Quantifying Community Response to Drought: a Trait Based Analysis of the Xeric Tallgrass Prairie in Boulder, Colorado

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Quantifying Community Response to Drought: a Trait Based Analysis of the Xeric Tallgrass Prairie in Boulder, Colorado

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A thesis submitted to the University of Colorado at Boulder
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Abstract

Increased severity and duration of drought events in Colorado pose a threat to grassland systems. Utilizing plant traits to analyze community responses to environmental disturbance serves as an accurate mechanism in addressing climate change influences on grassland ecosystems. In this project, I aim to quantify the relationship between five plant traits and drought intensity over time, in order to see if plant traits can capture changes in community structure in response to drought. I calculated the mean value of traits at the community level as well as the amount of variation observed in those values, in order to analyze community trends and detect instances of environmental filtering. The effects of current annual drought and lagged annual drought showed significant relationships with certain traits. Current annual drought had a positive influence on final plant height (P=0.037) and lagged annual drought (t-1) had an adverse effect on root mass ratio (P=0.004) and a positive effect on root dry matter content (P=0.04). Current year drought also had a significant influence on the amount of variation in final plant height (P=0.002), and lagged annual drought had a significant influence on the amount of variation in root mass ratio values (P=0.02), suggesting a filtering effect of decreased investment in root traits after a non-drought year and the favoring of shorter plants during current drought years. The results from this experiment show that traits can be used to indicate changes in community composition. Root traits demonstrated to be the most sensitive to changes in drought. Future studies should continue to utilize traits to analyze interspecific variation in response to climate change, though my results imply the need for caution when using individual traits to quantify change at the community level. Trait values of dominant species have the potential to influence the mean value observed across the community, which highlights the need for attention to detail when utilizing traits to make inferences about the community.
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Introduction

Predicting changes in plant ecosystems is an essential ecological challenge as climate change intensifies. Global temperatures are increasing, and although precipitation responses will be variable, it is likely that weather events, in general, will become longer and more intense (Knapp et al., 2015). In order to adapt to a changing climate and the effects of potentially altered biodiversity, it is essential to understand how plant systems respond on a local scale. Until recent years, many studies aimed to quantify the effects of climate change on different plant systems via broad changes in community composition. This level of analysis is the first step in understanding general community responses, however, executing studies at the level of functional group underestimated the ability of individual species to respond differently to environmental pressures compared to similar plants of the same functional group. Today, an increasing number of studies worldwide assess the role of plant traits -- measured within and/or among species -- as more useful indicators of vegetation changes in ecosystems (Cornwall & Ackerly, 2009, Kolodziejek, 2017, Lavorel & Garnier, 2002). Utilizing plant traits as a basis to understand and predict community responses allows for a more meaningful in-depth, quantitative assessment of the biological changes occurring to plant ecosystems.

The city of Boulder, Colorado, manages thousands of acres of public grasslands with biological, economic, and cultural values that managers aim to sustain in a changing climate. Climate data shows increasing temperatures in Boulder over the last twenty-five years with no significant corresponding increase in precipitation (Figure 1). Early snowmelt, hotter temperatures, and the potential for more prolonged, more severe droughts pose a threat to grassland ecosystems like those in Boulder (EPA, 2016). If plant traits can accurately depict
community responses to climate change, this will contribute to the growing understanding of how functional traits are useful in grassland conservation and management efforts.

My research question asks do changes in plant communities in response to climate change occur as a function of specific plant traits? In other words, can we predict changes to plant community structure based on the traits present in that community? To answer this question, I aim to assess the relationship between five plant traits and drought intensity over time within a xeric tallgrass community, to see if traits can capture shifts in community structure. I utilize three datasets including a Boulder Open Space monitoring dataset which has collected species cover and abundance annually since 1991, a trait dataset which includes trait measurements for over fifty species in Boulder Open Space, and a climate dataset which quantifies measurements of drought, precipitation, temperature, storm count, in each year of the monitoring dataset.

