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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 – may be a stronger driver of net primary 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 using rainout shelters in which we manipulated drought amount and timing (early-season drought, late-season drought, continuous drought and ambient precipitation) over three years and assessed plant responses: aboveground net primary production (ANPP), phenological timing of peak production and senescence, and community composition.

3. Overall, early-season and consistent drought treatments had lowest productivity, while late-season and consistent drought treatments senesced earlier. Plots with functionally diverse communities shifted community composition and had a significant ANPP response to precipitation treatments. In contrast, communities dominated by a single resource-acquisitive grass species did not 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 green longer (particularly under the early-season drought treatment) compared communities dominated by one grass species, which senesced earlier (particularly under the late-season drought treatment).

5. *Synthesis*. Our study demonstrates that drought patterns may indirectly drive ANPP via plant community responses in composition and phenology. This suggests that the combination of species composition and vegetation phenology could jointly alter ecosystem-level sensitivity to precipitation seasonality 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 to predict ANPP responses to intra-annual precipitation.

Key words: Mediterranean grassland, rangeland, drought, stability mechanisms, dominant species, functional diversity, plant-climate interactions, determinants of plant community diversity and structure

1. Introduction

Predicting plant productivity is challenging within ecosystems (Adler & Levine, 2007; Lauenroth & Sala, 1992; Sala et al., 2012). Both the timing and amount of precipitation is key to within-site productivity patterns due to plant species’ differing sensitivity to resource needs throughout the growing season (Cleland et al., 2013; Hallett et al., 2019; A. K. Knapp et al., 2002; Pitt & Heady, 1978; Zeppel et al., 2014). Thus, intra-annual precipitation patterns – not only how much precipitation occurs, but when – may predict within-site productivity responses better than total annual precipitation alone (A. K. Knapp et al., 2002; Alan K. Knapp et al., 2008). While seasonal 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 directly determine 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 annual net primary productivity (ANPP; 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 ANPP (Chelli et al., 2016; Craine et al., 2012; Hossain & Beierkuhnlein, 2018) due to the critical need for water to initiate and support early growth. Drought 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 & Hady, 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 ANPP 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 may depend 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 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). Such shifts in species composition may ultimately affect end-of-season ANPP due to different plant functional groups' growth capacities (Dudney et al. (2017). On the other hand, community changes could potentially moderate production responses to seasonal swings in precipitation.

Community responses to both precipitation amount and timing might buffer the sensitivity of productivity due to biotic stability mechanisms. For example, temporal niche partitioning, in which different species or functional groups vary in their responses to precipitation timing and amount, can generate a pattern of species tradeoffs (i.e. compensatory shifts in the relative abundance of plant species as a result of precipitation) that enhances the stability of ANPP 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 ANPP responsiveness to intra-annual precipitation. If dominant species are relatively unaffected by precipitation variability, they may dampen the overall sensitivity of ANPP to precipitation because dominants contribute the largest proportion of the biomass (Grime, 1998; Hillebrand et al., 2008). If species tradeoffs control ANPP responses to precipitation, 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, ANPP 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 ANPP. Here, species turnover and composition patterns are on an annual timeline and precipitation is highly variable within and between growing seasons. Drought occurs frequently but varies in seasonality and intensity. Using a 3-year field experiment to partition the effects of early-season, late-season, and continuous drought from a control, we asked: 1) How does drought timing affect the timing and quantity of production (i.e., senescence and ANPP, respectively)? We expected that a late-season drought would induce earlier senescence and limit ANPP, because of low water availability during peak growth. 2) How does plant community composition respond to drought timing? We hypothesized that early season drought would determine community composition, where early-season drought would select for drought tolerant forbs, but a wet early-season would select for competitive annual grasses (e.g. species tradeoffs). And 3) Do plant compositional responses amplify or buffer the response of ANPP to drought timing, and what biotic mechanisms underlie this effect? If species tradeoffs are in effect, we would expect high community turnover and indirect effects of drought timing on ANPP via plant community composition changes. Alternatively, if dominant stability is in effect, we would expect low community change but direct effects of drought on ANPP.

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. Drought 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). To create these drought

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 92nd 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 m² 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 m² quadrat in April and May of each spring. For subsequent analyses, we took the maximum value for each species or functional

group each year. 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 greenhouse reared plants (Butterfield & Suding, 2013; Hallett et al., 2017). 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 drought treatments on quantity and timing of ANPP

We tested for effects of drought treatments over time on the quantity (i.e. ANPP) and timing (i.e. senescence) of ANPP. 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 drought treatment, year, and their interaction 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 drought 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 drought treatment, time point, and their interaction 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 treatments

To test for community composition responses to drought 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 drought 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 formed 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 grouped with community clusters (function “multipatt” in package indicpecies; de Cáceres & 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 change in community composition 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 ANPP responses*

We used linear mixed effects model to test if communities amplify or buffer the response of ANPP to drought timing, where drought treatment, cluster, and their interaction were fixed effects and block nested within year was a random effect. We built similar mixed effects models to test cluster and treatment effects on functional diversity, cover of the dominant grass *A. barbata*, and functional group biomass (grass, forb, N-fixer). We then tested ANPP and functional group biomass (grass, forb, N-fixer) responses to drought treatments within each cluster individually to identify if community composition determined responses to drought treatments. We used linear mixed effect models to test drought 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 block nested in year were random effects, and drought treatment, cluster, time point, and their interactions were fixed effects. If communities with the greatest functional diversity had the most stable ANPP over time and in response to drought treatments, especially early drought, the species tradeoff mechanism would be supported. If communities had low functional diversity, high dominance, and a negative response in ANPP to drought, the dominant stability mechanism would be supported.

