**State-Transition Manuscript**

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

OR

Drought effects on California grasslands are contingent on prior patterns of community assembly

OR

Something else entirely?

**Abstract:** In plant communities, climate change is forecast to influence composition through shifts in average climatic regimes and increased frequency of extreme events. Compositional responses to this change will likely be constrained by patterns of community assembly, wherein responses differ based on the diversity and identity of locally interacting species. These controls are known to operate strongly in arid- and semi-arid systems, where communities fluctuate between many discrete vegetation states. In this study, we observed the composition of various plant community types in California grasslands during a ten year period including a drought of historic magnitude. 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 evidence 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 dependent on state assignment. Strong persistence of native perennial communities across a range of environmental conditions and reduced persistence of invasive annual grasses under drought suggest potential use of priority seeding and targeted interventions, respectively, to achieve management goals under a changing climate.

**Introduction**

Across ecosystems, elevated greenhouse gas inputs are 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 (Smith 2011, Felton and Smith 2017). As systems are increasingly influenced by climate change, the ability to predict changes in the composition of ecological communities is at a premium – unprecedented impacts will require new paradigms for continued conservation and management (Hobbs et al. 2009).

Critical to understanding the effects of climate change on plant communities is the capture of contingencies based on prior patterns of community assembly. At the individual scale, conditions imposed by heatwaves, droughts, and extreme cold may lead to decreased plant growth rate, shifted phenology, or mortality, depending on species tolerances to different stressors (Parmesan and Hanley 2015). At the community scale, however, changes in abundance will be constrained by interactions between a species’ climatic niche and the biotic environment in which it resides (Tylianakis et al. 2008, Fukami 2015). Key processes governing species abundances are known to depend on the emergent properties of different species assemblages, such as richness, functional diversity, and the identity of dominant taxa (Alexander et al. 2015). Particularly in systems where communities fluctuate between multiple states, site responses to climate change are expected to depend on community configuration present prior to perturbation.

Applied ecologists have long recognized the importance of these contingencies, particularly in arid- and semi-arid systems where vegetation naturally fluctuates between multiple equilibria. Conceptual models often used to guide management in these systems capture vegetation dynamics through transitions between various compositional states (state-transition models; Bestelmeyer et al. 2003). Given that states differ in their persistence or likely direction of change, managers may seek to facilitate vegetation transitions away from undesirable states or enhance the persistence of desirable ones.

In systems where vegetation dynamics may be effectively decomposed into fluctuations between distinct community types, a variety of organizing perspectives may be used to group taxa. In state-transition models, partitions are often made on the basis of expert opinion, formed by long-term observation (Bestelmeyer et al. 2003). Other perspectives, based on shared functional characteristics or other physiological traits, are also commonly employed in other contexts (Lavorel et al. 1997, Suding et al. 2008). However, the validity of such grouping schemes is limited by both the total species pool and range of compositional drivers considered during their construction (Diaz and Cabido 1997).

Climate change is expected to pose a number of challenges to effective community classification and associated management efforts (Hobbs et al. 2009). Unprecedented environmental extremes are likely form novel species assemblages, which in turn, may exhibit markedly different properties based on the frequency and identity of interacting taxa (Williams and Jackson 2007). Under these circumstances, previously defined species groups must be reflect new patterns of community turnover.

Modern computational tools offer a unique opportunity to redefine core species groups in responses to changing climate. Though still limited by the climatic variation captured available data, algorithmic partitioning approaches may rapidly be deployed as to evaluate or supplement models generated using prior observations. 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, their application to community dynamics under shifting climate patterns appears limited.

Mediterranean grasslands, characterized by long, hot summers with little precipitation, exhibit vegetation dynamics that depend strongly on both climate patterns and contingency in community assembly. California grasslands, in particular, often fail to exhibit predictable convergence to a single community type due to climate sensitivity (Hobbs et al. 2007), non-hierarchical competitive dynamics (Uricchio et al. 2019), and strong priority effects (Young et al. 2014). Given this dynamism, compositional turnover is often decomposed into variation between three species groups defined by shared life history strategy and history of colonization: naturalized exotic annual grasses, native perennial grasses and forbs, and recently invasive exotic annual grasses.

Differences in fecundity, phenology, and plant-soil feedbacks that distinguish species groups are thought to govern community turnover in California grasslands. While precipitation and temperature may provide favorable conditions for one group, their proliferation is dependent on the identity of previously dominant vegetation types; invasive annual grasses, for example, may enhance their persistence during unfavorable conditions through deposition of thick litter layers that suppress competitor growth (DiTomaso et al. 2008). Native perennials grasses, though broadly stress-tolerant, are known to exhibit seed limitation that may prevent colonization into environments occupied by other species groups (Seabloom et al. 2003b).

