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The Effects of Aridity and Herbivore Assemblage on Plant Functional Traits and Diversity

A Thesis submitted in partial satisfaction of the
requirements for the degree Master of Arts in
Ecology, Evolution, and Marine Biology

by

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September 2021

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by

Maggie Klope

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Mike, I would not be where I am today if it were not for your constant support and laughter – thank you.

ABSTRACT

The Effects of Aridity and Herbivore Assemblage on Plant Functional Traits and Diversity

by

Maggie Klope

Large herbivore communities are rapidly changing globally, with populations of large wild herbivores declining while large domestic herbivore populations are increasing exponentially. Along with climate change, these alterations in large herbivore communities are two of the most important impacts on ecosystem functioning in terrestrial systems. While large herbivores and climate are known to independently influence the cover and composition of herbaceous plant communities, manipulative experiments have rarely captured the interaction between realistic patterns of large herbivore assemblage change and climatic conditions. Critically, no studies to date have experimentally explored how these realistic changes in herbivore assemblages interact with climate to affect functional traits and functional diversity of herbaceous communities, even though these metrics have been demonstrated as some of the most useful proxies for ecosystem function.

Here, we use a multi-factor large herbivore exclosure experiment to simulate the three most common herbivore change scenarios globally, replicated along a topo-climatic gradient. We then explore the interaction between climate and herbivore assemblage on community-level functional traits and functional diversity of herbaceous plant understories in an oak savanna ecosystem.

Our findings demonstrate interacting effects between changes in large herbivore assemblages and climate. We found a shift between more drought tolerance traits to drought avoidance traits with increasing aridity, and found that plant community responses to grazing changed from an herbivore avoidance strategy at arid sites to a more herbivore tolerant strategy at mesic sites. Even over a relatively large temperature gradient within this landscape, we observed that the effects of herbivores on community-level traits can sometimes counteract those of climate. Finally, we found that cattle and large wild herbivores can differ in the magnitude and direction of effects on functional traits and diversity.

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I. Introduction

Large herbivores profoundly shape herbaceous plant communities, impacting plant abundance, biomass, survival, and reproduction (Díaz et al., 2007; Jia et al., 2018). These effects have been extensively studied using large herbivore exclosures to simulate the loss or removal of native large herbivore communities (Koerner et al., 2018). However, at the global scale, as large wild herbivore communities decline (Ripple et al., 2015) they are often replaced by domestic livestock at densities far exceeding the historic densities of their wild counterparts (Barnosky, 2008). While these changes in herbivore density and identity can have a substantial effect on plant communities and ecosystem function (Forbes et al., 2019; Malhi et al., 2016; Young et al., 2013), few experimental studies explicitly focus on realistic changes in herbivore assemblages by manipulating domestic and wild herbivores simultaneously (Forbes et al., 2019). Similarly, although it is well established that the effects of herbivores change across climate contexts, there are few, if any, experiments that have investigated how the effects of this type of realistic change in herbivores assemblages may vary across climate contexts, likely due to the logistical challenges of creating an ecological experiment which manipulates both herbivore assemblages and climate.

In this study, we explore the interactive effects of climate and realistic changes in large herbivore (hereafter referred to as “herbivore”) communities on plant functional traits and functional diversity. We focus on plant functional traits and functional diversity because they are frequently used to detect how both changes in climatic context and herbivores abundance or identity alter plant communities (De Bello, Lepš, & Sebastià, 2005; Díaz, Noy-Meir, & Cabido, 2001; Lavorel & Garnier, 2002). Critically, these metrics offer a powerful tool to understand the impacts of global change because they are often tightly tied to ecosystem

functions (Borer et al., 2014; De Bello et al., 2010; Díaz & Cabido, 2001; Funk et al., 2017; Lavorel & Garnier, 2002; Quétier, Thébaud, & Lavorel, 2007; Tilman, 1997; Zhu, Jiang, & Zhang, 2016).

The impacts of herbivores on plant functional traits have been studied in a variety of systems, and plant responses are typically placed into one of two strategies: herbivore avoidance and herbivore tolerance. In areas with a long history of grazing or at high grazing intensity, plant communities typically have a greater proportion of herbivore tolerant species (Del-Val & Crawley, 2005; Tahmasebi Kohyani, Bossuyt, Bonte, & Hoffmann, 2009). These species compensate for the frequent removal of biomass by quickly growing leaves and are characterized by high specific leaf area (SLA), low leaf dry matter content (LDMC), and high leaf nitrogen (Cingolani, Posse, & Collantes, 2005; Díaz et al., 2001). With low levels of herbivory there are often more plant species with herbivore avoidance traits (An & Li, 2014), characterized by shorter stature, smaller leaves, lower SLA, and higher LDMC (Landsberg, Lavorel, & Stol, 1999). However, the tradeoff between herbivore avoidance and tolerance strategies is dependent on herbivore identity and selectivity, ecosystem productivity, plant community composition, and nutrient availability (Augustine & McNaughton, 1998; Liu et al., 2015; Török et al., 2018; Tóth et al., 2016).

Existing research on the impacts of grazing on functional diversity has generated mixed results. Functional diversity has been shown to be positively correlated (Catorci, Cesaretti, Malatesta, & Tardella, 2014; Komac, Pladevall, Domènech, & Fanlo, 2015; Mandle & Ticktin, 2015; Niu, He, & Lechowicz, 2016a), negatively correlated (De Bello, Lepš, & Sebastià, 2006; Jäschke, Heberling, & Wesche, 2020; Rahmanian et al., 2019), and uncorrelated with herbivore presence (Jäschke et al., 2020; Niu, He, & Lechowicz, 2016a; Rahmanian et al., 2019). Such

differences in responses may be due to variation in grazing intensity and timing across studies, which can moderate the response of plant communities (Eldridge, Delgado-Baquerizo, Travers, Val, & Oliver, 2017; Pérez-Camacho et al., 2012; Rook et al., 2004)) and functional traits and diversity change (Tóth et al., 2016; van der Plas, Howison, Mpanza, Croomsigt, & Olf, 2016). Additionally, herbivore identity can affect the magnitude and direction of responses of plant communities and functional traits and diversity (Tóth et al., 2018). Therefore, to accurately predict the effects of changing herbivore assemblages on plant functional traits and diversity in an anthropogenic landscape, it is important to study the impacts of both native herbivore and livestock species. However, while studies have examined differential effects of specific livestock species on plant functional diversity and traits, few studies have explicitly compared differences in impacts to functional traits and diversity between native and introduced herbivores in the same system (but see van der Plas et al., 2016).