3. Results

3.1 *Characterizing plant communities*

Community composition did not differ by drought treatment (perMANOVA, $p = 0.26$, Table S1). Although communities did shift over time (Fig. 1a), there was no effect of year on these patterns (perMANOVA, $p = 0.19$, Table S1). The greatest change in community composition occurred in consistent drought treatments, while the least change occurred in late-season drought (Fig. 1b),

but these effects were not significant and not in any consistent direction (Fig. 1a). Cluster analysis of communities revealed two distinct clusters that did not group with treatments, blocks, or years (Fig. 1a; 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 (Fig. 1a). 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 (Fig. 2a) and greater productivity of forbs and N-fixers (Fig. 2b) compared to Cluster 2, which was composed of a mean 80% *A. barbata* cover (Fig. 2c). There was no difference in grass productivity between the two clusters.

Cluster membership remained fairly stable through time with three communities (two consistent drought and one ambient rainfall) shifting from the functionally diverse to the *A. barbata* dominated cluster (Fig. 1a). Only one member of the *A. barbata* dominated cluster shifted to the functionally diverse cluster in the final year (ambient rainfall treatment; Fig. 1a); this plot was among the lowest cover of *A. barbata* of all the *A. barbata* dominated communities. Within community clusters, we measured vector length as a proxy for community composition change and found that 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 (Fig. 1c).

3.2 Plant communities moderate ANPP responses to drought treatments

There were significant main effects of drought 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 drought treatment and year was not significant (Figure 3a and Fig. S1b). Total ANPP was highest in control and late drought treatments and was lowest in early and consistent drought treatments (Fig. 3a). 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 ANPP was lowest for the 2015 growing season, the same year as the lowest annual precipitation.

While there were detectable overall effects of drought treatment and year on ANPP, these effects were driven by the functionally diverse plant communities (i.e., Cluster 1). Functionally diverse communities' ANPP differed by drought treatments and was significantly lower in early and consistent drought treatments compared to the control (Fig. 3b). Meanwhile, *A. barbata* dominated communities' ANPP did not respond to drought treatments (Fig. 3c). Additionally, the diverse communities were less stable, with greater variation in ANPP over time compared to the *A. barbata* dominated communities (Fig. S5). There were significant main effects of drought 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 ANPP ($F_{1,29} = 9.86$, $p = 0.004$, Table S2) and N-fixer ANPP ($F_{1,29} = 6.90$, $p = 0.01$, Table S2) were significantly affected by cluster membership, where both were more productive in the functionally diverse cluster (Fig. 2b).

3.3 Plant communities moderate senescence timing in response to drought treatments

There were significant main effects of drought 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 (Fig. 3d). Although total ANPP was not affected by late drought, plant senescence occurred earlier in late and consistent drought treatments compared to control precipitation and early drought treatments, effectively shortening the active growing season for the former treatments (Fig. 3d).

The effects on plant senescence differed by community cluster, where the early drought treatment remained active (i.e. greener) longer and the consistent drought treatment senesced earlier for functionally diverse communities (Fig. 3e). For *A. barbata* dominated communities, the late drought treatment senesced earlier than all other treatments (Fig. 3f).

3.4 Functional groups respond differently to treatments across clusters

Both cluster 1 and 2 were grass dominated (Fig. 4a and 4b). Grasses that dominated Cluster 1 varied, but included *Festuca bromoides*, *Festuca perennis*, or *Cynodon dactylon*. In Cluster 2, only grass *Avena barbata* dominated (Fig. 1a). There were shifts with drought treatments in functional group abundance within the functionally diverse cluster (Cluster 1), where forb cover was greater under late drought (Fig. 4a), and these shifts were consistent across years (Fig S4). There were no shifts in functional groups for the *A. barbata* dominated cluster (Fig. 4b). There was no overall change in functional group abundance (% cover) by treatment or year (Fig. S3).

4. Discussion

Intra-annual precipitation variability is an important driver of ANPP, but predicting its effects is difficult because precipitation timing may both directly and indirectly influence ANPP via community composition and community phenology (e.g. senescence) responses. Here we

experimentally partitioned the effects of early versus late-season drought in a Mediterranean ecosystem. Critically, the sensitivity of ANPP to drought timing depended on the underlying community composition (Fig. 3b, Fig. 3c, Fig. S5). We observed two distinct communities, one characterized by a functionally diverse and dynamic set of species, and another dominated by a single, productive grass, *Avena barbata*. The functionally diverse communities were more dynamic in their response to drought timing, resulting in greater swings in peak ANPP but also a consistently longer growing season than the dominant-driven communities. In contrast, stability of the dominant grass *A. barbata* buffered the sensitivity of ANPP to drought, but also curtailed the maximum potential ANPP relative to functionally diverse communities. Overall we found that early-season and consistent drought decreased ANPP (Fig. 3a, b; a response driven by the functionally diverse community), whereas late-season drought shortened the growing season via earlier senescence (Fig. 3d-f, a response especially strong in the *A. barbata* dominated community). As both frequency and intensity of drought is predicted in the future (IPCC 2013), our results highlight that predicting ANPP responses will require characterizing the plant community and understanding the mechanisms that govern its response to precipitation.

