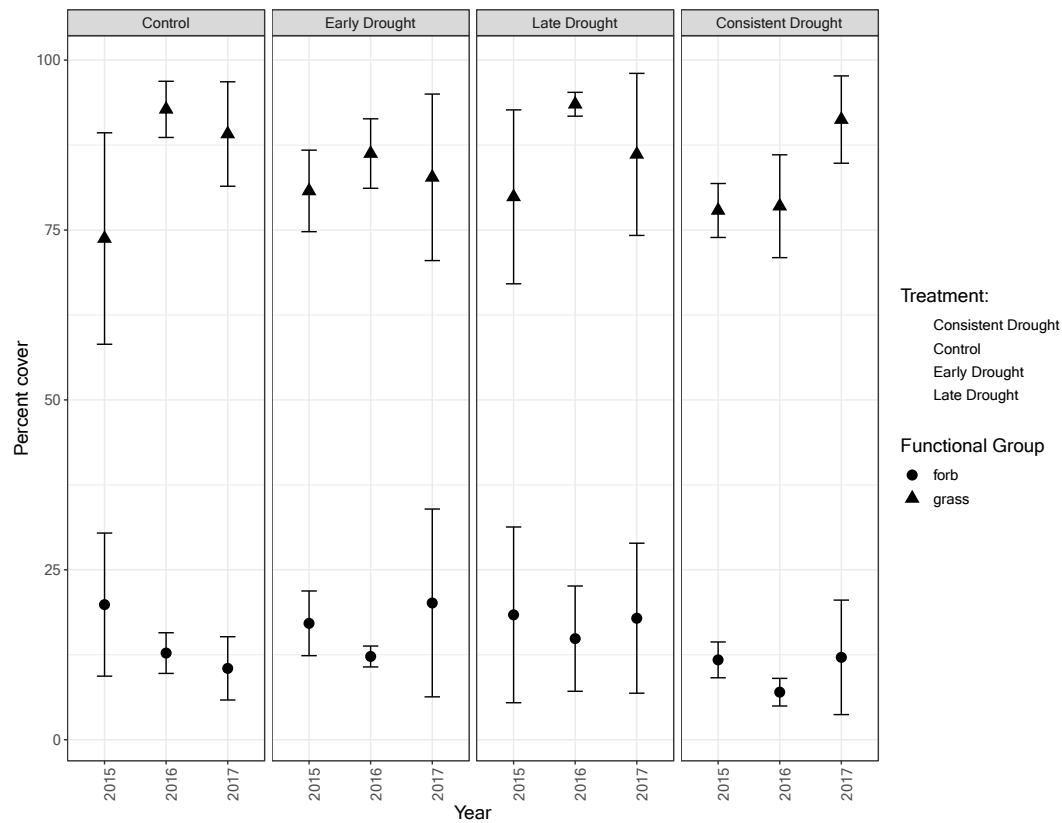


2  
 3 Figure S1. a) Water-year precipitation from 2015-2017 where early and late season are total  
 4 precipitation for September to January and February to May, respectively. Data are from the  
 5 California Irrigation Management Information System weather station at SFREC in Browns  
 6 Valley, CA (Lat/Long: 39.252561, -121.315670) and b) annual net primary productivity by year  
 7 across all plots, different letters denote significant differences between years. See Figure 1 for  
 8 differences in ANPP by treatment.



10 Figure S2. Volumetric soil moisture by treatment over time for a) water year 2015, b) water year  
11 2016, and c) water year 2017. Colored bars in show time periods consistent, early, and late  
12 drought treatments, matching colors shown in the figure legend. Control received all ambient  
13 precipitation shown in Figure S1.

14



15

16 Figure S3. Mean percent cover ( $\pm$  standard error) of functional groups forbs and grasses by  
 17 treatment and year. There were no significant changes in plant functional group composition  
 18 over time.