Plant functional traits and diversity are also strongly influenced by climatic conditions. At a global level, plant functional traits vary with climate (Asner, Knapp, Anderson, Martin, & Vaughn, 2016; Moles et al., 2014; Wright et al., 2005), while at a local level, differing responses to climate are seen based on plant communities and functional groups (Ahrens et al., 2020; Diaz, Cabido, & Casanoves, 1998; Török et al., 2018; Wellstein et al., 2017). Globally, vascular plants generally experience decreased leaf area, SLA, leaf Nitrogen with higher levels of aridity (Niinemets, 2001; Wright et al., 2005; Zheng, Li, Lan, Ren, & Wang, 2015). However, for extremely arid conditions and Mediterranean climates, the opposite pattern may occur (Ackerly, Knight, Weiss, Barton, & Starmer, 2002). This is due to an increase in the amount of drought-tolerant species in these systems, which are characterized by high leaf area (LA) and SLA, whereas more mesic systems typically have more drought-avoidant species

characterized by with low values of LA and SLA. Climate effects on the functional diversity of herbaceous communities are variable. Some studies have shown functional diversity to be higher at arid sites (De Bello et al., 2006) and to increase with long-term drought (Griffin-Nolan et al., 2019), while others have shown that it may be uncoupled from climate (Gallagher, Hughes, & Leishman, 2013; Rahmanian et al., 2019); however, the latter studies may not have sampled sufficiently arid climates to detect alterations to functional diversity.

Table 1. Terms, abbreviations, and definitions.

Term	Abbreviation	Definition
Leaf Area	LA	One-sided leaf area (mm ²)
Specific Leaf Area	SLA	leaf area / dry mass (mm ² mg ⁻¹)
Leaf Dry Matter Content	LDMC	leaf dry mass / fresh leaf mass (mg1g ⁻¹)
Seed mass		Weight of dry seed (mg)
Leaf Nitrogen Content	LNC	Total leaf nitrogen content per dry mass of leaf matter (mg1g ⁻¹),
Community-Weighted Mean	CWM	Community mean of each species' trait value weighted by their site-specific abundance
Functional Richness	FRic	The convex hull, or volume, of plant community's functional trait space
Functional Divergence	FDiv	Distance of abundance-weighted trait values from the center of the communities' functional space
Functional Evenness	FEve	The regularity of abundances of each species within the functional space
Functional Dispersion	FDis	The average distance of species to centroid weighted by their abundance
Intraspecific Trait Variation	ITV	Variation in trait values between member of the same plant species

Plant community responses to herbivores are also known to be dependent on climate (De Bello et al., 2006; Koerner et al., 2018; Orr et al., in press.; Pérez-Camacho et al., 2012; Young et al., 2013). Therefore, we expect there to be an interaction between climate and herbivore assemblage on functional trait and diversity responses. Grazing has previously been found to enhance functional diversity at arid sites, but decrease functional diversity at more mesic sites (De Bello et al., 2006). Similarly, Zheng et al (2015) found that community-weighted means (CWM) of SLA and leaf nitrogen content (LNC) increased in response to grazing at arid sites, but decreased in response to grazing at mesic sites. However, the studies that have investigated the effect of herbivores and climate together on plant functional traits manipulate all herbivores solely via presence/absence, rather than separating the impacts of wild herbivores and livestock.

Not only do climate and herbivory alter plant functional traits and diversity within communities, but they also alter variability in traits within species (intraspecific trait variation; ITV) (Lang et al., 2020; Niu, Zhang, & Lechowicz, 2020). However, not all species respond with the same level of variability with regards to climate gradients (Albert et al., 2010) and not all traits show the same level of plasticity (Cornelissen et al., 2003). For example, specific leaf area (SLA) shows more variability within species than leaf dry matter content (LDMC) (Garnier et al., 2001), and the percent of species that respond to grazing with higher ITV of SLA has been found to increase along a precipitation gradient (Lang et al., 2020). The role of ITV in moderating the effects of climate and herbivory is critical to understand because ITV has been found to affect ecosystem processes (Westerband, Funk, & Barton, 2021) and affects the response of CWMs and functional diversity to disturbance and environmental change (Jung et al., 2013; Siefert & Ritchie, 2016; Zheng et al., 2015).

Climate and herbivory are ubiquitous drivers that shape terrestrial ecosystems, and the impact both have on ecosystems is changing due to anthropogenic effects. As such, conducting empirical studies in an experimental system that not only manipulates herbivore density and identity in realistic patterns, but is replicated across a climatic gradient, is essential to further piece together the impacts of herbivory on ecosystems. By understanding how and when functional traits and diversity change with different climates and herbivore assemblages, we can better understand how anthropogenic change will alter ecosystem function.

A. Questions & Hypotheses

In this study, we experimentally manipulated ungulate composition to examine the effects of three common forms of herbivore communities in the Anthropocene – total wildlife loss (or removal), wildlife without livestock, and wildlife with livestock – on the composition and diversity of plant functional traits at three topo-climatic conditions (hereafter referred to as “climate”) across a landscape. Using six commonly examined functional traits (Leaf Area - LA; Specific Leaf Area - SLA; Leaf Dry Matter Content - LDMC; Leaf Nitrogen Concentration - LNC; and seed mass, Table 1) that are known to be linked to various metrics of ecosystem function, we ask the following questions.

1) How do climate, herbivore assemblage, and their interaction affect plant functional trait composition within a site? We predicted that with increasing access by herbivores, plant communities would experience increases in community-weighted means of SLA, LA, and LNC and decreases in LDMC and seed mass, due to increasing abundance of herbivore tolerant plant species. However, if the abundance of herbivore avoidant species increased, the opposite trends should occur. We expected that these effects would be stronger in more arid climates because species adapted to high levels of aridity have a lower capacity for regrowth after

biomass removal (low tolerance) (Paruelo, Lauenroth, Burke, & Sala, 1999) and environmental stress and grazing produce synergistic effects (Louthan, Doak, Goheen, Palmer, & Pringle, 2013; Oñatibia, Amengual, Boyero, & Aguiar, 2020; Quiroga, Golluscio, Blanco, & Fernández, 2010).