We expected that drought timing – in particular early-season drought – would drive shifts in community composition. Instead, we found two distinct community clusters present at our site that were not grouped by drought treatment: 1) a dynamic, 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. The two community types differed in their drought sensitivity, such that the functionally diverse cluster shifted in community composition by drought treatment (e.g. long vectors, Fig 1c), especially in the late drought treatment, which had a significantly higher abundance of forbs. The *A. barbata* dominated community had little

compositional change over time or in response to treatments (e.g. short vectors, Fig 1c). All clusters were mostly stable through time and by the end of our study, three functionally diverse plots had become *A. barbata* dominated, while only one *A. barbata* dominated plot had moved into the functionally diverse cluster (Fig. 1a).

While community composition was measured after drought treatments had been applied for one growing season, we expect that the two community clusters were not a product of the drought treatment, but rather, appeared to reflect community starting conditions as clusters were distributed across all treatments. These initial differences in composition, especially in the *A. barbata* dominated community, may be due to trait selection under drying climate conditions (Sandel et al., 2010), or different responses to disturbance or grazing history at the site (HilleRisLambers et al., 2010; Seabloom et al., 2003). Such patterns of dominant *A. barbata* patches could also be due to strong feedbacks (e.g. forming a litter layer or soil microbial feedbacks) that help non-native grasses establish large monodominant patches in these systems (Hillebrand et al., 2008; Lamb, 2008). How these patches respond to different precipitation scenarios, especially over time, may determine regional community composition via metacommunity source-sink dynamics (Hillebrand et al., 2008). Furthermore, the sensitivity of ANPP to precipitation variability, including drought, 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). 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 has been found in this system (Pitt and Heady 1978, Hallett et al. 2017, 2019). We found that the underlying, or

starting, plant community and its respective dynamics determined the sensitivity of ANPP to intra-annual precipitation timing. Comparing the two clusters, ANPP was more stable in the *A. barbata* dominated community, but maximum production was reached in the functionally diverse community under control precipitation (Fig 3). While the functionally diverse community was dynamic over time in its response to drought treatments, these shifts in composition (corresponding to increasing forb abundance) only acted as a stabilizing mechanism for maintaining ANPP levels in the late drought (Fig. 4a and Fig. 3b). Without shifts in functional composition, we found large swings in ANPP where consistent and early-season drought had much lower production than control for the functionally diverse cluster (Fig. 3b). In contrast, we found that *A. barbata* dominated communities had no changes in composition and produced consistent ANPP regardless of drought treatment (Fig. 3c). 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). Alternatively, the dominant species could be 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.

We hypothesized that the late-season drought would be a stronger driver of ANPP than an early-season drought in California grasslands, because the majority of plant growth occurs at this time (i.e. spring). However, we found that occurrence of early-season drought had a negative

effect on ANPP in functionally diverse communities, in particular (Fig. 3a and 3b). The strong relationship between early-season drought and ANPP suggests that drought limits growth investments early in the season, curtailing species' abilities to maximize ANPP (Chelli et al., 2016; Jongen et al., 2019; Murphy, 1970). Our results mirror other studies in Mediterranean ecosystems that have found that early rain is key to green-up (Esch et al., 2019) and that early drought decreases total biomass, potentially 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 ANPP may be amplified by its effect on community composition, as high 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 for known plant communities in advance based on early-season precipitation.

Drought timing was also 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 drove senescence approximately 2-3 weeks earlier than other drought 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

(Ratcliff and Heady 1962). As such, species tradeoffs across precipitation regimes depend on the *in situ* community and our results indicate that functionally diverse communities were composed of species with varied phenological responses to any given drought scenario. Consequently, species phenological shifts 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, despite shifting intra-annual patterns under climate change. Our study demonstrates that intra-annual precipitation patterns, in particular the variability and timing of 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 drought seasonality under future climate change. Here we address a few drought scenarios in a three-year experiment, but it is uncertain how communities will respond to increasingly large shifts in intra-annual precipitation over the long term. Communities dominated by a single species, such as *A. barbata*, may not be able to maintain a stable ANPP in response to increasingly large variability over time. In the long term, it is possible that

functionally diverse communities might better compensate for shifting intra-annual precipitation despite large swings in ANPP by shifting their phenology and functional groups. Here, 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