I hypothesize that in response to drought, certain species within grassland communities will invest in their root traits either in the form of longer or denser roots, thus giving them an advantage of increased abundance during dry years. If below ground resources such as water availability are limiting, this could also favor species investing less in above ground resources leading to a decrease in overall plant height in the community. Specific leaf area (SLA) is often associated with soil nutrients or light availability; therefore I do not predict to see any significant relationships between SLA and drought. Seed mass is associated with more than one plant function (reproduction, seed recruitment); thus the implications of drought are also unclear.

**Background**

Grasslands provide a wide array of ecological benefits including drought and flood mitigation and protection from soil erosion. The xeric tallgrass prairie, in particular, provides a
habitat for hundreds of species and is a critical factor in maintaining biodiversity— an essential element of plant communities, as different species contribute various beneficial ecological services (Isbell et al., 2011). This project focuses on the xeric tallgrass ecosystem in Boulder Open Space, which constitutes 6,000 acres of land throughout Boulder (City of Boulder, 2010).

Efforts to conserve this ecosystem date back to the 1980s when most of the area was deemed a State Natural Area in response to environmental degradation due to construction (Baker, 1985). The xeric tallgrass prairie is unique to Boulder and must continue to be protected under climate change conditions. Climate preparedness in the conservation and management of these systems is a major priority in the city's plan in order to restore native vegetation and habitats (City of Boulder, 2010). Most ecosystems within Boulder Open Space have been altered in the past 150 years, and because of climate change, it will be difficult to restore these ecosystems to their “historic range of variability” (City of Boulder, 2010). Thus, it is essential to figure out which species are thriving under new climate conditions for future land management. Considering the significance of plant systems in sustaining life as we know it, it is crucial to conduct local studies to quantify the effects of climate change on grassland systems.

The following sections focus on grassland ecosystems and climate change in Boulder, Colorado. I then highlight examples of trait-based analyses and community level responses in order to provide insight into trait functioning in grassland systems.

*Tall Grass Ecosystems and Drought*

The drought of 2012 that spanned across the central United States remains to be the fourth most extensive drought since 1895. The drought served as an accurate basis to study the effects of drought on grassland regions because it was similar in severity across most of the central plains (Knapp et al., 2015). Two main approaches in response to drought found in
herbaceous species are dehydration tolerance and dehydration avoidance. Tolerant plants are often found in severe drought areas and are associated with slower growth and productivity as well as broader, deeper roots to increase accessibility of water (Balachowski & Volaire, 2016). Avoidance, on the other hand, includes continually taking up water at a slower rate to delay the process of dehydration (Balachowski & Volaire, 2016). Per Tucker (2017), Knapp et al. concluded that arid grasslands are the most sensitive to drought but that within six grass species analyzed, sensitivity to drought varied by a factor of two (Knapp et al., 2015). Grasses are “more than three times more sensitive” to water vapor deficit compared to precipitation, which demonstrates a need for greater investment into how grasslands respond to environmental changes in order to protect them (Tucker, 2017). Grassland ecosystems tend to respond in similar ways despite being located in different biomes, but certain species are more resilient to drought and display unique response strategies and characteristics (Koerner & Collins, 2014).

**Climate Change in Boulder**

It has been estimated that land temperatures in Colorado are predicted to increase by 2.5° to 5°C by 2050 (Kennedy, 2014).
Over time, trends in SPEI and precipitation appear to show a general upward trend in Boulder, Colorado; however, neither relationship is significant overall (Figure 1). SPEI stands for “Standardized Precipitation Evapotranspiration Index” and is a widely used tool in determining drought measurements (Vincente-Serrano, 2015). SPEI is useful because it captures the effects of increasing temperatures on water supply in addition to changes in precipitation; thus it is utilized throughout this project as the chosen drought metric (Vincente-Serrano, 2015). The uncertainty surrounding precipitation and drought events adds to the complexity of understanding how plant communities will respond. Scientists have agreed that increased variability of precipitation patterns will result in a changing species abundance within plant communities as well as an altered competition gradient in regards to resource acquisition;
however, it is unclear what exactly that will look like in Boulder’s tallgrass ecosystem. (Thibault & Brown, 2008, Knapp et al., 2003).

