**State-Transition Manuscript**

**Title:** Drought drives turnover between dominant species groups in California grasslands

**Abstract:** Climate change is forecast to influence plant community composition through shifts in average climatic regimes, climate variability, and increased frequency of extreme events. In arid- and semi-arid grassland systems, climate-driven changes in species abundance are known to depend on prior community configurations, where communities dominated by different species groups may vary in their resistance to compositional change. These contingencies are likely to act as an important driver of vegetation dynamics under climate change; their capture may enhance forecasts of community change and identify targets for active management. In this study, we planted various California grassland plant community types and observed changes in their composition during a ten-year period that included a drought of historic magnitude, followed by one of the wettest years on record. Using algorithmic partitioning methods and multistate modeling, we evaluated both the number of discrete vegetation types that best captured community turnover and the probability of transition between them. We found that compositional variance was best partitioned in 4 discrete groups, distinguishing between two sets of annual grasses often considered as one species group in expert models. Moreover, vegetation states differed in their persistence under variable climate conditions, and often exhibited directional patterns of transition. When native perennials were able to become dominant, they demonstrated strong persistence across a range of environmental conditions, suggesting that native grass restoration can aid in grassland resilience to a changing and more variable climate. Noxious invasive grasses, which are a core target for conservation and rangeland managers, decreased in response to lower rainfall, suggesting that eradication efforts should focus on these years.

**Introduction**

Across ecosystems, climate change forecasts emphasize the increasing frequency of extreme events, in addition to changes in average climatic conditions (IPCC 2014). Changing climatic extremes are observed to be important drivers of compositional dynamics, responsible for shifts in species distributions, invasion events, and biodiversity loss (Smith 2011, Felton and Smith 2017). As ecological communities are increasingly subject to climate patterns outside historical bounds of variation, capturing the effects of unprecedented climatic extremes will be critical to generating new paradigms for conservation and management (Hobbs et al. 2009). However, given the complexity of many factors that control species abundances, these changes are often difficult to predict.

While species may exhibit varied tolerances to conditions imposed by heatwaves, droughts, and extreme cold, climate-driven changes in species relative abundances are also constrained by local interactions that govern community assembly (Tylianakis et al. 2008, Fukami 2015). Compensatory responses to climate change, for example, may be limited by competitors that inhibit growth and colonization (Alexander et al. 2015). At the community scale, these local interactions depend on key emergent properties that vary as a function of community attributes, including species richness, functional diversity, or dominant taxa (Chapin et al. 1997, Emery and Gross 2007). As a result, compositional responses to climatic events are likely to depend on prior community configuration, where the responses of different species assemblages vary in magnitude and direction (Fukami 2015).

These complex interactions between climatic drivers and species assemblages are often summarized through conceptual models that attempt to capture major drivers of ecological change (Galatowitsch, Ogden et al. 2005). Conceptual models in arid- and semi-arid systems often emphasize the importance of contingency in community assembly, where vegetation naturally fluctuates between multiple distinct types. In these systems, applied ecologists often base management action on “state-transition models” that identify the properties of different species groups (“states”) and their likely direction of change under various contexts ("transitions"; Bestelmeyer et al. 2003).

Contingencies in community assembly appear particularly important in capturing climate change effects on arid- and semi-arid systems where vegetation naturally fluctuates between multiple distinct types. In these systems, applied ecologists have long characterized pathways of vegetation turnover by organizing communities into groups made on the basis of correlated abundance, shared functional characteristics, or other physiological traits (Lavorel et al. 1997, Bestelmeyer et al. 2003, Suding and Goldstein 2008). When effective, distillation of community dynamics into variation between different community types captures major gradients of change, simplifying complex dynamics.

Grouping schemes, in turn, often form the basis for ecosystem management. In response to changing climate patterns, managers may use these models to predict which community states are likely to persist under climate extremes or reduce incursion of unfavorable vegetation types. However, novel climatic conditions are expected to complicate their application, as the validity of vegetation groups is limited by both the total species pool and range of compositional drivers considered during their construction (Diaz and Cabido 1997).

