**State-Transition Manuscript**

**Title:** Will add

**Abstract:** Will add

**Rough Outline of Key Points:**

**Introduction**

1. Climate change is expected to be an important driver of ecosystem structure + functions
2. We know that events like drought can impact stress individual plants, but it’s hard to often predict how these stresses impact the relative abundance of different species.
3. This is largely because community change is complicated – there are a bunch of different species and their abundances are the function of a complex network of biotic interactions.
4. To help make sense of this complexity, we usually simplify species into a set of constituent groups that share similar responses.
5. These groups are valuable, but can perform poorly under climate change. We should test how well these groups function + re-evaluate them to get a better sense of community dynamics.
6. California grasslands are a great system to test this in – communities are diverse, functionally varied, and we have a strong set of group predictions that we can test. Moreover, we know that climate is a strong driver of community composition in this system.
7. California experienced a severe drought between 2011 – 2016 – how did this impact species composition? Do our prior groups do a good job of describing major changes in vegetation? What do the emergent patterns of vegetation change suggest about key processes in this system?

**Methods**

1. Basic study set-up and methods
2. Why SPEI to capture precipitation change
3. Why cluster vs. keep track of each species
4. How clusters are used to characterize vegetation change

**Results**

1. Communities were highly dynamic, but could be pretty well described by a number of core vegetation groups
   1. However, we found 4 groups instead of the expected three.
2. Community composition flipped between groups quite a bit, which was influenced by key factors – state identity, initial seeding composition, and climate
3. Fitting a multi-state model showed a variety of interesting patterns. Certain state transitions were more likely than others, and a number of transitions showed different affinities to drought stress.

**Discussion**

1. Species and community responses to novel climate conditions
   1. While classic models of California grasslands have depicted a three-state system, we found evidence for four states.
   2. This is likely due to the unique context of our observations – the intense drought was far more significant than anything on record. While the three state description may work under most conditions, drought may have crossed previously unobserved stress thresholds or had unique influence on species interactions.
   3. This is known to be the case in many other global change studies. Emergent complexity is important.
   4. We should continue to re-evaluate our approaches to understanding species dynamics, as they may not hold under novel conditions.
2. Community transitions and response to drought
   1. A central to challenge to understanding community responses to drought is to determine how different drivers control composition, and which of these are likely to change under drought.
   2. Our observations illustrated a number of key vegetation transitions, some of which showed sensitivity to drought. These transitions seem to imply different mechanisms of vegetation change, reflected in the characteristics of dominant species in each group.
   3. Long-term studies are critical to determining these sorts of effects; community responses to climate change are complex, and sufficient data is needed to distinguish these patterns.
3. Management implications
   1. Climate change is expected to have a number of detrimental effects related to community composition, but also unique opportunities for management. Understanding these complex dynamics is therefore important.
   2. In our study, we found that species groups tended to exhibit different mechanisms of change – native species tend to be able to persist, increasing in abundance under stressful conditions. Attempts to increase establishment may have long-term consequences.
   3. Invasive species show negative relationships with drought. We can use this information for targeted management.
   4. To better restore and manage communities, attempts to understand community dynamics + the unique climatic niches of different groups are likely useful.

**Introduction**

Across ecosystems, global change is forecast to produce shifts in climate regimes. Changes in average climatic conditions, as well as the frequency and magnitude of extreme events , have been linked to changes in species’ distributions, invasion events, biodiversity loss, and compositional change (IPCC 2014, Smith, Smith and Felton). As systems are increasingly influenced by these novel conditions, the ability to predict changes in the composition of ecological communities is at a premium – the reorganization of species into novel assemblages will require new paradigms for continued conservation and management.

In plant ecosystems, conditions imposed by heatwaves, droughts, and extreme cold may lead to decreased plant growth rate, shifted phenology, or mortality, depending on species tolerances to specific stresses (Parmesan and Hanley 2015). However, community assembly is not only determined by differences in stress tolerance between species, climate-driven changes in community composition are also a function of recruitment dynamics, biotic interactions, and prior system conditions (Gilman et al. 2010, Walther 2010).

Given the complexity of these drivers, analytical approaches to predicting climate-driven changes in composition benefit from attempts to group taxa to simplify community dynamics. Particularly in species-rich systems, predictions of community change are often facilitated by grouping species that share similar responses to specific environmental factors, functional form, or other physiological characteristics (Lavorel et al. 1997, Díaz and Cabido 2001, Suding et al. 2008, Díaz et al. 2013).

Grouping schemes, in turn, are commonly used as the basis for ecosystem management. Resilience-based management frameworks, such as state-transition models (Bestelmeyer et al. 2017), often partition community turnover into a series of discrete vegetation states characterized by different taxa. Management action may be designed to facilitate transition from one state to another, or maintain the persistence of a desirable community type.

Climate change poses a number of challenges to effective species classification and associated management. Impacts of novel climate regimes on species’ stress thresholds and community interactions are likely to reduce the utility of species groups defined under different conditions (Díaz and Cabido 2001, Lavorel et al. 1999). As such, management of novel ecosystems requires approaches that may rapidly update core species groups as new data becomes available. Extreme drought events, for example, may drive distinctions between species responses not observed under historic norms.

In contrast to classic approaches that rely on expert opinion, modern computational tools may rapidly update species groups as new data becomes available. Algorithmic clustering methods have demonstrated utility a test of expert models and assessment of community turnover under novel conditions; in arid and semi-arid grassland systems, quantitative approaches to species classification have been used to characterize vegetation dynamics under species invasion (Bagchi et al. 2012) and varied grazing regimes (Stein et al. 2016).

In Mediterranean systems, long, hot summers with little precipitation act as an important abiotic driver of community assembly**. California grasslands, composed primarily of annual grasses, are highly sensitive to interannual climatic variation (George et al. 1992, Hobbs and Mooney 1995, Hobbs et al. 2007). While California is forecast to experience increases in mean annual temperature, climate projections emphasize shifts in the frequency of midwinter droughts and summer heatwaves (Yoon).**

Climate projections in California emphasize increasing frequency and intensity of drought events (Pierce et al. 2012), though the effects of these stressors on grassland community composition are uncertain.

California grasslands have long been a focal system in the study of **nonequilibrium dynamics in plant communities -- in contrast to more mesic, perennial-dominated systems, California grasslands often fail to exhibit predictable convergence to a single community type due to climate sensitivity, non-hierarchical competitive dynamics (Uricchio et al. 2019), and strong priority effect**s (Young et al. 2014).