Climate change effects, however, may complicate the use of these classic conceptual models. From 2011-2014, California experienced the driest period in recorded history, in concordance with a forecasted 50% increase in extreme events by the end of the 21st century (Yoon et al. 2015). This drought was observed to strongly influence species abundances in grasslands, potentially acting as a critical ecosystem tipping point (Shaw et al. 2009, Prugh et al. 2018). By virtue of its magnitude, the 2011 drought is may likely have produced non-intuitive effects on processes of community assembly, through generation of novel community types and interactions with complex drivers of compositional turnover.

In coming decades, land managers are expected to be increasingly concerned with meeting targets — such as establishment of native species and reduction in invasive species abundance — to promote key ecosystem services and ecosystem resilience. To this end, the application of modern computational tools to common management frameworks may prove increasingly valuable. 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 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 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 were repeated twice in the early fall of 2007.

Seeds were planted to establish vegetation treatments 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, 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 for each species was used in analysis.

**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, which were subsequently removed. 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. 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.

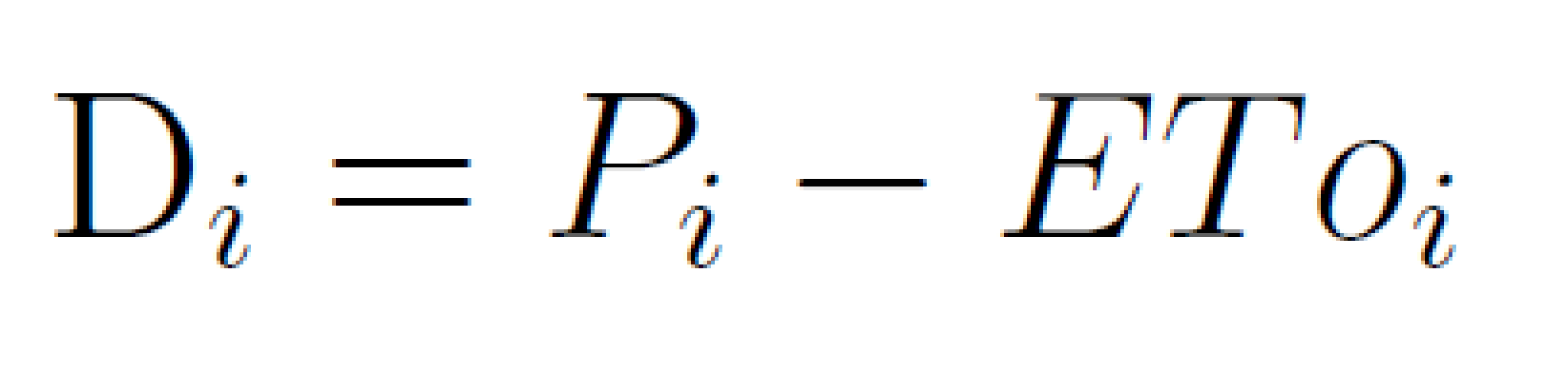
Because the number of relevant clusters in our study was not pre-defined, we applied K-medoids clustering across values of *k* from 2-10, yielding a number of clustering solutions. We then subjected the output of each of these clustering solutions to a battery of tests—Hartigan, CH, Beale, KL, Cindex,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