Despite variable precipitation patterns, trends suggest increasing temperatures over time (P=0.009). In Boulder, in particular, the implications of recent drought and rising temperatures have led to drier soil which poses a threat to natural systems (EPA, 2016). Additionally, a temperature increase without the certainty of an increase in precipitation is a likely contributor to more intense summer heat waves and increased severity of droughts. This finding suggests the need for a more mechanistic approach via the utilization of plant traits to captures the interspecific variation of the community.

**Traits**

For decades, researchers have tried to use knowledge about form and function to generalize and predict how species respond to the environment. Because communities have many plants, readily determined functional groups are often used to represent form and function (life history, life form, plant family, etc.). Conducting community analyses at the level of functional group assumes that species of the same type respond to environmental changes, in the same way, thus leaving out the element of intraspecific variation. As shown in many studies, it is evident that certain grasses respond differently (Tucker, 2017, Knapp et al., 2003). A trait-based analysis breaks down the community into distributions of continuous traits rather than plant type in order to more usefully represent the different ecological strategies represented by plants based on physiology (Tucker, 2017).

To understand the relationship between individual plants and their traits, it is essential to recognize what constitutes a trait as well as how different traits are organized and grouped to represent similar functions or tradeoffs in ecological strategy. Definitions of the word “trait”
vary throughout scientific literature, but for this thesis project, I will define trait to mean “any morphological, physiological, or phenological heritable feature measurable at the individual level...without reference to the environment or any other level of organization,” (Garnier, Navas, & Grigulis, 2015). Hundreds of different traits are measured and analyzed across scientific literature; often multiple terms can indicate the same functional trait or similar traits can be related to the same plant strategy. The unification of trait definitions is relevant to be able to compare traits in communities across different environmental gradients. Three subcategories of traits relate to resource acquisition, (e.g., leaf efficiency), plant stature, (e.g., vegetative height) and sexual regeneration (seed mass) (Garnier et al., 2015). A common measurable trait to represent leaf efficiency is specific leaf area (SLA) which determines the distribution of leaf biomass relative to leaf area (Caine &Dybzinski, 2013). The “three axes of variation” represent independent aspects of a species’ ecological strategy, and provide a useful start for selecting traits of interest to represent unique aspects of plant function.

Still, traits must also be in accordance with the environmental processes in which they are related (Pérez-Harguindeguy et al., 2013). Is the research question related to a specific environmental disturbance? Will this shift the point of focus to above or below ground trait aspects? (Pérez-Harguindeguy et al., 2013).

Previous work has been done to analyze the relationship between environmental gradients and functional plant traits. Cornwell and Ackerly looked at the mean value and spread of values for fourteen plant traits in a coastal California ecosystem. They identified the strongest predictor of mean trait value to be soil water content measured at the end of April (end of the growing season), concluding that the movement from dry to wet soil increases the mean trait value of specific leaf area (Cornwall & Ackerly, 2009). They also found that the range of values
for maximum plant height increased across a soil water gradient from low water content to high. In contrast, specific leaf area showed opposite results. They observed less diversity in values of specific leaf area when soil water content was high, suggesting the influence of an environmental filter (Cornwall & Ackerly, 2009). Interestingly, the study found no significant trend in species richness across the environmental gradient of water availability. Typically, studies show increasing species richness in response to greater water availability. It was speculated that the observed increase in the range of final height values is due to the presence of both trees and species that reach full maturity while in the understory (below canopy height). In dry soils, species appeared to show mid-range plant heights, and no observable woody species were reaching full maturity in the understory. In wetter soils, however, the inclusion of woody plants in the understory results in the apparent variation in final height.