As climate change effects continue to mount, management efforts are expected to increasingly rely on models that capture vegetation dynamics under “no-analog” conditions (Williams and Jackson 2007, Hobbs et al. 2009). While classic state-transition models have often been based on expert opinion, challenges associated with management in a novel environment have increased the demand for data-driven approaches (Allen-Diaz and Bartolome 1998, Bartolome et al. 2008). Though still limited by available data, these computational methods may better capture causal mechanisms of change and rapidly update predictions as new information becomes available. In grassland systems, clustering algorithms have shown promise in tests of expert models and in the tracking of community responses to variable grazing regimes and species invasions (e.g. Jackson and Bartolome 2002, Stringham et al. 2003, Bagchi et al. 2012, Stein et al. 2016). However, there appear to be few tests of their application to climate-driven vegetation turnover.

In California, climate change is predicted to produce a 50% increase in the frequency of extreme events by the end of the 21st century (Yoon et al. 2015). California grasslands are expected to be particularly sensitive to climatic extremes, given compositional dynamics defined by a predominantly annual life history, climate sensitivity (Hobbs et al. 2007), non-hierarchical competitive relationships (Uricchio et al. 2019), and strong priority effects (Young et al. 2014). In this system, state-transition models often decompose compositional turnover into variation between three species groups defined by shared life history strategy and history of colonization: (1) naturalized exotic annual grasses and forbs, (2) native perennial grasses and forbs, and (3) recently invasive exotic annual grasses.

Compositional shifts in California grasslands are thought to be governed by differences in fecundity, phenology, and plant-soil feedbacks that characterize these species groups (Corbin et al. 2007). While this functional variation may govern responses to interannual climate variation (Pitt and Heady 1978), communities composed of different dominant species may also exhibit emergent properties that constrain subsequent compositional change. Invasive annual grasses, for example, produce thick litter layers that suppress competitor growth (DiTomaso et al. 2008). These litter feedbacks may enhance invasive grass persistence when future climatic conditions favor other species groups, particularly those that may exhibit limited recruitment capacity, such as native perennial grasses (Seabloom et al. 2003a).

While warming average temperatures in California are forecast to produce increases in the distribution and abundance of annual grasses across the state (Sandel and Dangremond 2012), the effects of changing climate variance are less understood. Recent extreme climatic events, however, may provide insight into future vegetation dynamics. A drought from 2011-2015, which included the driest period in recorded history, was observed to produce significant changes in the composition and diversity of many grassland communities (Harrison et al. 2015, Prugh et al. 2018). Provided variation in community assembly prior to this event, tracking species abundance changes across different vegetation types may effectively characterize the validity of previously defined grouping schemes and the interaction between climatic drivers and the properties of these groups.

In turn, the capture of these contingencies may actively inform ecosystem management. Often focused on the establishment of native species and reduction in invasive species abundances, management of California’s grasslands under novel climatic conditions is likely to benefit from the application of modern computational tools to characterize vegetation change. Quantitative description of community transitions between dominant species groups may supplement largely qualitative models generated during climatic norms. Are certain desirable species groups more resistant to variable climatic conditions than others? Can extreme climatic events provide opportunities for targeted management action?

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. 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 was set 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 previously established seedbank, soil was disked, irrigated to stimulate germination, and sprayed with a broad-spectrum herbicide (glyphosate). Irrigation and herbicide treatments occurred twice in the early fall of 2007.

Seeds were planted to establish vegetation treatments representing commonly used species groups in California’s grasslands — native perennial grasses and forbs (“native”), naturalized annual grasses and forbs (“naturalized”), and invasive annual grasses (“invasive”; Appendix 1). Each group was planted alone, in all possible 2-group combinations, and all together in a 3-group combination. 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 maximum percent cover for each species when varying in phenology. The highest percent cover value in each year for each species was used in analysis.

**State Classification**

Prior to vegetation group classification, plant community observations were filtered to include only 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 (largely *Convolvulus arvensis)* 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), resulting in statistical groupings that are contingent upon the climatic regime and starting conditions imposed in experimental design.