2) How much are community traits influenced by species turnover and intraspecific trait variation (ITV)? We expected that community average traits, or abundance-weighted Community Weighted Mean traits (CWMs) will be influenced by both species turnover and ITV, but do not know the relative contribution of each to community-level trait variation. We predicted the effects of climate would be predominately explained by species turnover, while the effects of herbivore treatment within the same climate would be primarily driven by ITV because we expected aridity to act as a stronger environmental filter than herbivore assemblage.

3) How do climate, herbivore assemblage, and their interaction affect plant functional diversity within a community? We predicted that increases in environmental stress (aridity) may lead to reduced functional diversity (lower values of Functional Richness [FRic], Functional Divergence [FDiv], Functional Evenness [FEve], and Functional Dispersion [FDis]) with a larger effect observed with increased access to grazing if aridity and herbivore presence act as filters and cause species to converge on specific trait values (as outlined in question one). Conversely, herbivory may increase functional diversity if grazing acts as a release from a dominant competitor (Koerner et al., 2018).

II. Methods

A. Study Site

We conducted this study at the Tejon Ranch Enclosure Experiment (TREE) located at Tejon Ranch in Kern Co. CA (34°5'80" N, 118°3'50" W). Established in 2016, TREE consists of 27, 1-hectare plots which include three replicates (blocks) of three herbivore treatments at each of three topo-climate conditions (Figure 1). The treatments simulate some of the common forms of herbivore compositional change globally and regionally: 1) no large herbivores (Total enclosure, simulating defaunated lands), 2) wildlife-only (Partial enclosure, simulating conserved lands not grazed by livestock), and 3) cattle and wildlife present (Open, unfenced, indicative of managed grazing lands). These treatments are repeated across three aridity/climate types: mesic (high water availability), intermediate, and arid (low water availability). Details on the site's three climate types are in Table 2 and Supplement 1, and have been described in detail in Orr et al (in press). Vegetation across the sites consists of oak savanna, with the predominant canopy consisting of blue oak (*Quercus douglasii*), valley oak (*Q. lobata*), and black oak (*Q. kelloggii*), with density and species of oak varying with climate type. The majority of the understory consists of non-native grasses (*Bromus diandrus*, *B. hordeacous*) in arid sites, non-native grass (*B. diandrus*) and native woody shrubs (*Ericameria nauseosa*) at intermediate sites, and native woody shrubs (*Ribes californicum* var. *hesperium*) in mesic sites. Soils are loamy granite residuum Haploxerolls across all sites. Mesic sites are sloped north-facing, Intermediate sites are sloped south-facing, and Arid sites have minimal slope. Large herbivores common in the region consist of mule deer (*Odocoileus hemionus*),

introduced Rocky Mountain elk (*Cervus elaphus nelsoni*), invasive wild boar (*Sus scrofa*), and cattle (*Bos Taurus*).

This experiment provides an ideal scenario for detecting the effects of realistic herbivore change by controlling access to cattle and wild herbivores across climate contexts, allowing us to investigate herbivore assemblage interactions with climate on plant communities. Notably, the climate treatments of this experiment were selected to represent three probable future climate change scenarios that oak savannas will experience in California (Orr et al., in press). Previous research at this location has shown strong changes in plant diversity and cover which change interactively with herbivore assemblage and climate, but has not explored the effects on plant functional traits (Orr et al., in press).

Figure 1. A) Location of the Tejon Ranch Enclosure Experiment (TREE) in south-central California, B) Location of the 27, 1-hectare plots across three climate and three herbivore treatments (not drawn to scale)