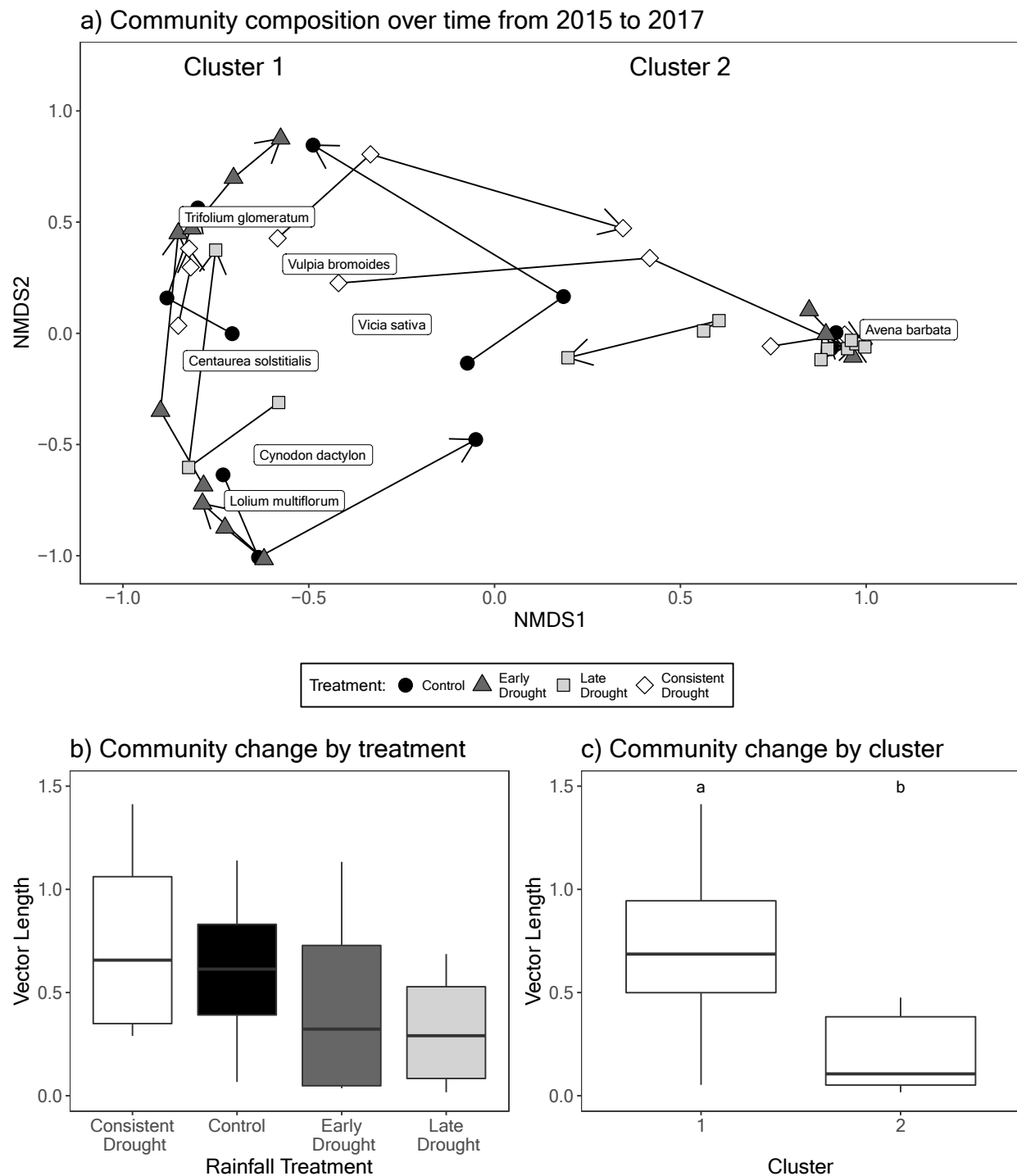
Figure 1. Panel showing a) NMDS ordination of communities by treatment with directional vectors for change in community composition for each plot from 2015-2017. The results of cluster analysis of these communities identified two clusters, which are indicated by a hull plotted around each cluster. Indicator 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) precipitation treatment, and c) cluster membership. Different letters denote significant differences.

Figure 2. Community characteristics of each cluster: a) Functional diversity, measured as Rao's quadratic entropy, of communities within each cluster; b) the productivity of forb and N-fixers by cluster; and c) the percent cover of *A. barbata* within each cluster. Different letters denote significant differences between clusters.

Figure 3. Effects of precipitation treatments on ANPP (a-c) and plant senescence (d-e) across all years (a) for all treatments; and the effects of precipitation treatments on ANPP within community clusters for (b) the functionally diverse cluster, and (c) the *A. barbata* dominated cluster. Significant differences between treatments are denoted with different letters within each cluster. Differences in ANPP by year are shown in Figure S1b. The effects of precipitation treatments on plant senescence, measured as percent greenness as plants senesce at the end of the growing season, (d) for all treatments; and the effects of precipitation treatments on plant senescence within community clusters for (e) the functionally diverse community, and (f) the *A. barbata* dominated community. Here 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).

Figure 4. Mean percent cover (\pm standard error) of functional groups (grass and forb) by treatment for a) the functionally diverse cluster and b) the *A. barbata* dominated cluster.