Multiple organizing perspectives have been used to partition vegetation into core species groups within this system. Distinctions are often made between species’ origins (native / naturalized / newly invasive), growth form (grass / forb / legume), lifespan (annual / perennial), and phenology (both germination and seed set). **Most frequently, distinctions are made between (1) naturalized exotic annual grasses, (2) native perennial grasses and forbs, and (3) recent annual invasive grasses with later-season phenology than the naturalized annuals. While species groups tend share general life history strategie**s, there is often considerable interspecific variation of certain traits therein.

Past work has established general response patterns between different groups that may be used to predict community-level responses to changing climate regimes (Corbin et al. 2007, Harpole et al. 2007, Abraham et al. 2009). Phenological differences are thought to play a strong role during the growing season. Rapidly germinating, large-seeded exotic annuals outcompete smaller-seeded native and exotic taxa at the seedling stage, though are sensitive to mid-winter breaks in precipitation. Species with more delayed phenology, in contrast, may be better disposed to take advantage of increasingly frequent late-season precipitation, but wilt under prolonged droughts that limit water availability during flowering periods (Pitt and Heady 1978, Reever Morghan et al. 2007).

Species groups also differ in recruitment ability and response to temporal priority. Highly fecund exotic and invasive annual grasses may produce seed densities as high as 200,000 seeds/m2 (Bartolome 1979, Young et al. 1981), while native species are often recruitment-limited (Seabloom et al. 2003). Native perennials are robust competitors once established, however, and may effectively resist invasion by invasive species with similar phenological patterns of water use (Young et al. 2009). Invasive species appear to exhibit positive feedback loops by inhibiting growth of new colonists when assembly order or climatic conditions foster litter deposition.

**Current climate projections emphasize increased duration and intensity of drought events in California which may act as critical tipping points in grassland ecosystems (Shaw et al. 2009, Pierce et al. 2012, Prugh et al. 2018**). To maintain system resilience in coming decades, land managers have increasingly emphasized certain targets — such as establishment of native species and reduction in invasive species abundance — to promote key ecosystem services. However, it is unclear if prior definitions of core species groups adequately capture vegetation responses under novel conditions, and how multiple drivers interact to control community composition. Will extreme climatic events stymie existing management efforts in this system? Or can severe droughts present an opportunity for targeted treatments?

From 2011-2014, California experienced the driest period in recorded history, producing shifts in species abundances in grassland systems (Prugh et al. 2018). Given the complexity of processes in California annual grasslands, a redefinition species groups in a drought context is likely needed to accurately assess how climate interacts with multiple drivers, such as competitor identity, temporal priority, and recruitment dynamics. Previous research in Meditteranean and semi-arid grasslands has shown that algorithmic partitioning methods may be useful in determining species response groups and major patterns of community change in a novel context (Bagchi et al. 2012, Stein et al. 2016).

Here, we assess interactions between community assembly and climatic variation on vegetation composition in California annual grasslands across a 10-year period encompassing extreme drought and potential recovery. Using data from experimental plantings of three key grassland species groups – naturalized annual, native perennial, and invasive annual grasses — we test key assumptions of grassland community dynamics under extreme drought stress. Specifically, we aim to identify (1) the species groups that best partition compositional change, and (2) how drought interacts with other drivers of vegetation turnover — assembly order and biotic resistance — to affect community composition.

**Materials and Methods:**

**Study site**

Plantings were conducted in research fields at the University of California, Davis (38.545751, -121.784780). Previously used in crop production, these fields were left fallow from 1985 to the start of experimental plantings in 2007. 75% of the experiment is on Reiff series soil (coarse-loamy, mixed, superactive, nonacid, thermic Mollic Xerofluvents); with the rest on Brentwood soil series (fine, smectitic, thermic Typic Haploxerepts) with a 0-2% slope (USDA Web Soil Survey).

In order to minimize the seedbank, in the early fall of 2017, soil was disked, irrigated to stimulate germination of the seedbank, and received a broad-spectrum herbicide (glyphosate), with the irrigation and herbicide treatment repeated twice.

Seeds were planted to establish vegetation treatments were representing commonly used grassland species groups — native perennial grasses and forbs (“native”), naturalized annual grasses and forbs (“naturalized”), and invasive annual grasses (“invasive”; Appendix 1). Each group was planted alone, all together in a 3-group combination, and in all possible 2-group combinations. Plots were 1.5m x 1.5m (2.25 m2), with 1m buffer between plots, and 8 replicates per treatment ( 56 plots total), laid out in a randomized block design. In each plot, a total of 139 grams of seed was added, reflecting an average of 8,000 plants/m2, a typical mature plant density in this system (Heady 1958). For each monotypic community (e.g. native vs. invasive vs. naturalized), an equal proportion of seeds of each species were added. For community mixtures, an equal proportion of community type seed was added (e.g. in invasive + naturalized, 50% invasive, 50% naturalized seed), with equal proportion of individual species within each community type.

From 2008 - 2018, total areal cover of all species was estimated to the nearest 10%. Cover observations for each species were performed in early and late spring to capture the season of maximum percent cover for each species to account for variation in species phenology, and the highest percent cover value for each species was used.

**State Classification**

Prior to vegetation group classification, plant community observations were filtered to those species present within initial seeding mixtures and *Bromus diandrus*, a locally abundant annual grass that self-recruited into the experiment and is an important component of the California grassland type. Despite regular weeding, a number of agricultural weeds occasionally recruited into plots from the seedbank and nearby fields and roadways over the course of our experiment . Due to potential effects of weeding and rare occurrence in California annual grasslands at large, these species were removed from community analysis. The resulting dataset captured 93% of the total vegetation abundance observed over the course of the experiment.

Algorithmic partitioning was used to determine core species groups that correlated in abundance over the course of our study. It is important to note that partitioning is limited to the suite of observations made between 2008 - 2018, capturing *n* = 560 plot:year combinations. This period includes a historic drought (2011-2015) and significantly wet year (2017), so the statistical groupings are contingent upon the climatic regime and starting conditions imposed by experimental design.