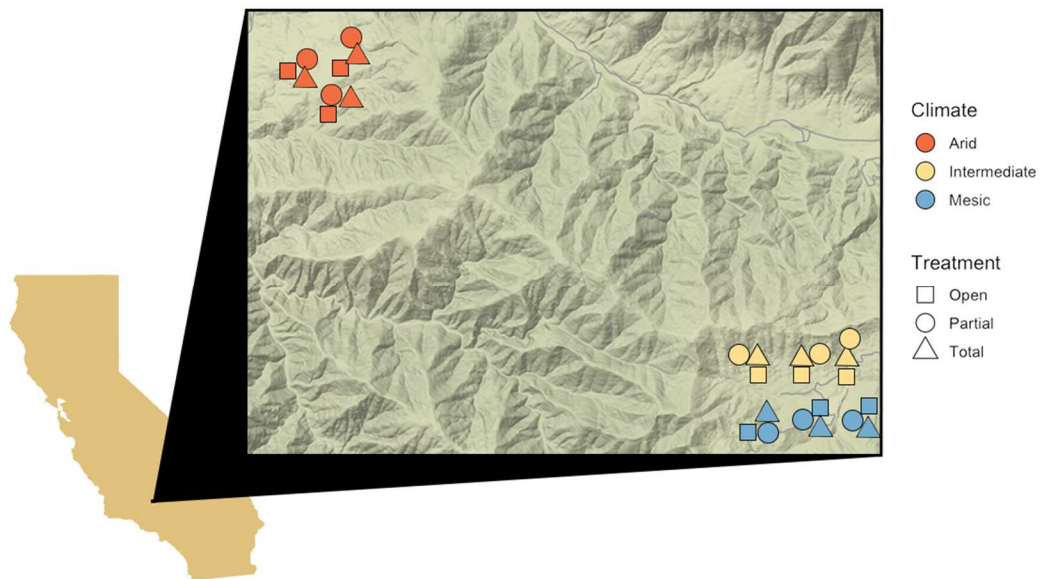


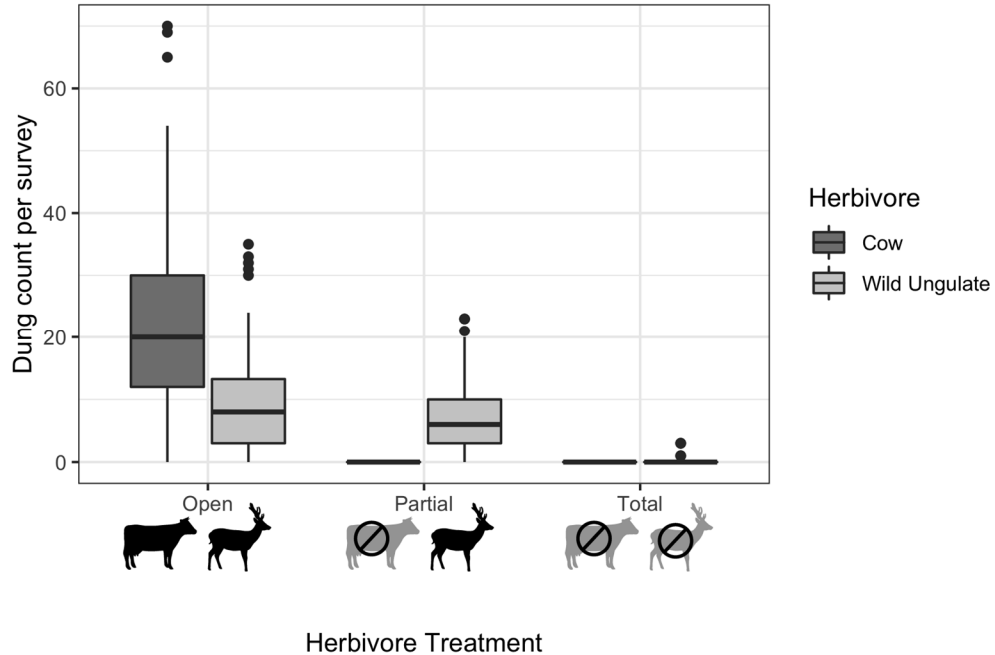
Table 2. Climate data using 30m downscaled PRISM data (Davis, 2018; McCullough et al., 2016) for 1983-2013 averaged across all plots at a climate (Supplement 1).

Climate	Elevation (m)	Total Annual Precipitation (mm)	Mean daily minimum temp. (°C)	Mean daily maximum temp. (°C)	Climate Water Deficit (CWD)	Potential Evapotranspiration (PET)
Arid	848.78	366.58	9.26	21.96	1155.95	1515.61
Intermediate	1581.78	428.28	6.23	17.92	1002.37	1483.80
Mesic	1668.11	431.94	6.25	17.99	882.10	1303.40

B. Herbivore Community

Dung counts conducted within each plot throughout 2017 and 2018 were used to determine herbivore density and composition (Orr et al., in press). These data show that herbivore treatments successfully reduced total herbivore densities and that those densities did not significantly differ between climate levels. Critically, total densities of wild herbivores were not affected by the fenced Partial enclosure and Total enclosures effectively excluded all large herbivores. Therefore, impacts from cattle can be considered additive (Figure 2).

Figure 2. Dung density by herbivore treatment (data from Orr et al., in press). Total wild ungulate dung counts did not differ between Open and Partial Treatment. Upper and lower limits of the box represent the first and third quartiles, lines represent 1.5 times the interquartile range, and points represent outliers.



C. Plant Functional Trait Collection

In order to determine how herbivore and climate alter plant functional traits, we chose a suite of easy-to-measure functional traits that are indicative of how both biotic and abiotic change impact ecosystem function: specific leaf area (SLA), leaf area (LA), leaf dry matter content (LDMC), leaf nitrogen content (LNC), and seed mass (Table 1).

Plant traits were collected in Spring 2017 for common species at one block per treatment/aridity level (n=9). Common species included those comprising at least 90% of the total understory plant cover in each plot based on spring transect vegetation surveys (Supplement 2). Species abundance was determined from vegetation surveys conducted in Spring 2019 within two weeks of each site's peak NDVI. Methods are detailed in Orr et al. (in

press), but briefly, a 1m² quadrat was placed at 10-meter intervals along six 50-meter transects in each plot (36 m² per plot) to determine species cover (up to 100% for each species).

Collection of functional traits for community trait analysis followed Cornelissen et al. (2003) methods. Specifically, two mature leaves were collected from 10 individuals of each common species when possible from full-sun areas. Effort was made to spread leaf collection throughout the whole plot, with a minimum sampling distance of 5 meters between individuals, unless there were fewer than 10 individuals located within the entire plot. Plant samples were kept in a cooler box on ice until they could be placed into beakers of water and kept in a large refrigerator (4 °C) for up to 48 hours before processing.

Leaf area and fresh and dried leaf weights were calculated in order to determine LA, SLA, and LDMC. LA was determined by scanning leaves with a digital scanner and using ImageJ (Schneider, Rasband, & Eliceiri, 2012) to compute each leaf's area. Leaf samples were weighed fresh (after being wiped to remove any residual moisture), dried at 60 °C for at least 36 hours, and weighed again for dry weight.

LNC and seed mass values were obtained from the TRY Plant Trait Database (Kattge et al., 2020). Any missing trait values were substituted with additional trait collection in 2019, or by using closely-related species, genus-level or family-level records (substitutions outlined in Supplement 2).

D. Community-level Trait Analysis

We performed a community-level analysis to understand how the community expressions of traits was influenced by climate and herbivore assemblages. To do so, we calculated the Community-Weighted Mean (CWM) for each functional trait in each plot. These were calculated by taking the mean of each species' trait value at a plot weighted by their 2019

cover abundance ($CWM = \sum_i^n t_i * a_i$; where n = number of species in each plot, t_i = trait value for i th species, and a_i = abundance for the i th species at a plot).

To test the differences between CWMs across herbivore and climate treatments, we built linear mixed effects models (LMMs) using the glmmTMB R package (v1.0.1, Brooks et al., 2017) using combinations of climate, herbivore treatment, and their interaction as fixed effects and block as a random effect. We selected for best-fit models by minimizing Akaike information criterion adjusted for small sample sizes (AICc) values using the MuMIn R package (v1.43.17, Barkton, 2009). If AICc of multiple models were within two units, we chose the model with the fewest parameters (Burnham & Anderson, 2004). We verified that model assumptions were met by visually inspecting the normality of residuals using the simulateResiduals function from the DHARMA R package (v0.4.1, Hartig, 2021). Using the best-fitting LMM, we examined pairwise differences using the “emmeans” function as a post-hoc test (“emmeans” R package, v1.6.0, Lenth, 2021). When required, a $\log(x)$ or a $\log(x+1)$ transformations were performed in order to meet model assumptions.