Partitioning was performed using an unsupervised clustering algorithm, K-medoids clustering. The K-medoids algorithm clusters data into *k* unique groups by identifying *k* medoid samples that best partition the total distance-based inertia of all observations. Distance between observations was calculated using Bray-Curtis dissimilarity.

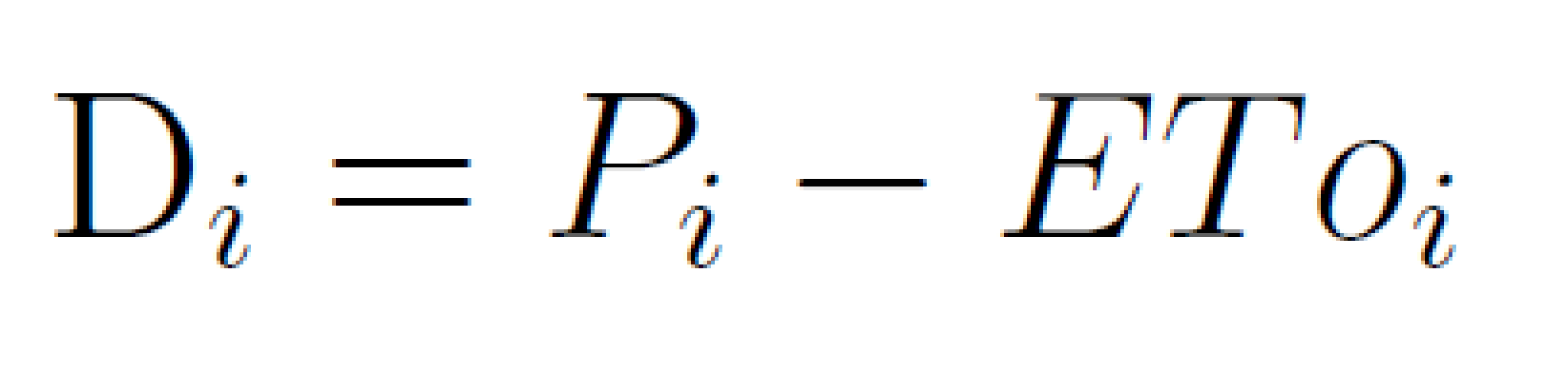
Because the number of relevant clusters in our study was not pre-defined, we applied K-medoids clustering across values of *k* from 2-10, yielding a number of clustering solutions. We then subjected the output of each of these clustering solutions to a battery of tests—Hartigan, CH, Beale, KL, Cindex, 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 vegetation 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. 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).