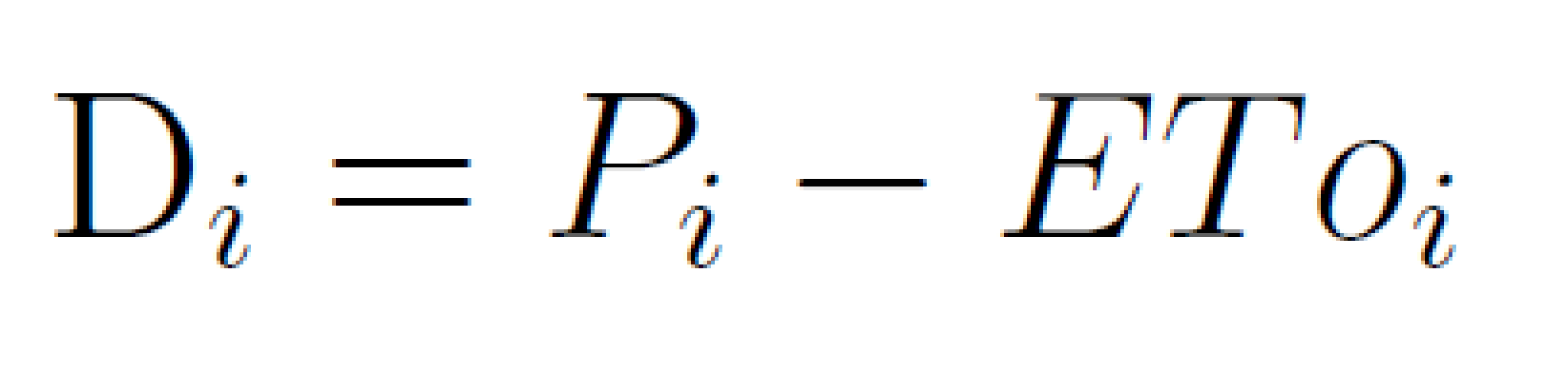
Partitioning was performed using an unsupervised clustering algorithm, K-medoids clustering. K-medoids clustering randomly selects *k* of *n* total datapoints as group “medoids” and computes the sum of distances between points and their associated medioid, based on Bray-Curtis dissimilarity. This algorithm then iteratively swaps medoids and recalculates summed distance to achieve a solution that best captures the total variance of the data. To determine the most appropriate number of states, we applied k-medoids clustering across values of *k* from 2-10. We then subjected the output of each of these runs to a battery of tests—Hartigan, CH, Beale, KL, Cindex, DB, Silhouette, and Duda indices (Charrad et al. 2014). The value of *k* with the best performance across all tests was chosen as the number of clusters that best represented discrete partitions within this dataset.

Following the partition of states, we then conducted indicator species analysis to establish which species are associated with each state. Indicator species analysis was performed using 9999 random permutations of state assignments to quantify statistical significance.

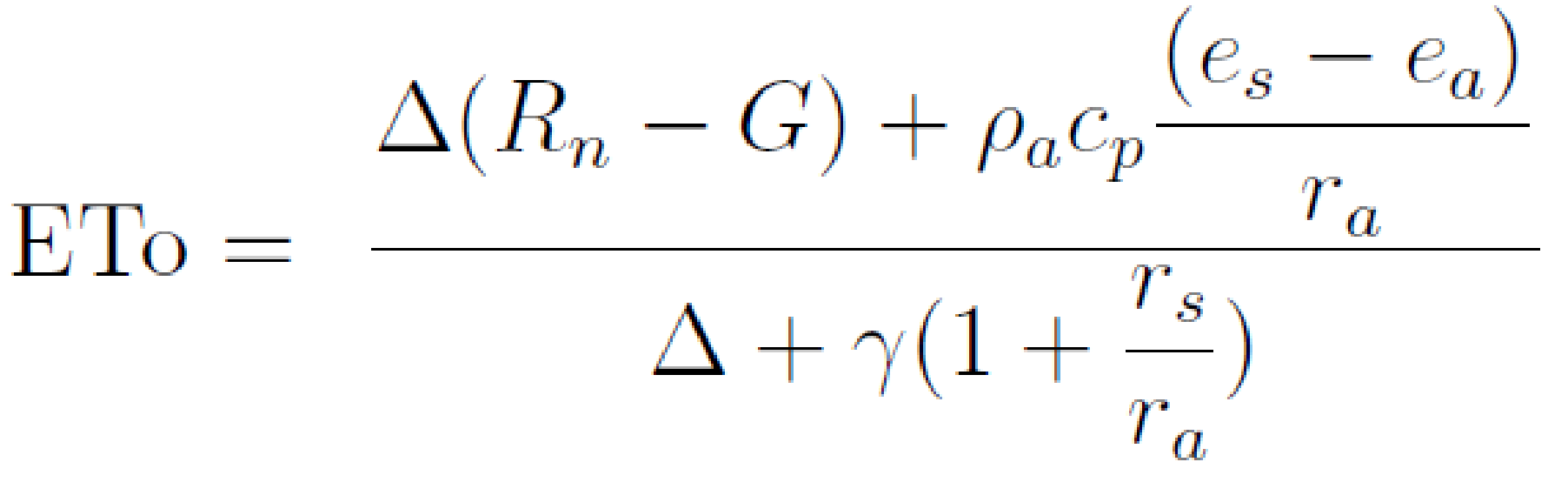
**Weather data**

Climatic variation has been shown to change dominant vegetation groups in California annual grasslands. To contextualize drought stress observed during our experiment, we quantified precipitation and evapotransporation using data provided by a local California Irrigation Management Information System (CIMIS) monitoring station in Davis, CA (38.535694, -121.777636). CIMIS automated dataloggers collect weather data on a minute-by-minute basis, including air temperature, soil temperature, precipitation, solar radiation, vapor pressure, and wind speed. We aggregated these data into monthly intervals, where we calculated Standardized Precipitation-Evapotranspiration Index (SPEI), a metric that can be used to quantify the magnitude of drought stress relative to historic norms (Slette et al. 2019).

Drought stress (*D*) at a given timepoint, *i*:



Where *Pi*represents observed precipitation and *EToi*represents estimated evapotransporation. *ETo* was calculated using the Penman-Monteith equation, defined as:



Where *Rn* is net radiation, *G* is soil heat flux, *(es – ea)* isthe vapor pressure deficit of air, *ρi* is the mean air density at constant pressure, *cp* is the specific heat of air, Δ is the slope of the saturation vapor pressure temperature relationship, γ is the psychometric constant, and *rs*and *ra* are the surface and aerodynamic resistances (FAO). SPEI offers flexible, variable timescale estimations of drought stress that can be used to quantify the effects of multi-year climate patterns (Vicente-Serrano et al. 2010).