E. Species turnover and ITV

To determine the relative contributions of species turnover and intraspecific trait variation (ITV) to community functional trait changes, we decomposed the variation of CWM values into variability from intraspecific trait variability, variability from species turnover, and their covariation utilizing methods from Lepš, de Bello, Šmilauer, & Doležal (2011), including the R function trait.flex.anova (see Lepš et al., 2011). Following their methods, we utilized three, two-way analysis of variance (ANOVA), or permutational analysis of variance (PERMANOVA) for non-normal data, one using “specific” averages, one using “fixed averages”, and one using ITV values. “Specific” averages weigh a species’ site-specific values

by their abundances, and are used to represent total variation. Therefore, we used our previously calculated CWMs as the response variable. “Fixed” averages weigh species’ abundances by an average, or fixed, trait value from all the locations where this species occurs and are used to represent Species Turnover. Therefore, we calculated the average trait value for each species from every plot where they occurred as the response variable. To calculate ITV, we subtracted our Fixed averages from our Specific averages. All ANOVAS and PERMANOVAS took the form: *response variable ~ climate * treatment*.

After performing these three ANOVAS for each of our traits, we used their total Sum of Squares (SS) to determine the relative contribution of Species Turnover and ITV to the trait variability by decomposing the amount of variability explained by climate, treatment, and their interactions and unexplained error ($SS_{\text{total}} = SS_{\text{climate}} + SS_{\text{treatment}} + SS_{\text{treatment:climate}} + SS_{\text{error}}$). Further following Lepš et al., we expect that $SS_{\text{specific}} = SS_{\text{fixed}} + SS_{\text{ITV}}$, with species turnover and ITV effects varying independently. By observing whether SS_{specific} is lower than expected, we can then look to see if SS_{fixed} and SS_{ITV} are positively or negatively correlated. If positively correlated, then SS_{specific} will be higher than expected, meaning they are selecting for the same trait values. When negatively correlated, SS_{specific} will be lower than expected, and they are selecting for conflicting trait values. Lepš et al expands on this further by determining their covariations as $\text{CovSS} = SS_{\text{specific}} - SS_{\text{fixed}} - SS_{\text{ITV}}$, where positive and negative CovSS values mean a positive and negative covariation, respectively. We used this method, and the `trait.flex.anova`, to perform the three ANOVAS for LA, SLA, and LDMC and decompose their variances. We did not evaluate seed mass or LNC due to a lack of site-specific trait values.

F. Plant Functional Diversity

To capture overall functional diversity, we calculated functional richness (FRic; the convex hull, or volume, of functional trait space; Villéger, Mason, & Mouillot, 2008). To capture variation in functional diversity, we calculated functional divergence (FDiv; species divergence from the mean; Villéger, Mason, & Mouillot, 2008), functional evenness (FEve; the regularity of abundances of each species within the functional space; Villéger, Mason, & Mouillot, 2008), and functional dispersion (FDis; the average distance of species to centroid weighted by their abundance; Laliberté & Legendre, 2010). Each metric was calculated using the FD package in R (v1.0-12, Laliberté, Legendre, & Shipley, 2014). For FEve and FDis, relative abundance values from the previously mentioned methods were used. We followed the method outlined above for CWMs and created one LMM for each diversity response metric, chose the model with the lowest AICc value (or the simplest model if within 2 values) to determine the inclusion of herbivory, climate, and their interaction as fixed effects, included block as a random effect, and used the emmeans R package for group comparisons.

IV. Results

A. Community-level changes in functional traits

As predicted, climate interacted with herbivore treatment to influence LA_{CWM} (Supplement 3). The total removal of larger herbivores had a positive effect on LA_{CWM} at Arid ($p = 0.0007$), a neutral effect at Intermediate, and a negative effect at Mesic ($p = 0.002$). The removal of only cattle had a neutral effect on LA_{CWM} at Arid and Mesic, and a positive effect at Intermediate ($p = 0.003$). LA_{CWM} increased with aridity, but only at the total herbivore removal treatments (Arid-Int: $p = 0.0001$, Int-Mesic: $p = 0.0026$, Mesic-Arid: $p < 0.0001$). Climate had no effect

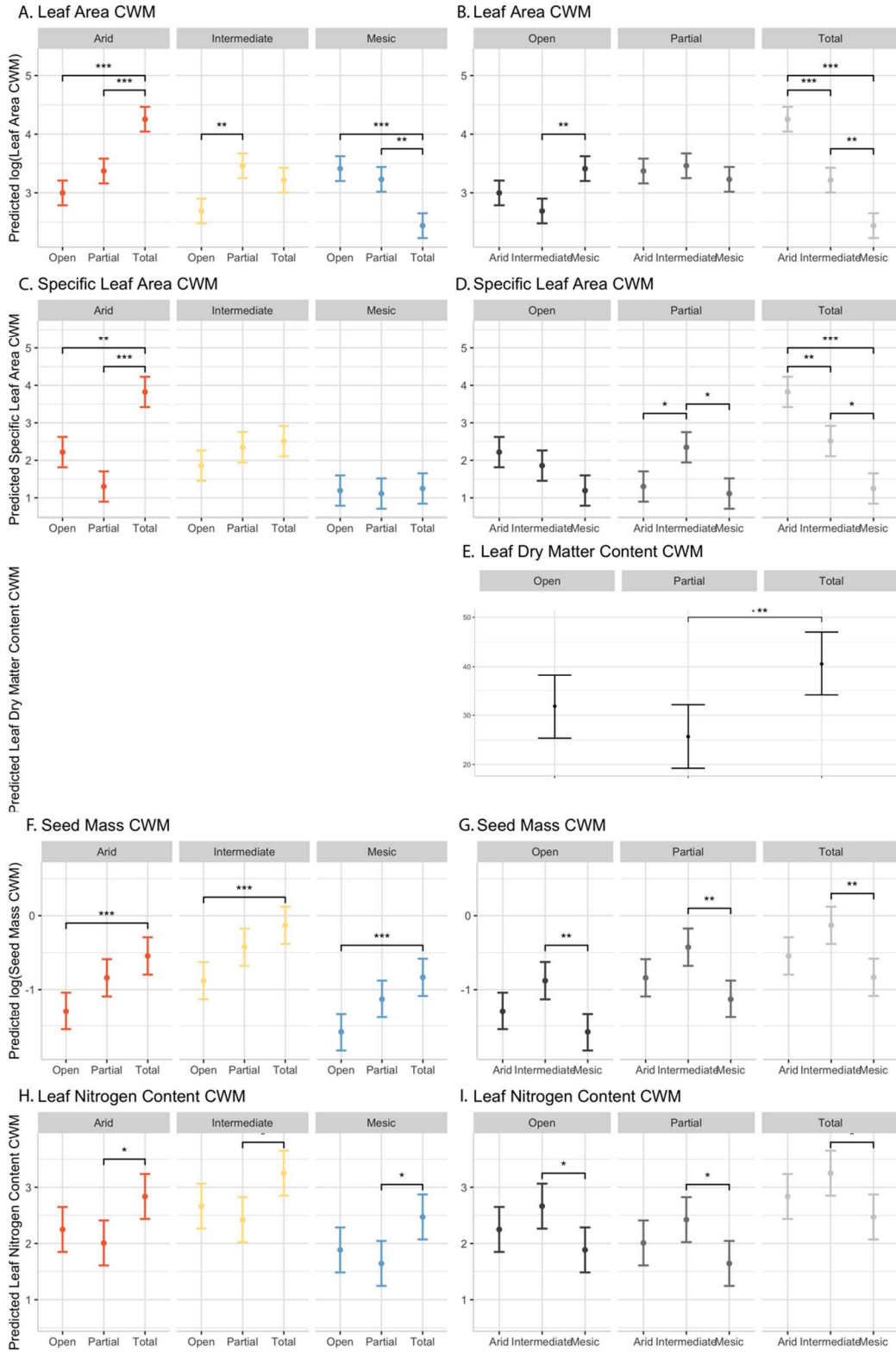
on wildlife-only plots. Between unfenced plots, LA_{CWM} was larger at Mesic than Intermediate ($p = 0.0051$).