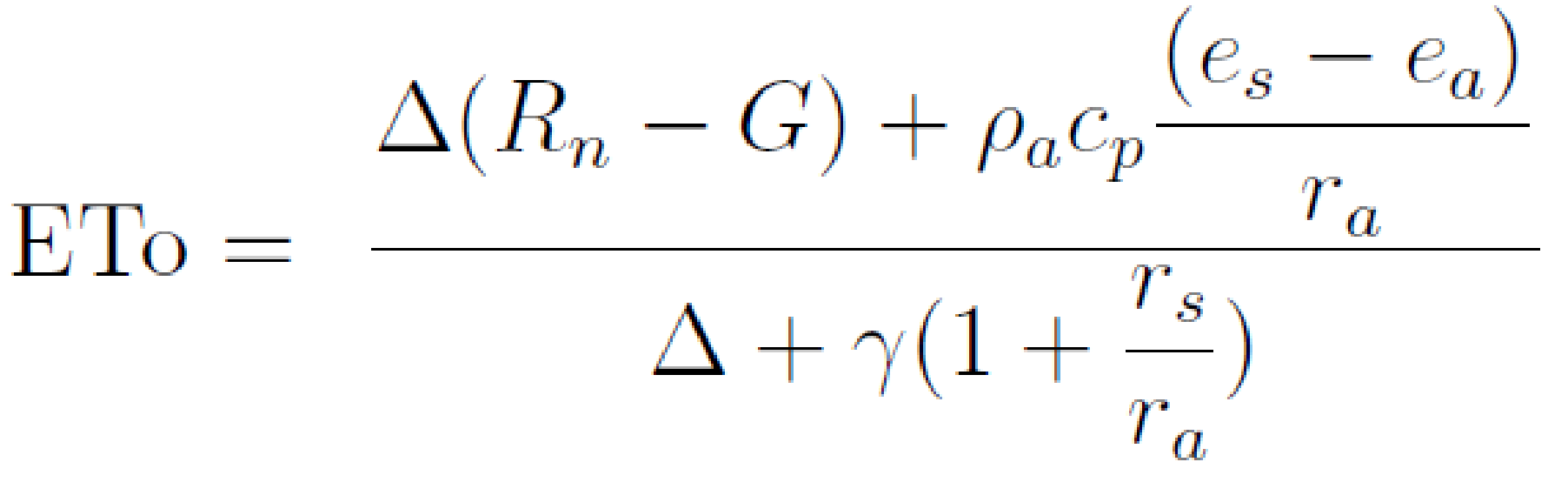
**Weather data**

To contextualize drought stress observed during our experiment, we quantified precipitation and evapotranspiration 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).

SPEI defines 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).

To contextualize observed climate patterns relative to long-term variation, we calculated SPEI for a 35-year span between 2018 and 1983, the first year sufficient climate data was collected by the CIMIS system. 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 of available data, 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. Resulting values of SPEI were centered at the mean drought stress across overall observations (D = 0), and individual years range between extreme droughts (D < -2) and significant water surplus (D > +2).

SPEI calculations were performed with the “SPEI” package (Beguirea and Vicente-Serrano 2017).

**Construction of Multistate Models**

To quantify the probability of vegetation transitions, we fit a multistate model (syn. Markov model) to community state assignments over time. In this model, the probability that a given plot transitions from one vegetation state to another is estimated by a transition matrix, whose terms may also interact with different covariates.

We fit 8 candidate multi-state models to our data, beginning with a baseline model consisting of a transition matrix without influence of any covariates. This base model was then further modified through inclusion of additional terms reflecting the influence of drought stress calculated over 1-, 2-, and 3-year intervals (SPEI), in addition initial planting composition (temporal priority effects). Temporal priority was defined as a binary (1/0) variable describing whether indicator species of a given state were a component of the seeded species mixture. We fit models consisting of only drought effects as covariates, temporal priority as a covariate, and models containing both drought and temporal priority as additive effects.

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. A table consisting of model descriptions and AIC scores is presented in Appendix 7. Multistate model fitting and model selection was performed using the “msm” package.(Jackson 2011)

All analyses were conducted in R version 3.06 (R Development Core Team).

**Results**

*Seeding treatment effects on community composition*

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 1). 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” treatment composition was also segregated from others

*Partitioning vegetation into discrete states*

As expected in a California annual grassland system, community composition observed in 2008 - 2018 was highly dynamic. On average, a plot compared between two consecutive years displayed roughly 50% of species’ relative abundances that changed, and 50% that remained the same (mean Bray-Curtis dissimilarity = 0.52 +/- 0.01 standard error). Clustering captured a substantial proportion of total compositional change (Pseudo-R2 = 0.39*;* Figure 1). Residual variation suggests that fluctuations in cover within clusters were still common, however, indicating that our method best captured broad changes in the dominance of correlated groups of species, rather than the varying abundance of individual species.

Contrary to classic approaches in California grasslands that classify vegetation in three discrete types (as included in our experimental design and displayed in the 1st year of the experiment) partitioning community variance into vegetation states indicated that vegetation was best characterized by 4 discrete clusters (Appendix 2-3). 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 (*B. hordeaceus.-Festuca* *Annuals*) and State 4(*Avena-B. diandrus* *Annuals*)reflected the partitioning of the “Naturalized Annual” group into two separate types.