Context for our observed climatic conditions was provided by comparison with prior climate patterns. We calculated SPEI for a 35-year span between 2018 and 1983, the first year sufficient climate data was collected. To account for potential temporal lag in the effects of climate variation on grassland species abundance (Sala et al. 2012, Dudney et al. 2017), we created drought indices across several cumulative water year durations. For each year, we calculated SPEI for a single water year (October – May; 8 months), two consecutive water years (20 months), and three consecutive water years (32 months). We then standardized these values by fitting the drought index series to a log-logistic distribution, wherein scaled drought indices reflect long-term norms in drought stress(0), extreme droughts (<-2) and significant water surplus(>+2).

**Construction of Multistate Models**

To quantify the probability of vegetation transitions between different states, we fit a multistate model (syn. Markov model) to panel data generated by tracking vegetation cluster assignments over time. Multistate models represent systems where subjects transition between a set of discrete classes over time and well-suited to expressing state-transition model concepts in a statistical framework.

In multi-state models, transition probabilities between states are modelled as a transition matrix. To explore transitions between states previously identified in clustering, we fit a transition matrix consisting of all possible transition directions, resulting in a base model of (*K-1) \* K*estimated parameters, where *K* is equal to the number of states.

In addition to a baseline model, we fit 7 candidate models that included the influence of planting composition (temporal priority effects) and climate (SPEI) on estimated transition probabilities. Temporal priority was defined as a 1/0 indicator variable of whether indicator species of a given state were a component of the seeded species mixture. We considered SPEI values generated from 1-, 2-, and 3-year cumulative drought stress indices. AIC scores were used to compare the relative fit of all potential candidate models. We selected the model with the lowest AIC score as our best fit model.

All analyses were conducted in R version 3.06 (R Development Core Team). SPEI calculations were performed with “SPEI” (Beguirea and Vicente-Serrano 2017). Clustering and diagnostics were generated using “cluster” (Maechler et al. 2019) and “nbclust” (Charrad et al. 2014). Community analyses were performed using “vegan” (Oksanen et al. 2019). Multistate model fitting and model selection was performed using the “msm” package.(Jackson 2011)

**Results**

In the first year of observation (2008), plant communities were highly segregated as a function of seeded species mixture (PERMANOVA, pseudo-F6, 49 = 32.815, P < 0.001; Appendix 2). Pairwise contrasts of community dissimilarity indicate a clear hierarchy in vegetation group establishment following seeding -- all planting mixtures containing the “naturalized annuals” group were similar in their species composition, as were mixtures composed of “invasive grasses” and “invasive grasses + native species”. The single-group “Native species” planting composition was also segregated from others.

*Partitioning vegetation into discrete states*

As expected in a California annual grassland system, community composition observed between 2008 - 2018 was highly dynamic. On average, a plot compared between two consecutive years shared roughly 50% of species’ relative abundances (mean Bray-Curtis dissimilarity = 0.52 +/- 0.01 standard error). Despite highly dynamic patterns of community turnover, clustering captured a substantial proportion of total compositional variation (Pseudo-R2 = 0.39*;* Figure 1).

Contrary to classic approaches in California grasslands that classify vegetation in three discrete types (as included in our experimental design) partitioning community variance into vegetation states indicated that vegetation was best characterized by 4 discrete clusters. Indicator species analysis of these assignments demonstrated that 2 of 4 vegetation states largely followed established conceptions of vegetation types within this system (Table 1). State 1*,* (hereafter, “Native Perennials”)was characterized by a group of native perennial grasses, while State 3(“Invasive Annuals”)was composed of the two planted invasive annual species. However, State 2 (“Transient Annuals”) and State 4(“Resistant Annuals”)reflected the partitioning of the “Naturalized Annual” group into two separate types. This division appears likely to be a function of the unique environmental context of our study, wherein extreme events may restructure pre-existing notions of species response groups.

Cluster assignments reflected consistent patterns in community composition; assignments reflected a 75% relative abundance of associated indicator species, on average. Fewer than one tenth of cluster assignments had indicator species relative abundances of less than 40%. Relative abundance of species by vegetation group is presented in Appendix 4.

*Frequency of state assignments over time*

Shifts in the frequency of state assignments over time reflected key processes structuring plant communities in California grasslands (Figure 2). Certain vegetation groups, such as Native Perennials, appeared roughly consistent in their relative frequency over time, while others, such as Invasive Annuals and Resilient Annuals, exhibit strong correlations with climate patterns.

Further inspection of individual plot assignments over time showed that transitions between vegetation states were common across all seeded species groups (mean number of transitions = 3.73 +/- 0.16 standard error). However, the frequency of transition events -- summarized in a contingency table (Table 3) -- varied both as a function of a plot’s prior state assignment and the direction of change (Plot-level state assignments presented in Appendix 1).

*Model selection*

To quantify potential drivers of state turnover, we fit 8 candidate multi-state models including a null model assuming constant transition probabilities between states, and models including the cumulative effect of drought stress (SPEI) in 1-3 year intervals and the influence of seeding composition. Comparison of model AIC scores indicated that best fit models included both the influence of initial seeding composition and climate variation (Table 4). While both 1-year and 3-year cumulative drought stress models provided comparable fits, here we present results from the former due to lower AIC score and greater parsimony. Chi-squared goodness of fit test of observed and expected state frequencies showed no significant deviations from model assumptions ( = 12, *p* > 0.20).

*State Transitions*

Multi-state modeling demonstrated a series of core patterns responsible for the observed frequencies of species groups over time. However, implied mechanisms of turnover — drought response, invasion resistance, and recruitment limitation — differed significantly between species groups.

As would be expected, with the data spanning a pre- during and post-drought period, the annuals which declined during drought(State 2) were the least persistent species group during our observations. Plots given this assignment were estimated to have a 58% probability to retain this same assignment in a subsequent year (95% CI = 0.48 - 0.65; Table 5, Figure 3). Despite a lack of persistence, these species were capable of dominating vegetation following seeding. All plots containing naturalized annual species in seeding mixtures assumed this state in the first year of observation, comprising 32 of 56 plots. However, by the 5th year of sampling (2012) all of these plots experienced at least one assignment transition.