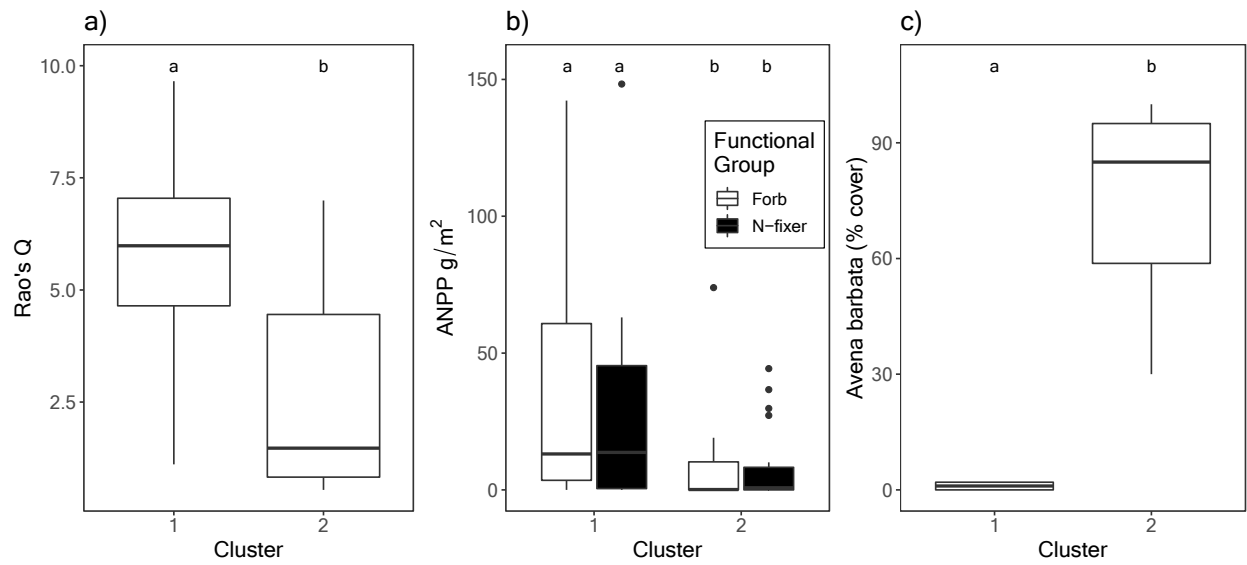
649 Figure 1



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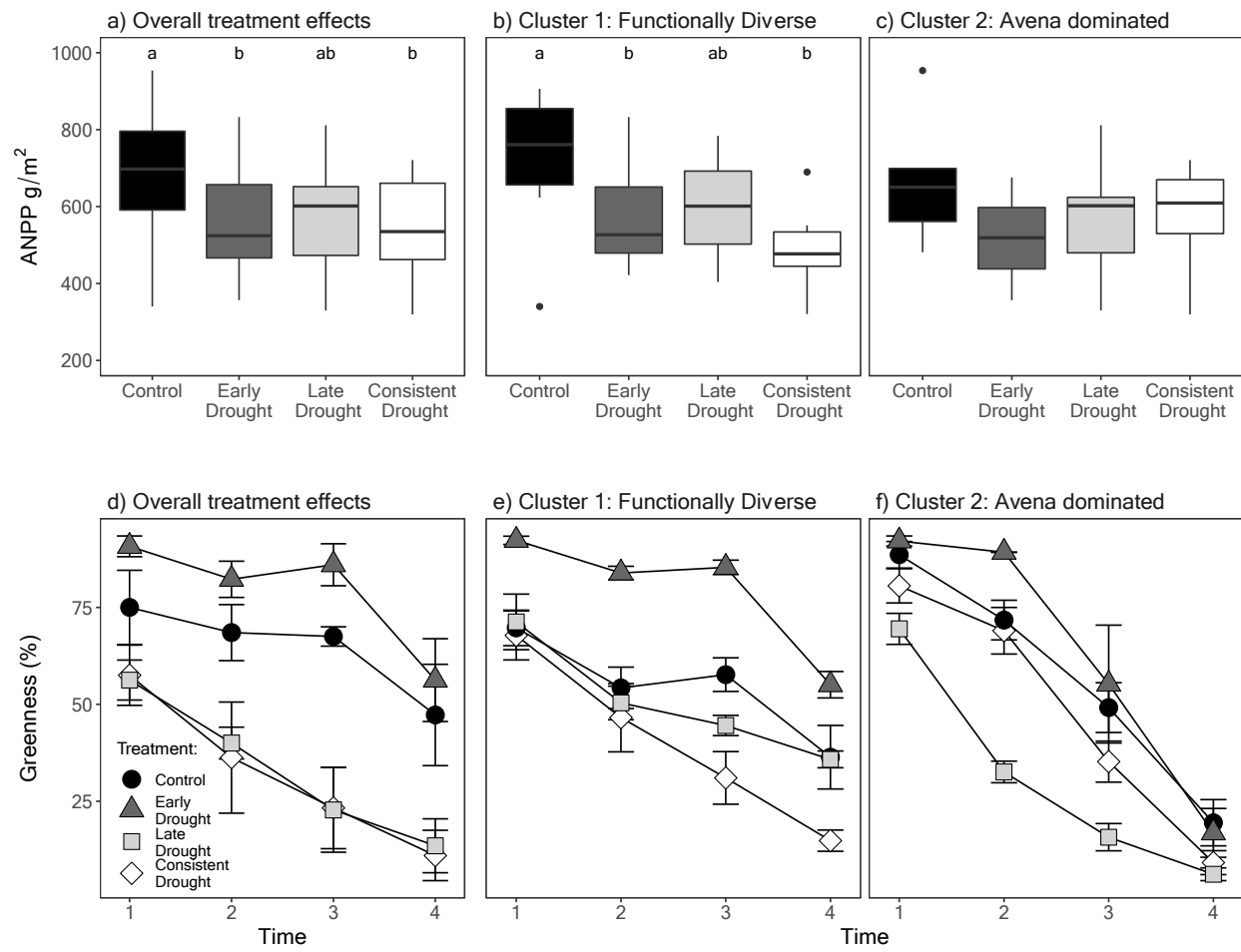
652 Figure 2