Another study looking at the relationship between traits across an environmental gradient is Balachowski (2018). The study analyzed tradeoffs between dehydration tolerance/summer dormancy and resource acquisition in a California Mediterranean-climate region and found resource acquisition strategies were associated with higher values of SLA and SRL. Their findings suggest the importance of increasing efficiency by growing leaves to gain more access to sunlight and to increase SRL to mitigate drought effects by investing in shallow soil for moisture rather than long term storage of deep root systems (Balachowski & Volaire, 2017). Studying plant functionality at the individual level is crucial because it serves as the basis for greater change within the population. Adaptation starts with the individual and leads to evolutionary changes in the long term (Garnier et al., 2000). Studying relationships between functional traits results in a more detailed analysis of how individual plants interact with their environment (Balachowski & Volaire, 2016).
Methods

The methods for my thesis project consist of acquiring three necessary datasets on species abundance, species traits, and Boulder climate to predict relationships between drought and plant trait distributions in the community. I hypothesized which traits would be an influencer in driving community change, tested said traits at the community level and recorded my findings.

Data Acquisition

The cover dataset belongs to Boulder Open Space and Mountain Parks (BOSMP) and was collected by BOSMP and ESCO Associates from 1991 to present. The title of the dataset is Tall Grass State Natural Area (TSGNA) permanent monitoring transects. The data includes eighteen fifty meter transects separated into areas three, six, and seven. Cover data was collected via the point-intercept method. If possible, vegetation was identified to the sub-species level, and non-living vegetation and ground cover (dead standing plants, litter, bare ground) were allowed cover values. There are 100 total points surveyed per transect, and species-level percent cover is calculated as the sum of all hits for a given species out of all cover hits on the transect.

Of the eighteen permanent monitoring transects, twelve were surveyed annually from 1991 to present, excluding 2013 and 2014 due to historic flooding. In 2013, they only monitored seven of the twelve transects, and in 2014 they did not collect any observations. The remaining six transects were surveyed annually from 1991 to 2005 and then surveyed every three years after 2005 through 2011 (2014 interrupted by flood damage). After 2015, these transects returned to annual monitoring. All transects in area seven were surveyed annually except for 2013 and 2014. In my analysis, I will only be analyzing area seven because I do not have enough trait data to quantify communities three and six at the level of traits.
The trait data were collected in 2017 and 2018 [unpublished data, J.Larson]. For the majority of species, they collected seeds from local populations within Boulder County, Colorado (exceptions: Oenothera villosa and Grindelia squarrosa were derived from Minnesota commercial sources). The amount of cover data captured by the trait dataset ranges for each study site. Across areas three, six, and seven the average percentage of cover data represented in the trait dataset is 70%. In area three, the cover is much lower at 45%. In area seven, however, trait data captures 90% of the cover. Transect eight within area seven had only 30% cover; thus I did not include it in my analysis (Figure S1). Area six only included two transects with roughly 50% cover in each.

To collect root and leaf traits, they collected five replicate seedlings per species. They grew the seeds for sixteen weeks in a standard set of greenhouse conditions, exposing the growing seedlings to cool early spring temperatures for the first six to eight weeks (approximately 12°C from December to March). Then, they transferred to warmer late spring conditions (approximately 21°C from April to June). They planted seedlings in deep pots (6.4 centimeters wide and 25.4 centimeters deep) filled with a 1:1:1 mixture of sand:perlite:vermiculite (to facilitate root harvesting) and inoculated the pots with approximately five milliliters of field soil from a local natural site. Pots were watered daily for the first six to eight weeks, and then every three days for the remainder of the growing period. Pots were also fertilized weekly with half-strength MiracleGro throughout the growing period.

After sixteen weeks, the plants were measured for final height and then harvested and gently cleaned of all soil debris. Plants were separated into root, leaf, and shoot tissue, and a standard subsample of leaves and roots were separated to collect areas (leaves only), fresh weights, and dry weights. For the leaves, typically three green, midsize leaves per plant were
collected, with more for small leaves. For roots, they used a standard branch of the crown or taproot. To collect leaf area, they collected fresh leaves and scanned and analyzed the images with ImageJ software to record area in square centimeters (Rasband, 1997). To collect fresh mass, they rehydrated the sub-sampled roots and leaves in a damp paper towel for twenty-four hours at 5°C before weighing. To collect dry mass, they oven dried these tissues for two days at 60°C and then re-weighed them. Remaining above- and below-ground tissues for each plant were also dried and weighed.