Following the short term predominance of the Transient Annual state, a majority of plots were defined by the remaining three states: *Invasive Annual* (State 3), *Native Perennial* (State 1), and *Resistant Annual* (State 4). These states were all found to be more persistent during our study, with estimated persistence ranging between 74% and 84% under average drought stress (SPEI = 0) (Table 5, Figure 3). The abundance of these three states during the majority of our observations suggests that these species are core elements of long-term vegetation change under drought and normal climatic conditions, barring the influence of other factors, such as disturbance. However, the ways in which model covariates affected transition probability and direction demonstrated distinct response patterns in these three groups.

The pronounced increase in *Invasive Annual* state frequency seen during the first 4 years of the experiment were driven primarily due to transition from the *Transient Annual* group. The high estimated probability of this change was not bidirectional or strongly affected by drought stress, indicating the presence of invasion dynamics that lead to Invasive Annual dominance that were not significantly affected by climate conditions. Drought reduced the overall persistence of *Invasive Annuals*, however (Table 5), with negative values of SPEI significantly increased the probability of transition to both Native Perennial and Resistant Annual states..

In contrast, *Resilient Annuals* increased in persistence under drought. Transitions from this state to *Native Perennial* state assignments increased significantly in response to positive values of SPEI. Transitions to other states from *Resilient Annual* communities did not show strong correlations with drought stress, though this may be due to a limited representation of normal precipitation conditions to capture covariate effects when this state was abundant.

Native Perennials exhibited a complicated relationship with both temporal priority and drought stress, reflecting broad environmental tolerances coupled with limited recruitment ability (Table 5, Figure 4). Priority generated by seeding composition positively affected transition probabilities to a Native Perennial state from both Invasive and Resilient Annual communities. These relationships were further compounded by drought stress effects that depended on the identity of a plot’s current assignment; elevated transition rates from Invasive Annual states under drought and Resilient Annual states during elevated precipitation? conditions demonstrated a general resilience of Native Perennial taxa to climatic extremes. However, the relatively low probability of transition when Native Perennials were not represented in the seeding mixture indicates that recruitment limitation strongly controls the relative abundance of these species. Native Perennials may only able to capitalize on extreme events when sufficient seed densities or established individuals are already present. As a result, Native Perennial community frequencies remained roughly constant over the course of the experiment, with no more than 25% of plots given this assignment.

**Discussion**

*Species response groups under climate extremes*

Decomposition of species pools into defined groups based on shared attributes, such as response or functional traits, are widely used to predict community change following environmental perturbation (Lavorel et al. 1999). While effective in capturing key mechanisms of community assembly, these approaches are sensitive to the biotic and abiotic context of their underlying observations; accelerating effects of climate change are likely to shift both the mean and variance of climatic conditions experienced by many ecosystems, potentially restructuring the core species groups needed to capture community responses.

In our study, patterns of community turnover during an extreme multi-year drought were best captured by four distinct species groups, as compared to expert models often describing a three-state system in California annual grasslands under more typical annual precipitation variations. Two identified species groups – dominated by native species and invasive annual grasses – largely followed the divisions made in initial seeding compositions and classic state-transition models of California annual grasslands. However, we found evidence to partition naturalized annual species into two separate vegetation groups.

This unique partitioning likely arose due to the unique conditions of our experimental study, defined by a historic drought. While classic species group definitions have proven useful under climatic norms, novel environmental contexts may drive distinctions between species with historically similar responses.

In our study, drought operates on existing trait variation present among naturalized annual species. *Avena fatua* and *Bromus diandrus*, primary constituents of the *Resistant Annual* state, are observed to have different positions along the leaf economic spectrum relative to other annual grasses such as *Bromus hordeacous* and *Lolium perenne*, key indicator species of the *Transient Annual* state (Sandel and Low 2019). Increased leaf thickness is observed to generally correlate with drought resistance (Poorter et al. 2009) and may predict vegetation responses in Mediterranean systems (Pérez-Ramos et al. 2012); however, plants exhibit varied functional strategies to cope with drought, and relationships between traits and drought tolerance are often complex (Fernández and Reynolds 2000).

Across ecosystems, novel environmental conditions are expected to produce outcomes that deviate from long-term observations. Shifting climatic means and variances have been observed to restructure dominance relationships in grassland systems (Kardol et al. 2010), differentially shift species phenology (Zavaleta et al. 2003), and generally produce complex relationships with drivers of ecosystem properties. In California annual grasslands, for example, productivity under simulated global change has been found to exhibit a unimodal response to precipitation, though this relationship varied with nitrogen availability and CO2 concentration (Zhu et al. 2016).

Critically, the ability to distinguish novel ecosystem responses is dependent on a sufficient range of observed environmental conditions (Lindenmayer et al. 2012). While able to capture the immediate effects of a historic drought on grassland plant communities, the scope of our study is focused on a relatively narrow time period that may be insufficient to capture long-term changes to vegetation dynamics. Continued observation, particularly over a broader range of climatic conditions, may further refine partitions between core species groups and better capture ecosystem recovery to extreme events.

*Contingency in vegetation dynamics*

Climate-driven changes in species composition are often characterized by dependence on a suite of other biotic and abiotic factors. A central challenge in predicting compositional change is to detect which processes respond to global change and contingencies that constrain outcomes (Smith 2011). Our analytical approach was particularly well disposed to capture this complexity, simplifying community variation into transitions between species groups to reflect the effects of community persistence, drought response, and historical contingency. As would be expected in an annual-dominated grassland, over the course of our observations, we detected a number of vegetation transitions, some estimated to exhibit strong correlations with climate, while others appeared to be largely independent of drought stress. In all cases, transition frequencies were linked to the ecological and functional characteristics of dominant species in each vegetation group.

Initial, frequent unidirectional transitions from *Transient Annual* to *Invasive Annual* states showed little estimated relationship with drought stress, instead supporting observations of invasion mechanisms in California grasslands. Species in the *Invasive Annual* group, *A. triuncialis* and *E. caput-medusae*, exhibit density-dependent litter feedbacks that suppress growth of competitors through reduced light competition and slowed nutrient cycling (Drenovsky and Batten 2007, Davies 2008). *Transient Annuals*, while effective colonizers in bare ground, appear unable to compete with invasive species in this context, leading to sustained *Invasive Annual* persistence.