Cluster assignments reflected a 75% relative abundance of associated indicator species, on average. Less than one tenth of cluster assignments had indicator species relative abundances of less than 40% ( Appendix 4).

*Frequency of state assignments over time*

The climatic conditions observed during our experiment included a period of normal to above-average water availability (2008 – 2011), followed by drought (2012 – 2016), and substantial water surplus (2017; Figure 1). 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 fluctuations that correlate with climate patterns (Figure 1).

While figure 1 displays the frequency of state assignments across all plots, further inspection of individual plot assignments over time showed that transitions between vegetation states were common across all seeded species groups (mean number of total transitions observed per plot = 3.73 +/- 0.16 SE). However, the frequency of transition events – summarized in a contingency table (Appendix 5) – varied both as a function of a plot’s prior state assignment and the direction of transition (plot-level state assignments presented in Appendix 6).

*Model selection*

Comparison of candidate multi-state models fit to state assignments indicated that best fit models included both the influence of initial seeding composition and climate variation (Appendix 7). 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.

*B. hordeaceus.-Festuca* *Annuals* (State 2) were the dominant vegetation following seeding of naturalized annuals (including *Avena fatua and Trifolium subteranneum),* with each of the 32 plots containing naturalized annual species in seeding mixtures assumed the *B. hordeaceus.-Festuca* state in the first year of observation (Figure 2, Appendix 1). However, the predominance of this community configuration was short-lived, and by the fifth year of sampling, each of these plots experienced at least one assignment transition. As a result, the estimated persistence of this state (0.58, 95% CI = 0.48 - 0.65) was the lowest of the four identified in our observations (Figure 3, Table 3).

Following the short-term predominance of the *B. hordeaceus.-Festuca Annual* state, a majority of subsequent observations were defined by the remaining three states: *Invasive Annuals,* *Native Perennials*, and *Avena-B. diandrus Annuals* (Figure 2, Appendix 6). Baseline transition matrix values in our model, which assume drought stress equivalent to the long-term average (i.e. SPEI = 0) and no effects of temporal priority, yielded estimated state persistence between 0.74 and 0.84 for these three groups (Figure 3, Table 3). Their abundance across the bulk of our later observations suggests that transition between these three community states are likely to form core patterns of vegetation turnover in response to our observed climatic variation, barring the influence of other factors, such as disturbance.

Estimated effects of model covariates – drought stress and planting composition – demonstrate distinct drivers of community turnover between vegetation states prior to, during, and post drought. In the first four years of our observations (2008 – 2011), compositional shifts were primarily driven by plot transitions from the *B. hordeaceous-Festuca Annual* to *Invasive Annual* states (Figure 2, Appendix 6). Importantly, this transition showed little evidence of bidirectionality, resulting in a directional shift in composition. Given average to slightly above-average rainfall patterns between 2008 - 2011, *Invasive Annuals* appear to favor non-drought conditions: transitions to this state from *B. hordeaceous-Festuca* communities were positively (though not significantly) correlated with SPEI, though a lack of statistical power likely results from limited observation of the *B. hordeceous – Festuca state* during drought years.

Transitions between *Invasive Annual* and *Avena-B. diandrus* states during drought provide further evidence for contrasting climate affinities between core species groups. Increased frequency of the *Avena-B. diandrus* annuals state between 2012-2017 produced significant negative correlations between SPEI and both *Avena-B. diandrus* persistence and probability of *Invasive Annual* transition to this state (Table 2).

In contrast to states which exhibited linearly correlated responses to drought stress, plots characterized by the *Native Perennial* state displayed complex interactions between effects of drought stress and initial planting composition (Figure 3, Table 3). Transition probabilities to the *Native Perennial* state significantly increased under both positive and negative values of SPEI, depending on prior community configuration: *Invasive Annual* communities were more likely to transition to a *Native Perennial* state under drought, while *Avena-B. Diandrus* communities were more likely to do so with increased water availability. Critically, these transitions were strongly affected by seeding treatments, where plots seeded with native perennial grasses increased transition probabilities by factors of 3.3 and 2.5, respectively (Table 3). This finding suggests that *Native Perennial* species may be broadly tolerant of climatic variation but significantly limited in their capacity to dominate communities when propagules are not supplemented.