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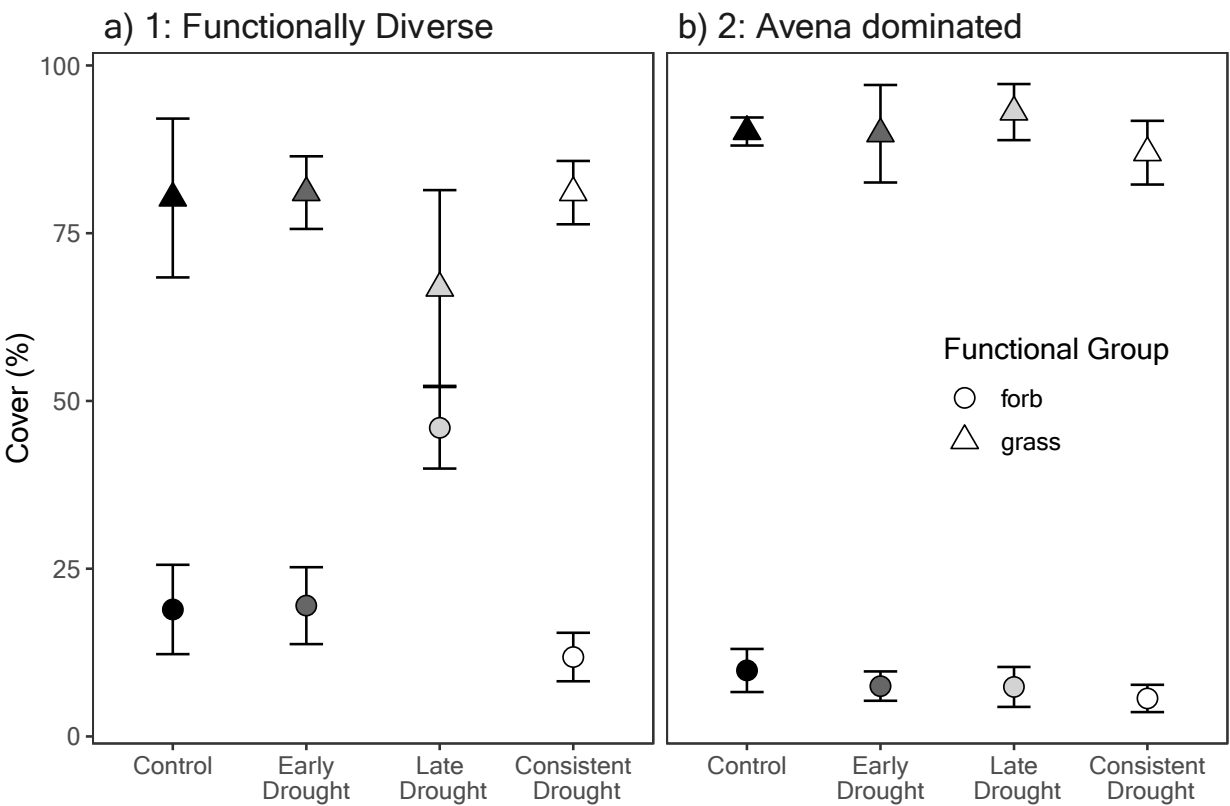
655 Figure 3



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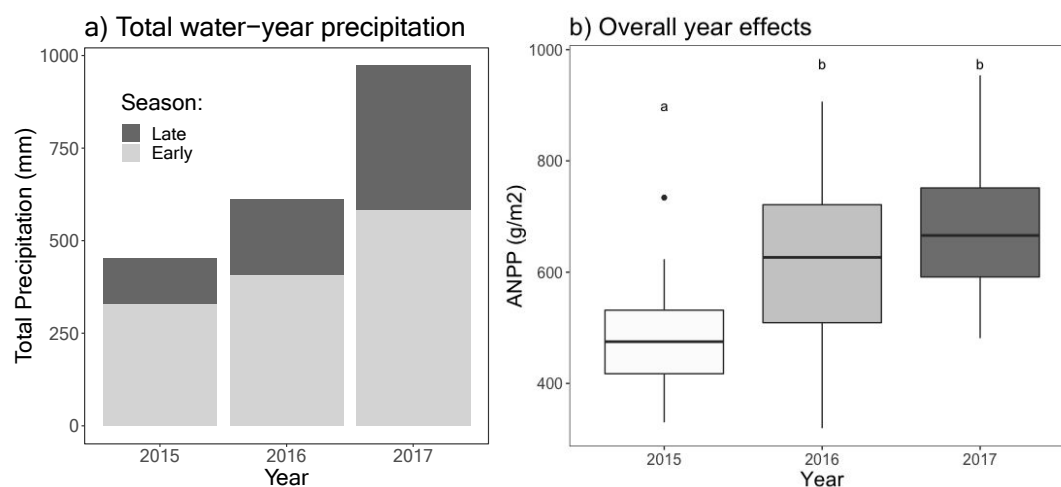
658 Figure 4