Subsequent transitions from the *Invasive Annual* state appeared to show a significant relationship with climate, when key species characteristics, such as delayed phenology, are thought to prompt severely reduced seed production under drought stress (Young et al. 1998). Species groups observed to respond positively to this effect – *Native Perennials* and *Resilient Annuals* – appeared to rely on separate mechanisms to increase in relative abundance under drought.

In many plots, *Invasive Annual* vegetation transitioned to the *Resistant Annual* state. *A. fatua* and *B. diandrus*,core species defining this state, are observed to exhibit comparatively early phenology in germination and seed set, and may be better predisposed to utilize limited winter precipitation before summer drought (Wainwright et al. 2012).

In plots where natives species were included in initial planting mixtures, however, transitions to the *Native Perennial* state were more common. Robust, stress-tolerant competitors once established, native perennial grasses in California produce are far less fecund than their annual counterparts -- seed limitation is a strong bottleneck to establishment in many contexts, though site-level variation in precipitation, fertility, and land use history may also exhibit strong controls (Seabloom et al. 2003, Orrock et al. 2008). As a result, vegetation changes under drought were contingent on prior patterns of community assembly, where previous native species establishment increases the probability of their future dominance.

Across ecosystems, biotic and abiotic interactions are known to constrain responses to global change (Tylianakis et al. 2008). Particularly in highly dynamic systems, short-duration studies may fail to recognize how these interactions shape community dynamics, as well as their interaction with climatic stress (Suttle et al. 2007, Walther 2010). The benefits of long-term observations are thus two-fold: by capturing community change across a range of biotic contexts and climatic conditions, long-term studies may better capture key contingencies in response, as well as distinguish which mechanisms of community assembly that act independently of climate. In California serpentine grasslands, long-term observations have proven instrumental in understanding compositional relationships with precipitation, disturbance, and invasion (Hobbs et al. 2007).

Such datasets also present unique analytical challenges. In our study, a focus on shifts between vegetation states served as a test of *a priori* species groups in California annual grasslands and characterization of dominant species shifts. Given that dominant species often control many ecosystem properties, such as productivity, this approach may be well-suited to a broad assessment of ecosystem responses to drought (Smith and Knapp 2003, La Pierre et al. 2016). However, methods predisposed to capturing the influence of infrequent species may provide a complementary perspective on the dynamics of subdominants and associated functions.

*Implications for Restoration and Management*

While drought is often linked to a number of negative ecosystem changes, such as reduced biodiversity and invasive species spread, the novel conditions imposed by extreme climatic events may also present opportunities for management (Hobbs et al. 2006, 2009, Seastedt et al. 2008)

The establishment of native perennial grasses is a common restoration target in California annual grasslands, though success is limited and highly contingent on year-to-year variation (Stromberg et al. 2007, Seabloom 2011). Many restoration efforts in this system utilize temporal or spatial priority to manipulate competitive relationships during planting -- such as seeding following removal of competitors or spatially aggregated plantings -- in the hope that early establishment delays or prevents encroachment by less desirable species (Grman and Suding 2010, Wainwright et al. 2012, Young et al. 2017). Particularly for native perennial grasses in California annual grasslands, we found strong evidence that priority seeding can assist in establishing and maintaining a desired community that remains relatively persistent after planting or provide the basis for subsequent dominance when conditions are favorable (Porensky et al. 2012).

In semi-arid systems, where spatial and temporal storage effects act as important mechanisms of species coexistence, attempts to facilitate growth of a desirable species or group are likely to depend on species’ climatic niches. Greater taxonomic and functional diversity in managed systems is likely to reduce periods where few species are adapted, mitigating the risk of invasion or persistent ecosystem state change (Funk et al. 2008).

In turn, management actions can benefit from targeted application during favorable periods. When climate causes transitions between an undesirable group to a desirable one to be more probable, species-specific attempts to facilitate these community shifts are likely to be more effective than a more general application (Funk and Zachary 2010). Our results suggest that invasive species control in this site, for example, may be enhanced during drought years. As the pace of global climate change accelerates, more effective use of limited management resources will benefit from deeper consideration of how dominant species groups fluctuate in response to climatic variation.

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**References:**

Abraham, J. K., J. D. Corbin, and C. M. D’Antonio. 2009. California native and exotic perennial grasses differ in their response to soil nitrogen, exotic annual grass density, and order of emergence. Plant Ecology 201:445–456.

Bagchi, S., D. D. Briske, X. B. Wu, M. P. McClaran, B. T. Bestelmeyer, and M. E. Fernández-Giménez. 2012. Empirical assessment of state-and-transition models with a long-term vegetation record from the Sonoran Desert. Ecological Applications 22:400–411.

Bartolome, J. W. 1979. Germination and seedling establishment in California annual grassland. Journal of Ecology 67:273–281.

Bestelmeyer, B. T., Andrew Ash, J. R. Brown, B. Densambuu, M. Fernández-Giménez, J. Johanson, M. Levi, D. Lopez, R. Peinetti, L. Rumpff, and P. Shaver. 2017. Rangeland Systems. Page Rangeland Systems, processes, Management and challenges.

Corbin, J. D., A. R. Dyer, and E. W. Seabloom. 2007. Competitive Interactions. Page *in* J. D. Corbin, M. R. Stromberg, and C. M. D’Antonio, editors. California Grasslands: Ecology and Management.

Davies, K. W. 2008. Medusahead Dispersal and Establishment in Sagebrush Steppe Plant Communities. Rangeland Ecology & Management 61:110–115.

Díaz, S., and M. Cabido. 2001. Vive la différence: Plant functional diversity matters to ecosystem processes. Trends in Ecology and Evolution 16:646–655.

Díaz, S., A. Purvis, J. H. C. Cornelissen, G. M. Mace, M. J. Donoghue, R. M. Ewers, P. Jordano, and W. D. Pearse. 2013. Functional traits, the phylogeny of function, and ecosystem service vulnerability. Ecology and Evolution 3:2958–2975.

Drenovsky, R. E., and K. M. Batten. 2007. Invasion by Aegilops triuncialis (Barb Goatgrass) Slows Carbon and Nutrient Cycling in a Serpentine Grassland. Biological Invasions 9:107–116.

Dudney, J., L. M. Hallett, L. Larios, E. C. Farrer, and N. Erica. 2017. Lagging behind: Have we overlooked previous-year rainfall effects in annual grasslands? Journal of Ecology 105.