Plant height was defined as the final plant height from soil to the tip of photosynthetic tissue. RMR captures the plant’s relative investment of resources belowground (i.e., acquiring water/nutrient resources) and was calculated as the ratio of total root dry mass relative to the whole plant dry mass. RDMC is an indicator of root toughness or density and was calculated as the ratio of dry root mass to fresh root mass. Specific leaf area (SLA) is an indicator of leaf efficiency and resource acquisition ability and was calculated as leaf area per dry leaf mass. Seed mass was also used as an indicator of regenerative strategy (many small seeds compared to few large seeds). There is a trade-off between seed size and the number of seeds dispersed among plant species. A massive dispersal does not necessarily indicate a healthy population; however, larger seeds tend to have higher rates of success in unfavorable environmental conditions likely due to their ability to take up increased nutrients (Garnier et al., 2015). Seed mass was the average mass per seed from three replicates of ten to thirty seeds, oven-dried for two days at 80°C. Where possible, they substituted missing seed masses with the average seed mass from the Kew Seed Information Database (Royal Botanic Gardens Kew, 2019). The dataset quantifies traits for fifty species (Table S1). The traits included in the dataset are RMR, RDMC, SRL, root diameter, leaf dry matter content, specific leaf area, and seed mass.
The third dataset I utilize is a climate dataset. Precipitation, drought, and temperature measurements were derived from NOAA/ the Boulder weather station. Data was subsetted from April 1st, 1991 to present. A small set of missing values for daily precipitation (six days in April 1996) and daily maximum temperature (October 27th, 1990) were substituted with values from the NOAA Global Historical Climatology Network daily (GHCND) summaries dataset. Both maximum temperature and precipitation values from the GHCND dataset have a +0.99 correlation with maximum temperature and precipitation values in the NOAA Boulder weather station dataset. Station locations are roughly 100 meters apart, approximately 4.5 kilometers northwest of the BOSMP monitoring area. The dataset quantifies environmental variables for both the growing season and the full year, including the number of dry days and wet days, storm frequency, average, maximum, and minimum amount of generated precipitation, etc. The growing season is defined from April to August and the annual window of September to August. The growing season window was determined through visually inspecting NDVI curves for 2012 to 2017 for each transect.

**Selection of Traits**

Specific traits of interest were selected to represent the three principal axes of variation and therefore the relevant aspects of a plant’s life cycle. I referred to the New Handbook for standardized measurement of plant functional traits worldwide (2013) as well as additional studies that looked at functional trait responses. I intended to choose traits that are not correlated to one another so that I can be sure the relationships I’m seeing are not influenced by similar traits. After creating a correlation table and referring to additional studies, I chose to include RMR, RDMC, SLA, seed mass, and plant height in my analysis (Table S2). Root traits including
RMR and RDMC were added to test my hypothesis that underground resources will be more heavily relied upon in times of drought.

**Selection of Environmental Variables**

I created a scatterplot matrix to assess the correlation between environmental variables described above and observed the relationships. With the predictable likelihood of increased drought in Colorado, understanding how plant communities will respond is necessary for restoration. Annual SPEI was selected to capture changes in precipitation as well as temperature and to account for potential strategies used by plants in winter months when productivity is lower. Annual lagged SPEi (t-1) was selected to detect drought sensitivity adaptation.

**Data Analysis**

To answer the question if traits can be used to indicate changes to community structure, we utilized two different metrics to quantify overall responses as well as variation within those responses. Community weighted means (CWM) represents the “mean of values present in the community-weighted by the relative abundance of taxa bearing each value” (Lavorel, 2008). CWMs are useful for observing general trends in the community over time. CWM was quantified at each transect; however, the responses were grouped to form one mega-community.