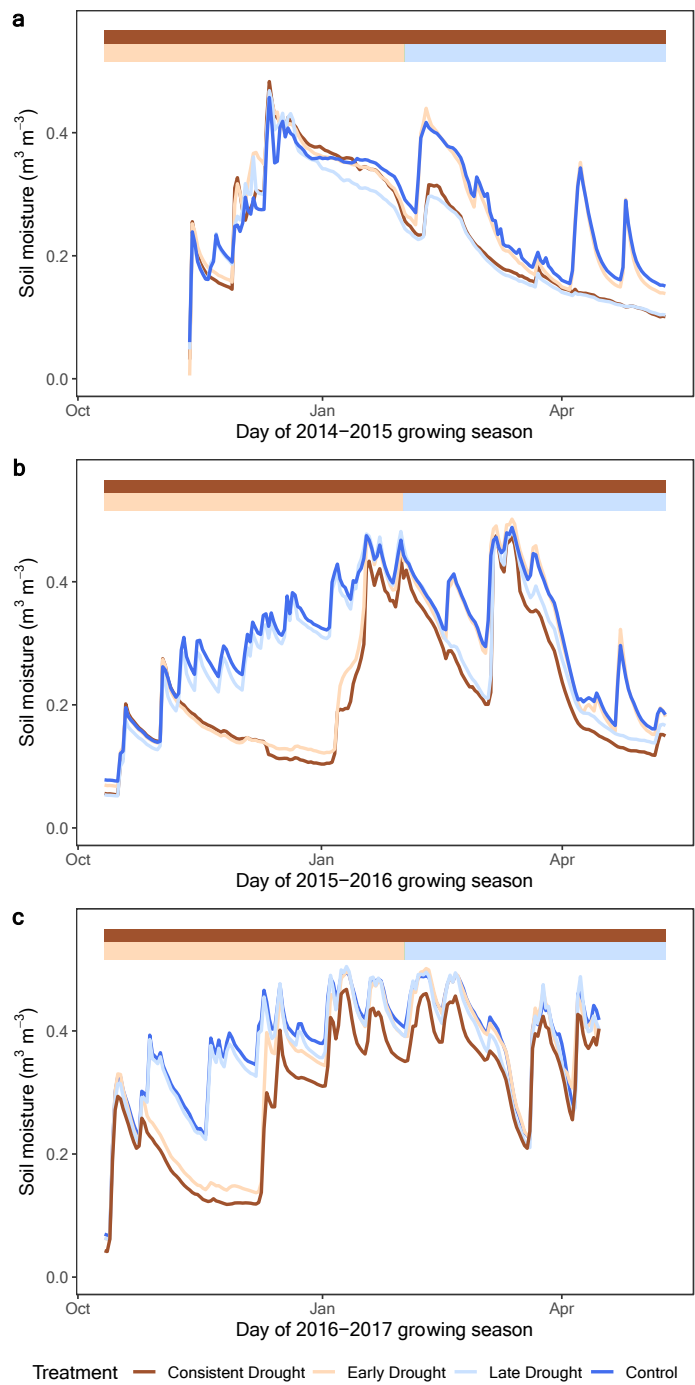
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1 Supplementary Tables and Figures



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.



9

Treatment — Consistent Drought — Early Drought — Late Drought — Control

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Figure S2. Volumetric soil moisture by treatment over time for a) water year 2015, b) water year

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2016, and c) water year 2017. Colored bars in show time periods consistent, early, and late

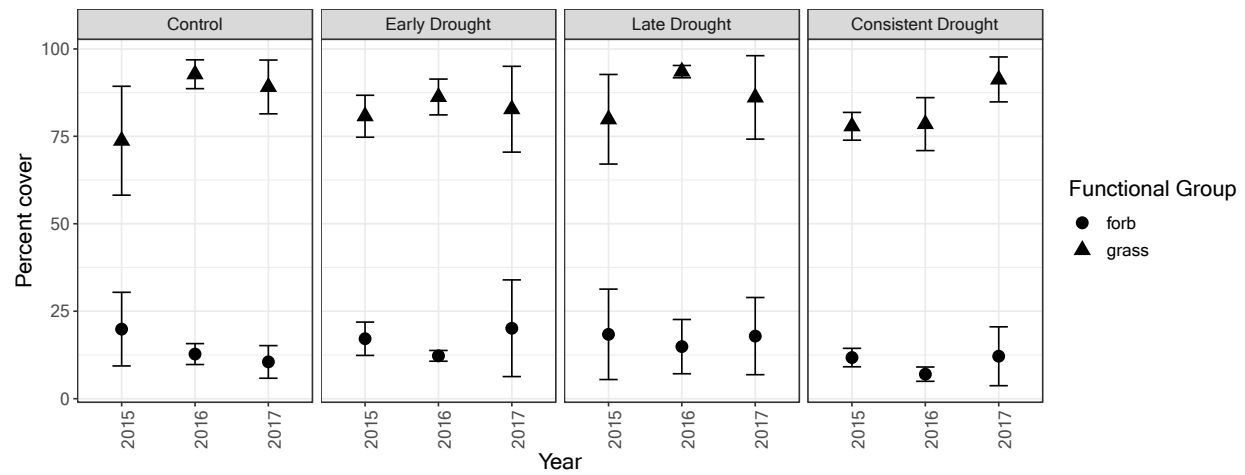
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drought treatments, matching colors shown in the figure legend. Control received all ambient

13

precipitation shown in Figure S1.

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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