Felton, A. J., and M. D. Smith. 2017. Integrating plant ecological responses to climate extremes from individual to ecosystem levels. Philosophical Transactions of the Royal Society B: Biological Sciences 372.

Fernández, R. J., and J. F. Reynolds. 2000. Potential growth and drought tolerance of eight desert grasses: Lack of a trade-off? Oecologia 123:90–98.

Funk, J. L., E. E. Cleland, K. N. Suding, and E. S. Zavaleta. 2008. Restoration through reassembly: plant traits and invasion resistance. Trends in ecology & evolution 23:695–703.

Funk, J. L., and V. A. Zachary. 2010. Physiological responses to short-term water and light stress in native and invasive plant species in southern California. Biological Invasions 12:1685–1694.

George, M. R., J. R. Brown, and W. J. Clawson. 1992. Application of nonequilibrium ecology to management of Mediterranean grasslands. Journal of Range Management 45:436–440.

Gilman, S. E., M. C. Urban, J. Tewksbury, G. W. Gilchrist, and R. D. Holt. 2010. A framework for community interactions under climate change. Trends in ecology and evolution 25:325–331.

Grman, E., and K. N. Suding. 2010. Within-Year Soil Legacies Contribute to Strong Priority Effects of Exotics on Native California Grassland Communities. Restoration Ecology 18:664–670.

Harpole, W. S., D. L. Potts, and K. N. Suding. 2007. Ecosystem responses to water and nitrogen amendment in a California grassland. Global Change Biology 13:2341–2348.

Hobbs, R. J., S. Arico, J. Aronson, J. S. Baron, P. Bridgewater, V. A. Cramer, P. R. Epstein, J. J. Ewel, C. A. Klink, A. E. Lugo, D. Norton, D. Ojima, D. M. Richardson, E. W. Sanderson, F. Valladares, M. Vila, R. Zamora, and M. Zobel. 2006. Novel ecosystems: theoretical and management aspects of the new ecological world order. Global Ecology and Biogeography 15:1–7.

Hobbs, R. J., E. Higgs, and J. A. Harris. 2009. Novel ecosystems: implications for conservation and restoration. Trends in Ecology and Evolution 24:599–605.

Hobbs, R. J., S. Yates, and H. A. Mooney. 2007. LONG-TERM DATA REVEAL COMPLEX DYNAMICS IN GRASSLAND IN RELATION TO CLIMATE AND DISTURBANCE. Ecological Monographs 77:545–568.

Hobbs, R., and H. Mooney. 1995. Spatial and temporal variability in California annual grassland: results from a long‐term study. Journal of Vegetation Science:43–56.

Kardol, P., C. E. Campany, L. Souza, R. J. Norby, J. F. Weltzin, and A. T. Classen. 2010. Climate change effects on plant biomass alter dominance patterns and community evenness in an experimental old-field ecosystem. Global Change Biology 16:2676–2687.

Lavorel, S., S. McIntyre, J. Landsberg, and T. D. . Forbes. 1997. Plant functional classifications: from general groups to specific groups based on response to disturbance. Trends in Ecology and Evolution 5347.

Lindenmayer, D. B., G. E. Likens, A. Andersen, D. Bowman, C. M. Bull, E. Burns, C. R. Dickman, A. a. Hoffmann, D. a. Keith, M. J. Liddell, A. J. Lowe, D. J. Metcalfe, S. R. Phinn, J. Russell-Smith, N. Thurgate, and G. M. Wardle. 2012. Value of long-term ecological studies. Austral Ecology 37:745–757.

Orrock, J. L., M. S. Witter, and O. J. Reichman. 2008. Apparent Competition With an Exotic Plant Reduces. Ecology 89:1168–1174.

Parmesan, C., and M. E. Hanley. 2015. Plants and climate change: complexities and surprises. Annals of Botany 116:849–864.

Pérez-Ramos, I. M., C. Roumet, P. Cruz, A. Blanchard, P. Autran, and E. Garnier. 2012. Evidence for a “plant community economics spectrum” driven by nutrient and water limitations in a Mediterranean rangeland of southern France. Journal of Ecology 100:1315–1327.

Pierce, D. W., T. Das, D. R. Cayan, E. P. Maurer, N. L. Miller, Y. Bao, M. Kanamitsu, K. Yoshimura, M. a. Snyder, L. C. Sloan, G. Franco, and M. Tyree. 2012. Probabilistic estimates of future changes in California temperature and precipitation using statistical and dynamical downscaling. Climate Dynamics 40:839–856.

La Pierre, K. J., D. M. Blumenthal, C. S. Brown, J. A. Klein, and M. D. Smith. 2016. Drivers of Variation in Aboveground Net Primary Productivity and Plant Community Composition Differ Across a Broad Precipitation Gradient. Ecosystems 19:521–533.

Pitt, M. D., and H. F. Heady. 1978. Responses of annual vegetation to temperature and rainfall patterns in northern California. Ecology Vol. 59:336–350 (article consists of 15 pages).

Poorter, H., Ü. Niinemets, L. Poorter, I. J. Wright, and R. Villar. 2009. Causes and consequences of variation in leaf mass per area (LMA): a meta-analysis. New Phytologist 181:517–531.

Porensky, L. M., K. J. Vaughn, and T. P. Young. 2012. Can initial intraspecific spatial aggregation increase multi-year coexistence by creating temporal priority? Ecological Applications 22:927–936.

Prugh, L. R., N. Deguines, J. B. Grinath, K. N. Suding, W. T. Bean, R. Stafford, and J. S. Brashares. 2018. Ecological winners and losers of extreme drought in California. Nature Climate Change 8:819–824.

Reever Morghan, K. J., J. D. Corbin, and J. D. Gerlach. 2007. Water Relations. Pages 87–93 *in* J. D. Corbin, M. R. Stromberg, and C. M. D’Antonio, editors. California Grasslands: Ecology and Management. First edition. University of California Press, Berkeley and Los Angeles, California.

Sala, O. E., L. A. Gherardi, L. Reichmann, E. Jobbágy, and D. Peters. 2012. Legacies of precipitation fluctuations on primary production: Theory and data synthesis. Philosophical Transactions of the Royal Society B: Biological Sciences 367:3135–3144.