Community weighted variance (CWV) measures the range of trait values observed in a given community and was used to analyze the spread of trait values in response to current and lagged drought (t-1). If the range of values is small, it could mean that only species with specific attributes can establish or persist. CWV was calculated via an existing R script created by Maud Bernard-Verdier (2012). To calculate CWV, I used the pooled data which includes area seven. All analyses were carried out via Rstudio.
**Statistical Analysis**

I ran a linear model to test whether CWM or CWV significantly changed as a function of annual SPEI. Because CWM’s were calculated at each transect, we also tested the inclusion of transect in the model as both an additive and an interaction term. The results of a log likelihood ratio test show the model of best fit to include transect as an additive term explaining trait CWMs rather than drought on its own. Adding transect as an interactive term did not improve the model. It is thus evident that there is a spatial component across transects, yet the implications of those findings are beyond the scope of this project. For the results below, I present findings from univariate models incorporating only the effect of environmental variables.

**Results**

The results from my analysis show certain traits as significant functional indicators of community structure in response to both current and lagged drought.

**Community Weighted Means**

Current annual SPEI had a positively significant effect on the mean value of final plant height across the community of area seven (P=0.037). Annual SPEI with a one year lag had a significant effect on RMR (P=0.004) and RDMC (P=0.04) across the community. RDMC increases with less drought while RMR values decrease with less drought.
Figure 2: Community weighted mean trait value across area seven in response to current annual SPEI (left) and annual SPEI lagged by one year (right).

**Community Weighted Variance**

Community weighted variance of final plant height across the community was significantly influenced by an increase in current annual SPEI (P=0.002). The trend suggests RDMC increasing with less drought-like conditions as well; however, this relationship is not significant. In regards to drought lagged by one year, the variety of RMR values throughout area seven significantly decreases with increasing values of annual SPEI (less drought) (P=0.02).
Heavy drought conditions during the previous year correspond to much less variation in the range of RMR values.

**Figure 3:** Community weighted variance of trait values across area seven in response to current annual SPEI (left) and annual SPEI lagged by one year (right).

**Discussion**

The experiment partially answered the proposed research question as well as highlighted essential implications for future research. The apparent traits in a community can accurately identify changes in community composition, however, it is relevant to test traits that directly relate to the environmental variable being studied. It is likely that I did not see relationships with seed mass and SLA because I was assessing those traits within an environmental context that
does not pertain to them. Within the xeric tallgrass prairie in Boulder Open Space, the significant relationship between current annual SPEI and plant height was expected. RMR also responded as predicted, and the results of RDMC suggests dominant species can influence community weighted means. We did not see any significant relationships between SPEI and seed mass or SLA.

**Height**

We see a significant relationship between community-weighted mean and community weighted variance of plant height and current annual SPEI, which suggests an environmental filtering effect. In drought years, the community gravitates towards shorter plants overall, and there is a clear trend in increased variation of height values as drought conditions become more abundant. In general, taller plants have a greater competitive advantage because they have greater access to light compared to their neighbors (Craine & Dybzinski, 2013; Garnier et al., 2015). This makes sense given my results, and it is likely that an increase in height in response to lower current annual SPEI relates to competition for resources. Additional forces that influence plant height apart from light and water include temperature and soil nutrient intake, and because the focus of my analysis is solely on drought, additional research is needed in order to better understand the interaction between these variables in response to drought and competition of resources. Studies have found that an increase in temperature is significantly correlated to an increase in plant height (Olson et al., 2018). In Boulder, temperatures have been increasing significantly over the past decades; therefore it makes sense that we see a filtering effect which allows taller plants to better persist overall (Figure 2). If we continue to observe drought in Colorado in the coming years, it is possible that the filtering effect of only enabling shorter
plants to persist in dry years will result in the phasing out of certain species altogether that are not equipped to thrive in a drier climate.