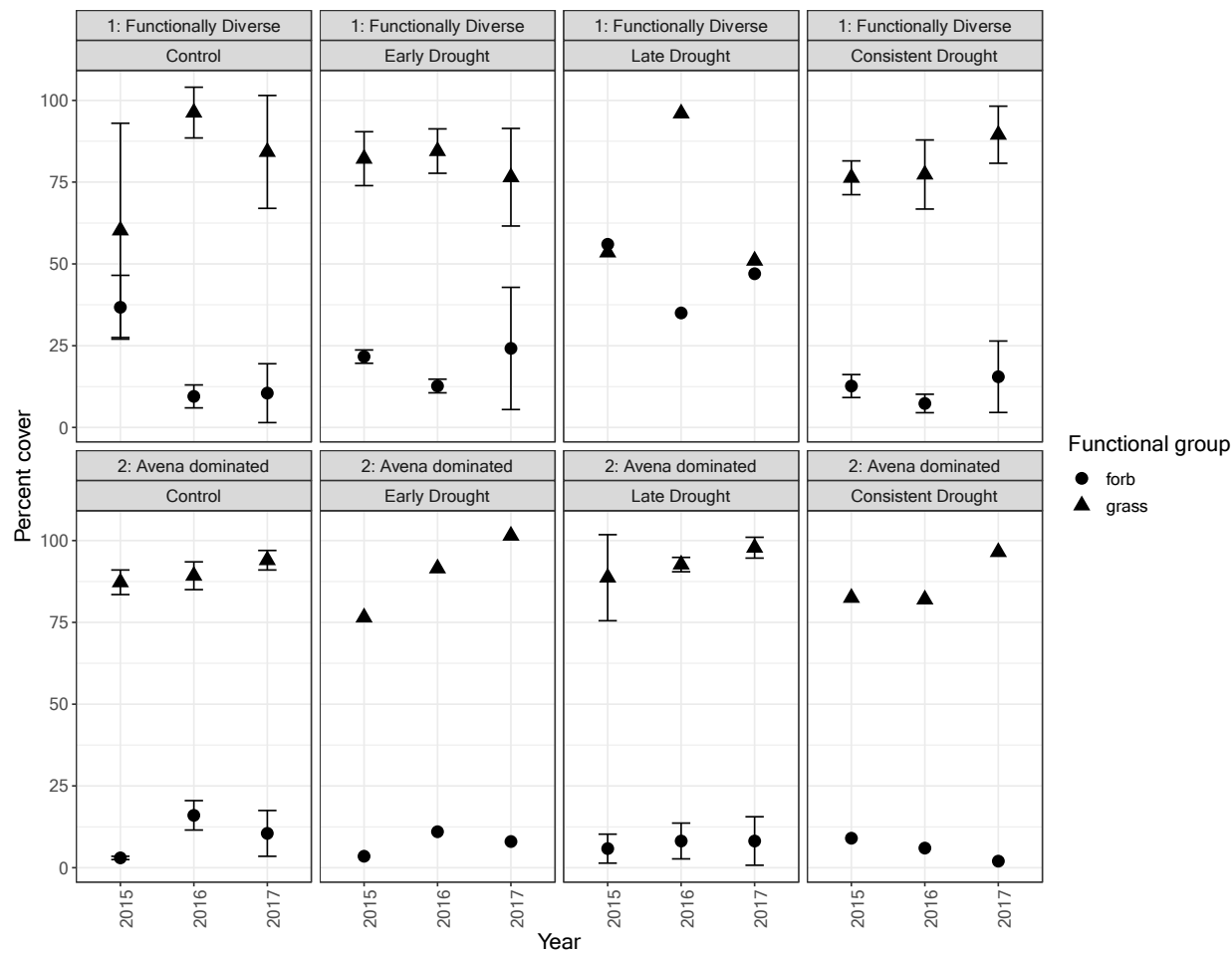


Figure S4. Mean percent cover (\pm standard error) of forb and grasses by cluster, treatment, and year. Cluster 1 is the functionally diverse and Cluster 2 is the *A. barbata* dominated cluster.

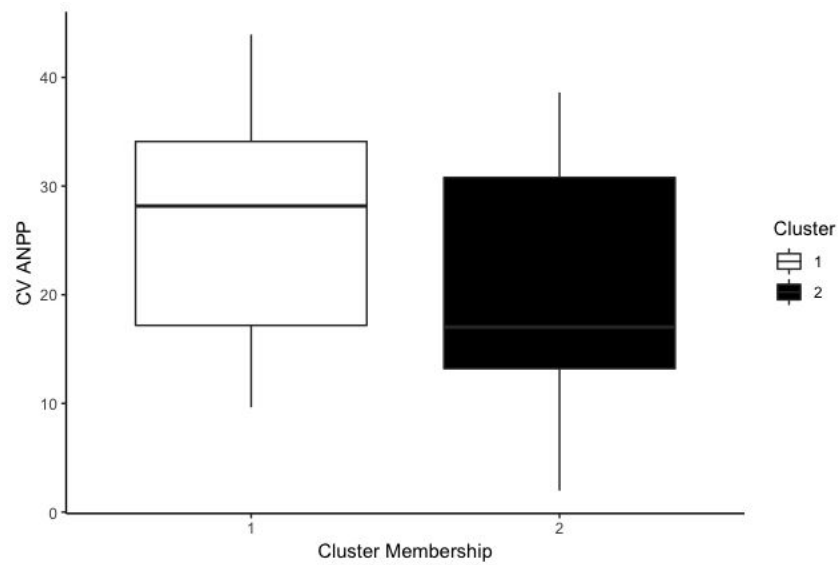


Figure S5. Coefficient of variation in ANPP by cluster membership. Cluster 1 is the functionally diverse and Cluster 2 is the *A. barbata* dominated cluster.

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 ²	Pseudo-F	P
a)						
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)						
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
a) ANPP			
Treatment	3,29	4.10	0.02
Cluster	1,29	0.06	0.81
Treatment*Cluster	3,29	0.21	0.89
b) Rao's Q			
Treatment	3,29	1.54	0.22
Cluster	1,29	26.09	<0.001
Treatment*Cluster	3,29	0.21	0.89
c) <i>A. barbata</i>			
Treatment	3,29	7.73	<0.001
Cluster	1,29	107.78	<0.001
Treatment*Cluster	3,29	2.34	0.09
d) Grass			
Treatment	3,29	3.86	0.02
Cluster	1,29	1.98	0.17
Treatment*Cluster	3,29	0.10	0.96
f) Forb			
Treatment	3,29	0.39	0.78
Cluster	1,29	9.86	0.004
Treatment*Cluster	3,29	2.16	0.11
g) N-fixer			
Treatment	3,29	8.40	<0.001
Cluster	1,29	6.90	0.01
Treatment*Cluster	3,29	0.45	0.72