Similarly, climate interacted with herbivore treatment to influence SLA_{CWM} (Supplement 3). The removal of only cattle had no significant effect on SLA_{CWM} . The removal of all herbivores increased SLA_{CWM} , but only at Arid ($p < .0001$). Similar to LA_{CWM} , we see a step-wise increase in SLA_{CWM} with Aridity, but only with the complete removal of herbivores (Arid-Int: $p = 0.0084$, Int-Mesic: $p = 0.0112$, Mesic-Arid: $p < .0001$). A similar, non-significant trend was observed within Open treatments. Within wildlife-only treatments, Intermediate was larger than both Arid ($p = 0.0477$) and Mesic ($p = 0.0140$).

Only herbivore treatment was present in the model for $LDMC_{CWM}$ (Supplement 3). Total herbivore removal plot showed larger $LDMC_{CWM}$ values than wildlife-only treatments ($p = 0.0016$), with no significant difference between unfenced and wildlife-only or total herbivore removal.

Both climate and treatment had important influences on seed $mass_{CWM}$ and LNC_{CWM} , but treatment effects did not vary by climate for these metrics (Supplement 3). For all climates, seed $mass_{CWM}$ was larger in total removal plots than unfenced ($p = 0.0009$). For all herbivore treatments, seed $mass_{CWM}$ values were larger at Intermediate than Mesic ($p = 0.0018$). Between herbivore treatments, LNC_{CWM} values were larger with total herbivore removal than wildlife-only plots for all climates ($p = 0.0308$). Across herbivore treatments, LNC_{CWM} was higher in Intermediate than Mesic ($p = 0.0478$).

Figure 3. Estimate Marginal Means of CWMs by climate and herbivore treatments. The first column shows relationships climate, and the second column shows relationships by herbivore treatment. Significance codes: 0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05.