**Discussion**

*Species response groups under climate extremes*

The emergence of unique community assemblages under climate change is expected to pose a major challenge to the study and management of natural systems in the near future (Hobbs et al. 2009). California, like many Mediterranean systems, is projected to experience increasing temperatures and fewer, more extreme rainfall events (Yoon et al. 2015). While unprecedented climatic extremes are expected to produce unintuitive patterns of community assembly that are poorly predicted by prior observations (Williams and Jackson 2007), contemporary observation of extreme events can shed light onto future dynamics.

In this study, we found evidence that core community assemblages under extreme drought differed from historic norms. Classic conceptual models that describe vegetation through three discrete state types failed to capture community turnover as effectively as a four-state model that partitioned the “Naturalized Annual Grasses” state into two separate groups defined by dominance of *B. hordeaceous* and *F. perennis*, or *A. fatua* and *B. diandrus*. Given the structure imposed by our initial planting composition, this result is particularly striking.

While exotic grasses in California are often expected to share similar climatic tolerances due to their annual life history strategy (Sandel and Dangremond 2012), the unique conditions imposed by extreme drought may have crossed previously unobserved thresholds to separate “winners” and “losers” within functional groups (Prugh et al. 2018). The mechanism of this partitioning is unclear, but it appears likely that extreme events may operate on secondary divisions within the “Naturalized Annual Grass” group. *B. diandrus,* for example, is a more common dominant in Southern California grasslands (Barbour et al. 2007), and may exhibit adaptations that provide a competitive advantage under severe drought. In contrast, *Lolium perrene* tends to be active later into the dry spring season than other naturalized annuals, and likely fares poorly under drought.

Our partitioning results highlight the potential difficulty in extending species-environment relationships to unobserved conditions (Nippert et al. 2006). Drought severity is defined by a suite of characteristics related to event size, frequency, and soil water content, whose combined effect on vegetation may not scale linearly with an aggregate measure of drought stress (Fay et al. 2008). In turn, drought responses of locally interacting species will be further controlled by factors such as resource competition, mutualism, and herbivory (Suttle et al. 2007, Tylianakis et al. 2008).

As a result, grassland responses to climatic variation are often inconsistent across sites. Drought may increase or decrease the abundance of dominant species (Hoover et al. 2014, Griffin-Nolan et al. 2019), depending on drought magnitude, functional diversity, and capacity for reorganization (Lloret et al. 2012, Ruppert et al. 2015). Complexities arising from local interactions may lead to unintuitive results that restructure species-environment relationships (e.g. Stampfli and Zeiter 2004, Kimball et al. 2010, Stuble et al. 2017). While this study provides evidence for a unique partitioning of species response groups under extreme drought, repeated application of our methods to different sites and environmental contexts may highlight variable results.

*Contingency in vegetation dynamics*

Beyond their potential role in structuring species response groups, local interactions are an important driver of vegetation dynamics under varying climatic conditions. In grassland systems, dominant species have often been observed to be the primary determinants of key community attributes, such as productivity (Smith and Knapp 2003), drought tolerance (Hoover et al. 2014), and resistance to invasion (Smith et al. 2004). Shifts in species dominance under drought, therefore, are likely to be constrained by community types present prior to perturbation – both the direction and magnitude of effect will depend on the resistance of a community to different pathways of change.

In our study, we found that climate operated on underlying patterns of persistence and transition across the four species groups. Despite considerable climatic variation, we found that community composition was generally persistent; on average, plots were more likely to retain their assignment in two subsequent observations than they were to change states. Given the dominance of annual species in most plots, this result was surprising, but may reflect a reduced soil seedbanks and a smaller species pool than many natural communities.