I did not see any relationships with seed mass. Seed mass relates to sexual regeneration and is most influenced by soil nutrient content as well as nutrient content during the growing season of the mother plant (Wulff, 1986; Kolodziejek, 2017). If anything, I expected to observe a relationship between increased seed mass in more intense drought conditions because larger seeds might have a better chance of survival (Garnier et al., 2015). It would be more likely to observe a relationship with seed mass if I included soil samples in my analysis.

**Root Traits**

I was interested in the trade-off between having denser roots to obtain more water (relates to RDMC) or having longer, thinner roots to maximize efficiency in low water environments (relates to root diameter and RMR). My results, however, are somewhat counterintuitive. My results show that RMR values decrease and the community gravitated towards lower RMR values overall when the previous year was a non-drought year. This makes sense intuitively because we would not expect plants to invest as much into their root systems during wetter years. However, the relationship between lagged SPEI (t-1) and RDMC was more surprising. As stated, RDMC measures root density, but the fact that non-drought like conditions during the previous year results in higher values of RDMC raises questions. If drought conditions are abundant, why would that result in both denser roots and a decrease in allocation towards root systems overall?

This finding led to a more in-depth analysis of community structure and of the relationship between the traits themselves and overall species abundance. It is common amongst plant communities to exhibit a high species richness with a considerable variation in abundance of species. Often, few species will represent a large portion of the overall cover, with many
different types of plant species occurring in low numbers. It is possible that certain dominant species within the community display substantially higher or lower trait values than average and as a result influence the mean value of the community. The correlation between RDMC and specific root length (SRL) is .828 which is much higher than expected (Table S2). SRL indicates root length, and higher SRL values indicate longer roots per unit mass area (Garnier et al., 2015). We would have expected to see a negative correlation between SRL and RDMC because long, dense roots is an odd combination as opposed to longer roots with a lower density. An analysis of the trait correlations at the community level indicates a positive relationship between SRL and RDMC; however, at the level of the individual, we see a different relationship.

The differences between trait correlations at the community level and the species level suggest implications for future research relating to the utilization of traits to predict changes in community structure. At the level of the individual, there appears to be no correlation between SRL and RDMC; however, at the community level, this changes drastically. A scatterplot matrix of the trait correlations themselves indicates certain species displaying odd trait combinations including low root diameter, high SRL, and high RDMC. This suggests that there are certain species with relatively thin, long, and dense root systems, which is a unique combination. As observed in the community-weighted mean output table, Poa agassizensis appears to be a dominant species, and there appears to be a temporal influence as well (Figure S2). It is possible that the community-weighted mean values of RDMC and SRL are being driven by individual species, one of which we identified to be Poa agassizensis. Poa agassizensis displays relatively high values of SRL, mid to upper range values in root diameter, and the highest value across all species in RDMC, favoring the idea that this species could be influencing community weighted values. Poa agassizensis is a C3 grass: a cool system grass that does well under high moisture conditions.
environments. Poa agassizensis is dominant during wetter years, and it is likely that this species adapted to these particular climate conditions over time. Our findings suggest the importance of taking precaution when using trait data to make inferences about the community because there is a potential for dominant species to impact community weighted means.

**Suggestions for Future Research**

Future research efforts should continue to observe community structure at the level of traits. When used in accordance with specific functions that they relate to, traits are accurate indicators of community response because they measure biological attributes of the species present in the community. Future research efforts should aim to include the spatial component across transects. Supplemental figures show community-weighted mean trait values in response to current annual and lagged drought split up by transect (Figure S3 & figure S4). It appears that specific transects respond differently to annual SPEI, although I did not test the significance of this phenomenon. Grazing was implemented in two of the transects in my analysis, and it is possible that grazing could influence community composition. One suggestion is for future studies to collect soil samples at each transect and include in their findings possible mechanisms of why transects show different relationships between traits and SPEI. It would also be interesting for future studies to look at major drought years in the record and then analyze community structure before and after the event. Figuring out which species are first to emerge or which are the most resilient will be beneficial in understanding how these communities respond and adapt to climate change.
Supplemental Information

Figure S1: Temporal mean relative transect vegetative cover split up by transect to represent amount of cover captured by trait dataset. Bars indicate ±1 standard error. Figure created by Caitlin White.
Table S1: Table of species included in trait dataset.