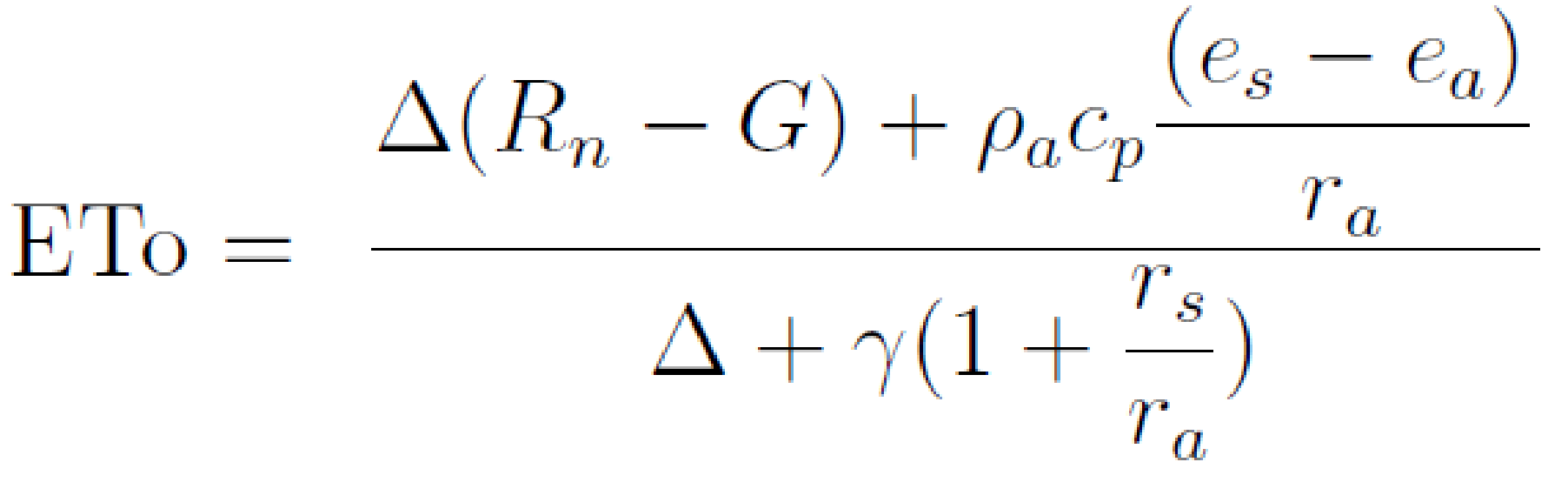
**Weather data**

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

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 with 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 Table 4. 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**

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” treatment 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 (*Bromus-Festuca* *Annuals*) and State 4(*Avena-Bromus* *Annuals*)reflected the partitioning of the “Naturalized Annual” group into two separate types.

Cluster assignments reflected consistent patterns in community composition; 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%. 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 SE). 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 transition (plot-level state assignments presented in Appendix 1). Despite considerable variation in species abundances, communities were likely to retain their state assignments for multiple years of observation. Fluctuations in species abundances within a given state assignment, particularly dominant taxa, appear likely an important component of community dynamics.

*Model selection*

Comparison of candidate multi-state models fit to observed state assignments 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.

Despite early dominance, *Bromus-Festuca* *Annuals* (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; Figure 3, Appendix 5). Despite a lack of persistence, these species were capable of dominating vegetation following seeding; each of the 32 plots containing naturalized annual species in seeding mixtures assumed the *Bromus-Festuca state* in the first year of observation. However, by the 5th year of sampling, all of these plots experienced at least one assignment transition.

Following the short-term predominance of the *Bromus-Festuca* *Annual* state, a majority of subsequent observations were defined by the remaining three states: *Invasive Annual* (State 3), *Native Perennial* (State 1), and *Avena-Bromus Annuals* (State 4). The baseline transition matrix values, which assume no effects of temporal priority and drought stress equivalent to the long-term average (i.e. SPEI = 0), estimated average state persistence to range between 0.74 and 0.84 for these three groups (Table 5, Figure 3). The abundance of these three states across the bulk of our later observations suggests that these species are core elements of long-term vegetation change, 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 *Bromus-Festuca* *Annuals* 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. While this transition was common during years with above-average precipitation, estimated climate relationships were non-significant, likely due to insufficient data on *Bromus-Festuca* state transitions under drought. However, drought did reduce the overall persistence of the *Invasive Annual* state, resulting in increased probability of transition to both *Native Perennial* and *Avena-Bromus Annual* states (Table 5).

In contrast, *Avena-Bromus 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 *Avena-Bromus 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 Perennial* transition probabilities exhibit significant relationships with both temporal priority and drought stress, reflecting broad environmental tolerances coupled with limited recruitment ability (Table 5, Figure 4). During wet or dry periods, *Native Perennial* species were more likely to become dominant in communities characterized by *Avena-Bromus Annuals* and *Invasive Annuals*, respectively. However, these transitions were far more likely when native species were a component of the seeded species mixture;colonization of *Native Perennials* into plots of other seeding compositions were rare, resulting in state frequencies that remained roughly constant over the course of the experiment, with no more than 25% of plots receiving this assignment in a given year.

**Discussion**

California, like many Mediterranean systems, is projected to experience increasing temperatures and fewer, more extreme rainfall events. While community responses to novel climatic regimes are often difficult to predict, contemporary observation of compositional changes following extreme events can shed light onto future dynamics.

Long-term datasets which capture community responses across a range of climatic conditions are likely to capture deviations from prior community dynamics produced by extreme events (Lindenmayer et al. 2012). However, the complexity of processes governing compositional change present unique analytical challenges -- particularly in highly dynamic, species-rich systems, complex interactions between biotic and abiotic drivers of species abundances may only be capture non-traditional statistical methodology. In this study, we present a combination of unsupervised clustering and multi-state modeling to partition vegetation into discrete community states and capture contingent patterns of turnover during a historic drought.