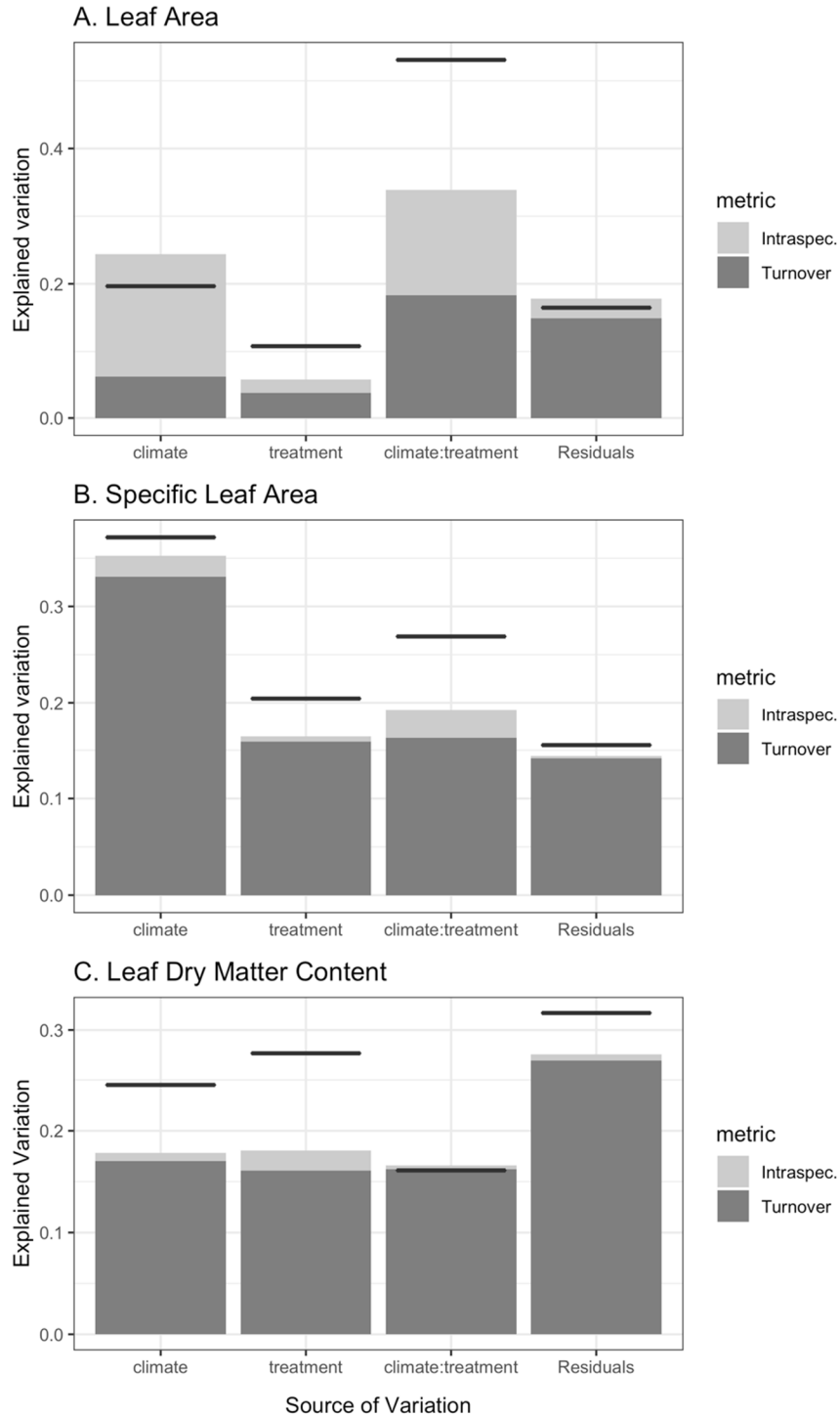
B. Species Turnover and ITV

For all traits, both species turnover and ITV accounted for the sources of variation within the community (Table 3, Table S-6), but the relative contribution of each differed between the measured traits. SLA_{CWM} and $LDMC_{CWM}$ variation were explained predominately by species turnover (79% and 76% of total variation, respectively), while LA_{CWM} variation was more evenly influenced by both species turnover and ITV (Figure 4). Species turnover and ITV positively covaried for total sources of variation. For SLA_{CWM} , species turnover and ITV were positively correlated for all sources of variation. Only for variation due to climate treatment for LA_{CWM} and variation due to climate and herbivory interaction for $LDMC_{CWM}$ did we see any negative covariation in experimental treatments.

Table 3. Relative contributions (%) of Species Turnover and intraspecific variation (ITV), their covariation, and the total variation.

CWM	Terms	Turnover	ITV	Covariation	Total
LA	climate	6.11	18.29	-4.75	19.65
	treatment	3.74	1.96	5.09	10.79
	climate:treatment	18.33	15.58	19.18	53.09
	Residuals	14.87	2.97	-1.36	16.47
	Total	43.05	38.79	18.15	100.00
SLA	climate	33.08	2.17	1.91	37.16
	treatment	15.86	0.57	4.01	20.44
	climate:treatment	16.29	2.98	7.61	26.88
	Residuals	14.13	0.26	1.13	15.52
	Total	79.37	5.98	14.65	100.00
LDMC	climate	17.01	0.79	6.70	24.51
	treatment	16.10	1.94	9.67	27.71
	climate:treatment	16.23	0.35	-0.48	16.11
	Residuals	27.02	0.59	4.06	31.67
	Total	76.37	3.68	19.96	100.00

Figure 4. Relative contribution of Species Turnover and ITV to sources of variation for community-weighted traits. Black line represents the total amount of variance. Any space between the column and the black line represents the covariation between Turnover and ITV. If the column surpasses the black line, then there is a negative correlation, and when it does not surpass the black line, there is a positive correlation.



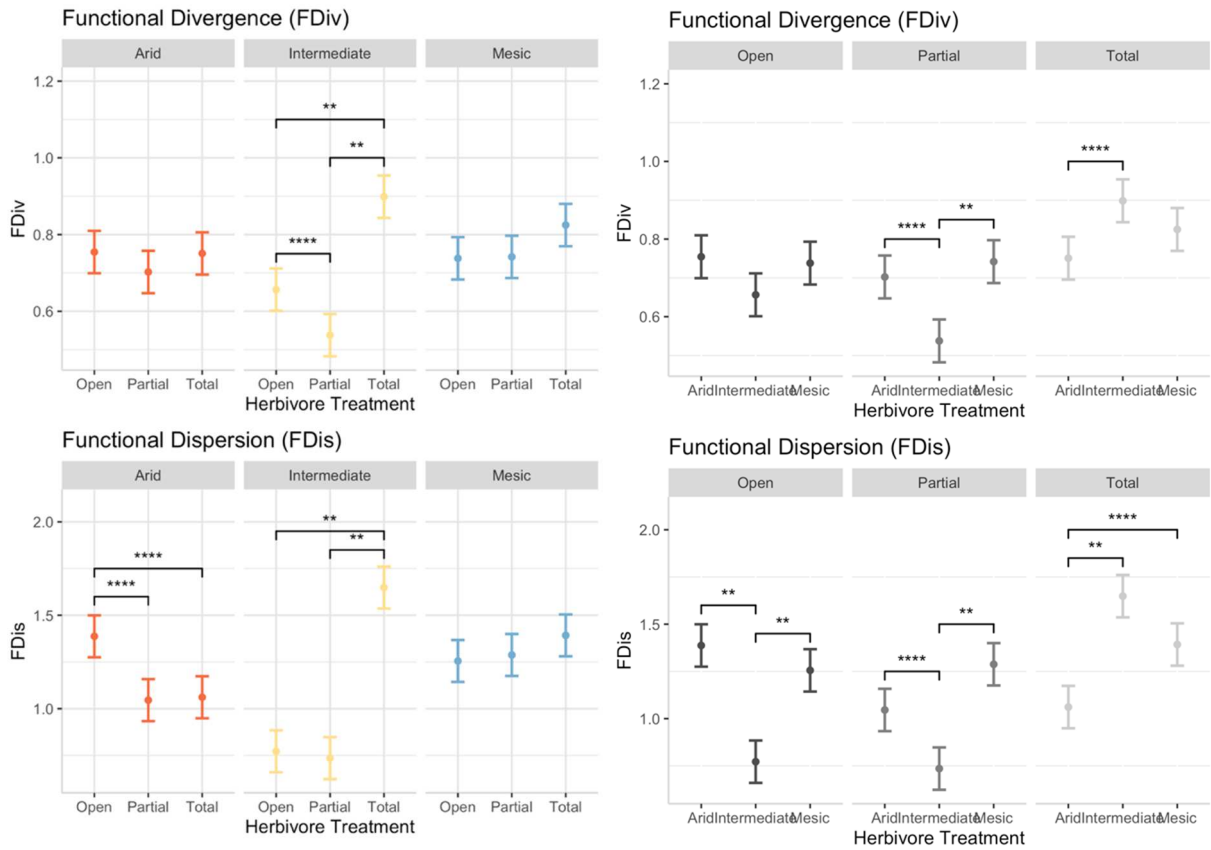
C. Functional Diversity

Metrics of functional diversity responded differently to climate and grazing treatment, and responses were not consistent across metrics. Best-fit models for FDiv and FDis included climate, treatment, and their interaction (Table S-4). However, neither climate or herbivore treatment significantly altered FEve and FRic, with the models including the intercept only.