<table>
<thead>
<tr>
<th>Scientific Name</th>
<th>Life Form</th>
<th>Life History</th>
<th>Scientific Name</th>
<th>Life Form</th>
<th>Life History</th>
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</thead>
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<td>Forb</td>
<td>Perennial</td>
<td>Juncus arcticus</td>
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<td>Lotus tenuis</td>
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<td>Annual</td>
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<td>Perennial</td>
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<td>Perennial</td>
</tr>
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<td>Heterotheca foliosa</td>
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<td>Bromus tectorum</td>
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<td>Annual</td>
</tr>
<tr>
<td>Heterotheca villosa</td>
<td>Forb</td>
<td>Perennial</td>
<td>Lesquerella montana</td>
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<td>Perennial</td>
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Table S2: Correlation table of mature traits included in trait dataset

<table>
<thead>
<tr>
<th>final_height_cm</th>
<th>RMR</th>
<th>RDMC</th>
<th>SRL</th>
<th>Rdiam</th>
<th>LDMC</th>
<th>SLA</th>
<th>seed_mass</th>
</tr>
</thead>
<tbody>
<tr>
<td>final_height_cm</td>
<td>1.000000</td>
<td>-0.6258252</td>
<td>0.65240547</td>
<td>-0.45613975</td>
<td>-0.7713273</td>
<td>0.20093199</td>
<td>0.2715000</td>
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<tr>
<td>RMR</td>
<td>-0.6258252</td>
<td>1.000000</td>
<td>-0.58257462</td>
<td>-0.76386781</td>
<td>0.9105776</td>
<td>-0.37547131</td>
<td>-0.4561096</td>
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<tr>
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<tr>
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</table>
Figure S2: Boulder Open Space xeric tallgrass summer cover (all transects) over time - includes species in trait dataset. Figure created by Caitlin White.
**Figure S3:** Community weighted mean of plant traits and current annual SPEI split up by transect.
Figure S4: Community weighted mean of plant traits and lagged annual SPEI (t-1) separated by transect.
**Table S3:** Model table results for community weighted mean traits and current annual & lagged annual SPEI.

<table>
<thead>
<tr>
<th>CWM Model</th>
<th>n</th>
<th>P value</th>
<th>adjusted R²</th>
</tr>
</thead>
<tbody>
<tr>
<td>height ~ SPEI</td>
<td>220</td>
<td>0.038</td>
<td>0.01513</td>
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<tr>
<td>height ~ lagged SPEI (t-1)</td>
<td>211</td>
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<td>0.00324</td>
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<tr>
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<td>RDNC ~ lagged SPEI (t-1)</td>
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<td>0.01608</td>
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<tr>
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<td>-0.0026</td>
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**Table S4:** Model table results for community weighted variance of traits and current annual & lagged annual SPEI.

<table>
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<tr>
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<td>RMR ~ SPEI</td>
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<td>RMR ~ lagged SPEI (t-1)</td>
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<td>0.16</td>
<td>0.04634</td>
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</table>
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Bibliography


Barbara J. Bentz, Jacques Régnière, Christopher J Fettig, E. Matthew Hansen, Jane L. Hayes, Jeffrey A. Hicke, Rick G. Kelsey, Jose F. Negrón, Steven J. Seybold; Climate Change and Bark Beetles of the Western United States and Canada: Direct and Indirect Effects, BioScience, Volume 60, Issue 8, 1 September 2010, Pages 602–613, https://doi.org/10.1525/bio.2010.60.8.6


City of Boulder Open Space and Mountain Parks (2010). Grassland ecosystem management plan.


Danielle A. Way, Ram Oren; Differential responses to changes in growth temperature between trees from different functional groups and biomes: a review and synthesis of data, Tree Physiology, Volume 30, Issue 6, 1 June 2010, Pages 669–688, https://doi.org/10.1093/treephys/tpq015