19

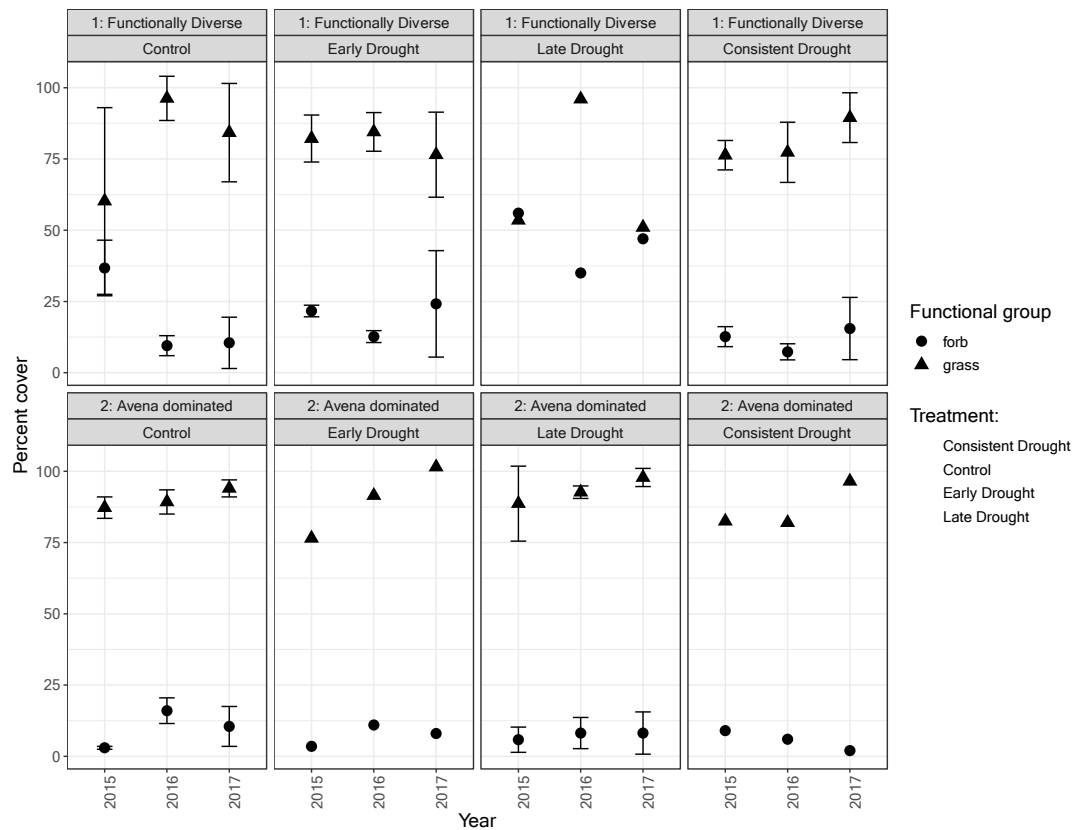


Figure S4. Mean percent cover ( $\pm$  standard error) of forb and grasses by cluster, treatment, and year. Cluster 1 is the functionally diverse and Cluster 2 is the *A. barbata* dominated cluster.

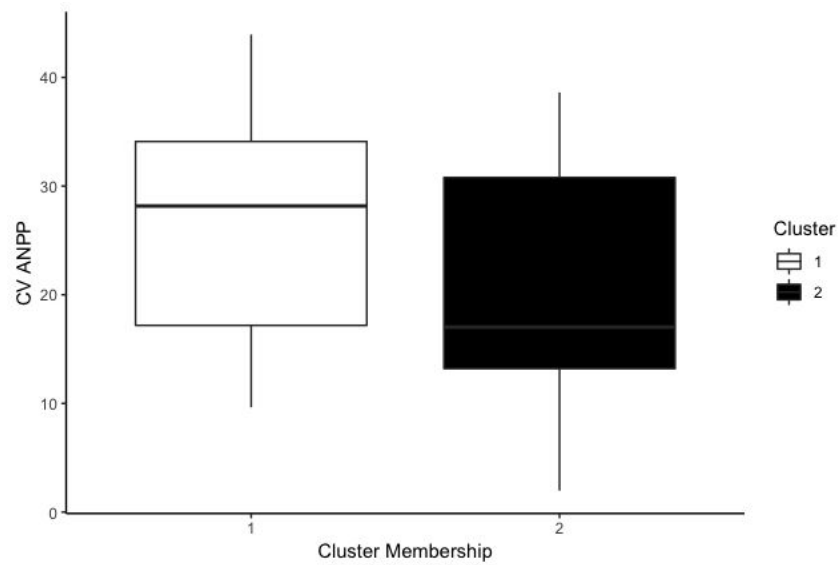


Figure S5. Coefficient of variation in ANPP by cluster membership. Cluster 1 is the functionally diverse and Cluster 2 is the *A. barbata* dominated cluster.

Table S1. Effects of treatment (a) and cluster (b) on community composition tested via permutational multivariate analysis of variance (perMANOVA) tests (1000 permutations), where block was a random effect. df= degrees of freedom, SS= sum of squares, MS= mean squares

	df	SS	MS	R <sup>2</sup>	Pseudo-F	P
<b>a)</b>						
Treatment	3	0.73	0.24	0.06	0.85	0.26
Year	2	0.57	0.28	0.05	1.00	0.19
Treatment*Year	6	0.45	0.07	0.04	0.27	0.89
Residuals	36	10.21	0.28	0.85		
Total	47	11.96				
<b>b)</b>						
Cluster	1	5.94	5.94	0.50	47.73	<0.001*
Year	2	0.53	0.27	0.04	2.14	0.06
Cluster*Year	2	0.26	0.13	0.02	1.06	0.37
Residuals	42	5.23	0.12	0.44		
Total	47	11.96				

Table S2. Results of two-way analyses of variance by treatment and cluster for a) ANPP, b) functional diversity (Rao's Q), c) *Avena barbata* percent cover, d) grass biomass, e) forb biomass, and f) N-fixer biomass.

	df	F value	P
<b>a) ANPP</b>			
Treatment	3,29	4.10	<b>0.02</b>
Cluster	1,29	0.06	0.81
Treatment*Cluster	3,29	0.21	0.89
<b>b) Rao's Q</b>			
Treatment	3,29	1.54	0.22
Cluster	1,29	26.09	<b>&lt;0.001</b>
Treatment*Cluster	3,29	0.21	0.89
<b>c) <i>A. barbata</i></b>			
Treatment	3,29	7.73	<b>&lt;0.001</b>
Cluster	1,29	107.78	<b>&lt;0.001</b>
Treatment*Cluster	3,29	2.34	0.09
<b>d) Grass</b>			
Treatment	3,29	3.86	<b>0.02</b>
Cluster	1,29	1.98	0.17
Treatment*Cluster	3,29	0.10	0.96
<b>f) Forb</b>			
Treatment	3,29	0.39	0.78
Cluster	1,29	9.86	<b>0.004</b>
Treatment*Cluster	3,29	2.16	0.11
<b>g) N-fixer</b>			
Treatment	3,29	8.40	<b>&lt;0.001</b>
Cluster	1,29	6.90	<b>0.01</b>
Treatment*Cluster	3,29	0.45	0.72