Observed vegetation transitions captured differences in both the inherent properties of different community states, as well as their response to seeding treatments and drought stress. Following early predominance of the *Fectuca – B. hordeaceous* community, subsequent shifts to *Invasive Annual* and *Avena – B. diandrus Annual* states appeared to be governed by climatic trends, where states were favored by above-average precipitation and drought, respectively (Figure 3). Rather than showing random or bidirectional patterns of change, the sequential nature of these shifts implies that vegetation dynamics were governed by state-specific differences in persistence and ability to colonize different communities. *Invasive Annuals* appeared highly resistant to colonization by *Festuca – B. hordeaceous* species (Table 5), for example, so many of the vegetation transitions observed early in our experiment did not reverse during drought.

Contingencies in vegetation dynamics were perhaps best illustrated by transitions to the *Native Perennial* state, where initial seeding composition had strong effects on the probability of vegetation transition to this state type (Figure 3, Table 3). The addition of native perennial grass seeds greatly increased the probability of their dominance under both above- and below-average drought conditions, where recruitment limitation likely acted as a bottleneck to the spread of a broadly stress-tolerant community state. Failure to account for this effect may lead to markedly different predictions of native perennial grass abundance under a changing climate.

Studies of California grassland community dynamics have identified similar state-specific differences in the probability of vegetation transition (Jackson and Bartolome 2002, Stein et al. 2016). In our study, the functional characteristics of dominant species exhibited correlations with observed state properties: Persistence of *A. triuncialis* and *E. caput-medusae* is likely to be facilitated through deposition of dense thatch layers that inhibit germination and growth of competitors (Eviner and Hawkes 2012). Native perennial grasses are known to be effective competitors once mature, though appear to exhibit seed limitation in some contexts that may limit colonization (Seabloom et al. 2003a, 2003b). This contrasts with many naturalized annual grasses, whose large investment into seed production may facilitate rapid growth and colonization, particularly after disturbance (Hillerislambers et al. 2010)

In grassland systems, the capture of these contingencies can improve predictions of community response and recovery following drought, where pathways of change govern resistance to perturbation and system recovery (Briske et al. 2003). While different vegetation types in California grasslands often appear to resist colonization by one another, changing environmental conditions are likely to cross thresholds that prompt community transition to a new state (Thomsen and D’Antonio 2007, Larios et al. 2017, Uricchio et al. 2019). Subsequent recovery thus depends on the probability of transition from a new state to previous community configurations, though can be limited by selective pathways of compositional turnover (Larios et al. 2013). This resistance may contribute to observed delays in ecosystem recovery, where return to pre-drought community composition is unlikely in the years immediately following disturbance (Harrison et al. 2018).

*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 facilitate management efforts (Hobbs et al. 2006, 2009, Seastedt et al. 2008). To better predict windows of opportunity and design effective interventions, our results may provide a foundation by quantifying the persistence of species assemblages under various contexts.

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, Young et al. 2014). 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 (Wainwright et al. 2012, Fry et al. 2017, 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 contrast, our study suggests that eradication of invasive annual grasses may be facilitated by targeted management during drought. Common interventions–grazing, herbicide application, and targeted burning–may increase in efficacy when conditions naturally disadvantage *E. caput-medusae* and *A. triucialis* (DiTomaso et al. 2008). However, given that vegetation states may vary in persistence, care must be taken to ensure that colonizing vegetation is robust to re-invasion. Growth of ruderal weeds appears common following management in California grasslands, which often do little to resist colonization of invasive grasses (Young 1992, DiTomaso et al. 2008).

Our findings underscore the potential value of maintaining functional and taxonomic diversity in restoration and management (Funk et al. 2008). Particularly in highly dynamic systems where environmental fluctuations drive turnover, long-term ecosystem health may depend on turnover among desirable community types – the maintenance of multiple potential vegetation states can maintain favorable pathways of compositional change following disturbance that may otherwise favor spread of undesirable species (Hoover et al. 2014, Griffin-Nolan et al. 2019, Wilcox et al. 2020).

*Future Directions*

Our findings underscore the need to employ analytical approaches capable of distinguishing novel assemblages as they arise. Reliance on long-standing divisions between species groups to characterize system responses to climate change may fail to capture emergent complexity. 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.

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