Sandel, B., and R. Low. 2019. Intraspecific trait variation, functional turnover and trait differences among native and exotic grasses along a precipitation gradient. Journal of Vegetation Science 30:633–643.

Seabloom, E. W. 2011. Spatial and temporal variability in propagule limitation of California native grasses. Oikos 120:291–301.

Seabloom, E. W., W. S. Harpole, O. J. Reichman, and D. Tilman. 2003. Invasion, competitive dominance, and resource use by exotic and native California grassland species. Proceedings of the National Academy of Sciences of the United States of America 100:13384–9.

Seastedt, T. R., R. J. Hobbs, and K. N. Suding. 2008. Management of novel ecosystems: Are novel approaches required? Frontiers in Ecology and the Environment 6:547–553.

Shaw, M. R., L. Pendleton, B. Morris, G. Bratman, D. Bachelet, K. Klausmeyer, J. Mackenzie, D. Conklin, E. Haunreiter, and C. Daly. 2009. The Impact of Climate Change on California ’ s Ecosystem Services. Page California Climate Change Center.

Slette, I. J., A. K. Post, M. Awad, T. Even, A. Punzalan, S. Williams, M. D. Smith, and A. K. Knapp. 2019. How ecologists define drought, and why we should do better. Global Change Biology 25:3193–3200.

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

Smith, M. D., and A. K. Knapp. 2003. Dominant species maintain ecosystem function. Ecology Letters 6:509–517.

Stein, C., W. S. Harpole, and K. N. Suding. 2016. Transitions and invasion along a grazing gradient in experimental California grasslands. Ecology 97:2319–2330.

Stromberg, M. R., C. M. D’Antonio, T. P. Young, J. Wirka, and P. Kephart. 2007. California Grassland Restoration. Page *in* M. R. Stromberg, J. D. Corbin, and C. M. D’Antonio, editors. California Grasslands Ecology and Management.

Suding, K. N., S. Lavorel, F. S. Chapin, J. H. C. Cornelissen, S. Díaz, E. Garnier, D. Goldberg, D. U. Hooper, S. T. Jackson, and M. L. Navas. 2008. Scaling environmental change through the community-level: A trait-based response-and-effect framework for plants. Global Change Biology 14:1125–1140.

Suttle, K. B., M. A. Thomsen, and M. E. Power. 2007. Species Interactions Reverse Grassland Responses to Changing Climate. Science 315:640–642.

Tylianakis, J. M., R. K. Didham, J. Bascompte, and D. A. Wardle. 2008. Global change and species interactions in terrestrial ecosystems. Ecology Letters 11:1351–1363.

Uricchio, L. H., S. C. Daws, E. R. Spear, and E. A. Mordecai. 2019. Priority Effects and Nonhierarchical Competition Shape Species Composition in a Complex Grassland Community. The American Naturalist 193:213–226.

Vicente-Serrano, S. M., S. Beguería, and J. I. López-Moreno. 2010. A multiscalar drought index sensitive to global warming: The standardized precipitation evapotranspiration index. Journal of Climate 23:1696–1718.

Wainwright, C. E., E. M. Wolkovich, and E. E. Cleland. 2012. Seasonal priority effects: Implications for invasion and restoration in a semi-arid system. Journal of Applied Ecology 49:234–241.

Walther, G. R. 2010. Community and ecosystem responses to recent climate change. Philosophical Transactions of the Royal Society B: Biological Sciences 365:2019–2024.

Young, J. A., R. A. Evans, C. A. Raguse, and ]. R. Larson. 1981. Germinable Seeds and Periodicity ofGermination in Annual Grasslands. Hilgardia 49:1–37.

Young, J. A., J. D. Trent, R. R. Blank, D. E. Palmquist, J. A. Young, J. D. Trent, and R. R. Blank. 1998. Nitrogen interactions with medusahead (Taeniatherum caput-medusae ssp . asperum ) seedbanks. Weed Science 46:191–195.

Young, S. L., J. N. Barney, G. B. Kyser, T. S. Jones, and J. M. DiTomaso. 2009. Functionally similar species confer greater resistance to invasion: Implications for grassland restoration. Restoration Ecology 17:884–892.

Young, T. P., K. L. Stuble, J. A. Balachowski, and C. M. Werner. 2017. Using priority effects to manipulate competitive relationships in restoration. Restoration Ecology 25:S114–S123.

Young, T. P., E. P. Zefferman, K. J. Vaughn, and S. Fick. 2014. Initial success of native grasses is contingent on multiple interactions among exotic grass competition, temporal priority, rainfall and site effects. AoB PLANTS 7:plu081-plu081.

Zavaleta, E. S., M. R. Shaw, N. R. Chiariello, B. D. Thomas, E. E. Cleland, C. B. Field, and H. a. Mooney. 2003. Grassland responses to three years of elevated temperature, CO 2, precipitation, and N deposition. Ecological Monographs 73:585–604.

Zhu, K., N. R. Chiariello, T. Tobeck, T. Fukami, and C. B. Field. 2016. Nonlinear, interacting responses to climate limit grassland production under global change. Proceedings of the National Academy of Sciences of the United States of America 113:10589–10594.

**R packages and Other Citations**

*Kept separate til citations finalized to not disrupt citation manager plugin*

Wickham, Hadley. *ggplot2: elegant graphics for data analysis*. Springer, 2016.

Jackson, Christopher H. "Multi-state models for panel data: the msm package for R." *Journal of statistical software* 38.8 (2011): 1-29.

Charrad, M., Ghazzali, N., Boiteau, V., Niknafs, A., & Charrad, M. M. (2014). Package ‘nbclust’. *Journal of statistical software*, *61*, 1-36.

Hagberg, A., Swart, P., & S Chult, D. (2008). *Exploring network structure, dynamics, and function using NetworkX* (No. LA-UR-08-05495; LA-UR-08-5495). Los Alamos National Lab.(LANL), Los Alamos, NM (United States).

Pachauri, R. K., Allen, M. R., Barros, V. R., Broome, J., Cramer, W., Christ, R., & Dubash, N. K. (2014). *Climate change 2014: synthesis report. Contribution of Working Groups I, II and III to the fifth assessment report of the Intergovernmental Panel on Climate Change* (p. 151). Ipcc.

Maechler, M., Rousseeuw, P., Struyf, A., Hubert, M., & Hornik, K. (2012). Cluster: cluster analysis basics and extensions. *R package version*, *1*(2), 56.