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.

*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). Unprecedented climate extremes and their impacts on species interactions may lead to unintuitive patterns community assembly, wherein previously observed dominance hierarchies and trait-environment relationships are rapidly restructured.

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 these species have often been assumed to share similar functional characteristics,

conditions imposed by a historic drought may have crossed previously unobserved thresholds to separate “winners” and “losers” across species once assumed to have similar climatic tolerances (Prugh et al. 2018). The mechanism responsible for this partitioning is not clear, but given the diversity captured by the “Naturalized Annual Grass” group, these species may exhibit far greater functional variation than is often considered. Only under significant departures from climatic norms may these differences become apparent.

Unanticipated shifts in dominance following extreme events have been reported in many terrestrial systems. Previously abundant species are known to become uncommon or locally extinct, while rare species may become dominant when resource fluctuations permit rapid growth and expansion (Brown et al. 1997, 2001). However, such changes are often highly complex, given a network of direct and indirect interactions that control species abundances; extreme climate events may be buffered in some systems, exhibit exaggerated responses in others, or produce entirely novel species-environment relationships. Increasing temperatures and decreased rainfall in the Chihuahuan desert, for example, has favored cold-adapted species capable of better utilizing delayed precipitation (Kimball et al. 2014).

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.

*Contingency in vegetation dynamics*

The identification of community types also serves to determine constraints on compositional change driven by the properties of species assemblages. Many studies have reported moderating effects of taxonomic and functional diversity on many community processes (Levine and Antonio 1999, Díaz and Cabido 2001). However, in grassland systems, dominant species have often been observed to be the primary determinants of key attributes, such as productivity, drought tolerance, and resistance to invasion. As a result, both the frequency and direction of compositional changes following drought are likely to be constrained by species assemblages present prior to perturbation.

In our study, we found that climatic variation interacted with underlying patterns of persistence and transition probability across different species assemblages. Despite considerable climatic variation, we found that community composition generally persistent; on average, plots were more likely to retain their assignment in two subsequent observations than they were to change states. A number of transitions, however, were largely unidirectional, such as transitions from *Bromus-Festuca* to *Invasive Annual* states. Others depended strongly on seeding treatment, such as *Native Perennials*, which were broadly stress-tolerant once established but rarely became dominant in plots when not represented at seeding.

These findings suggest that community composition in California annual grasslands is strongly contingent on prior patterns of assembly. Even when subject to extreme drought, species abundances appear unlikely to follow simple relationships and instead vary as a function of previously dominant vegetation groups. Similar dynamics have been reported in other studies of California grasslands, where response to other stressors, including grazing, was characterized by state-specific patterns of persistence and transition (Stein et al. 2016).

These patterns appear to reflect functional differences between species in each community state known to control community assembly. 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. 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 is in contrast to many naturalized annual grasses, whose large investment into seed production may facilitate rapid growth and colonization, particularly after disturbance (Hillerislambers et al. 2010).

As a result, contingencies in community response driven by dominant species groups are likely to control the probability and direction of ecosystem recovery following drought. Established communities of different vegetation types in California grasslands, generally, appear able to resist colonization by one another until certain thresholds are crossed (Thomsen et al. 2006, Larios et al. 2017). Upon return to normal conditions, however, certain species may be limited by the growth of others. Drought recovery in a patchy grassland consisting of both native and exotic species, for example, was stalled in communities that were once composed of native taxa (Larios et al. 2013). Relative persistence of drought-induced changes in species abundance may contribute to delays in ecosystem recovery, where return to pre-drought community composition is unlikely in years immediately following disturbance (Harrison et al. 2018).

*Implications for Restoration and Management*

1. Ecosystem management under a changing climate can be enhanced by recognizing the patterns of turnover in these species groups + planning accordingly.
   1. Certain vegetation confirmations may be more resistant to change under climatic variation
   2. More importantly, we might benefit from building in sufficient variation to maintain pathways of ecosystem change.

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 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 (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 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*. 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.

**Acknowledgements and Funding Information**

Funding was provided by the USDA NIFA NRI Controlling Weedy and Invasive Plants Program (grant number 2006-55320-17247), Kearney Foundation of Soil Science, Hatch Funding, Packard Foundation funding to the UC Agriculture Sustainability Institute, and by the USDA National Institute of Food and Agriculture, Agricultural Experiment Station Projects to VE (grant numbers CA-D-PLS-7641-H and 1013397). EB was supported by grants provided by the University of California, Davis, Department of Plant Sciences and Graduate Group in Ecology.

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