For FDiv, only Intermediate climate experienced an effect of herbivore treatment, with the removal of cattle causing a decrease in FDiv ($p = 0.0241$), and the removal of all wildlife causing an increase ($p = <.0001$). Between total removal treatments, FDiv was larger at Arid than Intermediate ($p = 0.0016$). Between wildlife-only treatments, FDiv was larger at both Mesic and Arid than Intermediate ($p = 0.0025$, $p = 0.0167$, respectively). There were no differences between unfenced herbivore treatments across the climates.

For FDis, values were significantly larger at Mesic than both Arid ($p = 0.016$) and Intermediate ($p = 0.0001$) when averaged over treatment. There was no effect of herbivore treatment at Mesic climate. At Intermediate, total removal plots had higher FDis than both unfenced ($p = <.0001$) and wildlife-only plots ($p = <.0001$). At Arid, unfenced plots had higher FDis than both wildlife-only ($p = 0.0142$) and total removal plots ($p = 0.0205$). Between unfenced treatments and between wildlife-only treatments, FDis was larger in Mesic and Arid than Intermediate ($p = 0.0001$, $p = 0.0297$, respectively), with no difference between Arid and Intermediate. For total removal treatments, FDis values were significantly smaller at Arid than both Mesic and Intermediate ($p = 0.0181$, $p = 0.0001$, respectively), with no difference between Mesic and Intermediate.

Figure 5. Estimate Marginal Means for functional diversity metrics (FDiv and FDis) by climate and herbivore treatment. Significance codes: 0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05.



V. Discussion

We found that both climate and herbivore treatment impacted plant functional traits and functional diversity. We frequently observed an interaction between climate and herbivore assemblage, and detected differences between wildlife-only treatments and those accessed by wildlife and cattle. Notably, the interaction effects sometimes changed not only in magnitude, but also the direction of the responses, even within this one oak savanna ecosystem. However, results did not always meet our predictions, mostly likely due to differences in plant community dissimilarity, changes in the dominance of plant functional groups, and herbivore type, the latter of which illustrates the importance for studying different herbivore assemblages.

The response of community-level trait means to grazing and climate

In the absence of large herbivores, LA_{CWM} and SLA_{CWM} showed large decreases from Arid to Intermediate to Mesic climate sites, indicates a switch from drought avoidant species in dry sites to more drought tolerant species at mesic sites, as is more frequently observed in Mediterranean climates (Ackerly et al., 2002). However, we see a divergence from this trend with the presence of wild herbivores and cattle.

We observed opposing effects of herbivore assemblage on LA_{CWM} and SLA_{CWM} . Contrary to other studies, LA_{CWM} and SLA_{CWM} decreased from total large herbivore removal to unfenced and wildlife-only plots at Arid. LA_{CWM} did follow predictions at Mesic with lower values at total herbivore removal. This opposite trend between more arid and mesic sites is likely driven by a shift from herbivore avoidance to herbivore tolerance strategies between climates. The higher values of SLA_{CWM} and LA_{CWM} with total herbivore removal at Arid suggest that the plant species with herbivore avoidance strategies increase with access to both wild herbivores

and cattle. However, the decrease in LAC_{WM} with total herbivore removal at Mesic suggests an herbivore tolerance strategy. Therefore, we do not seem to observe an additive effect of climate and herbivores assemblage as predicted.

This difference in responses to herbivore assemblage between climates may also be due to differences in plant community dominance. A study at the site by Orr et al. (in press) found that the plant community was dominated by invasive annual grasses at Arid, an invasive annual grass and a woody shrub at Intermediate, and a shrub and a native annual forb at Mesic. Additionally, Orr et al. found no difference in plant community dominance between herbivore treatments at Arid, but lower dominance in unfenced plots than wildlife-only at Mesic and Intermediate. Combined with our findings of high community dissimilarity between herbivore treatments at Arid (Supplement 4), differences in $SLAC_{WM}$ and LAC_{WM} at Arid may be led by an increase in abundance by annual non-native grasses, which increased in abundance in both Arid wildlife-only and total removal treatment plots (Orr et al., in press). Further, we may have observed lower levels of grazing intensity than other studies, which would reinforce this observation. At low intensity grazing, herbivores remove large leaves, but not to the degree that would increase the abundance of herbivore tolerant species, so it effectively decreases LA and SLA.

We detected differences in trait responses between cattle and wildlife-only treatments. For example, all $CWMs$ at Arid showed no significant difference with the removal of only cattle, while all but seed $mass_{CWM}$ were significantly higher between wildlife-only and full enclosure. In fact, of all treatments and climates, only LAC_{WM} at Intermediate was significantly impacted by the removal of only cattle. However, we lacked a cattle-only enclosure plot due to

feasibility, which does not allow us to fully explore the differences between cattle and wild herbivores at our study site.

The contribution of ITV and species turnover to community-level traits

Species turnover accounted for the majority of trait variability due to climate and treatment effects for SLA_{CWM} and $LDMC_{CWM}$, and almost half the variability of LA_{CWM} . This follows our prediction for the high contribution of species turnover to trait variability due to climate, and is consistent with other research that has shown that the relative contribution of species turnover increases across environmental gradients and with environmental harshness (Kichenin, Wardle, Peltzer, Morse, & Freschet, 2013; Niu et al., 2020); however, it does not follow our prediction that ITV would explain more variability for herbivore treatment. ITV accounted for a relatively small amount of the response of SLA_{CWM} and $LDMC_{CWM}$ variability to climate, treatment, and their interactions, which may be indicative of how leaf-level traits show less ITV than plant-level traits (Siefert et al., 2015). However, this does not hold true for the almost equal contributions of species turnover and ITV we observed for LA_{CWM} .

The positive correlation we observed between species turnover and ITV when explaining total variation suggests that climate and herbivory are changing community functional traits by both selecting for species with specific functional traits and by altering within-species trait values in a way that reinforces those community trait responses. However, it should be noted that we have high levels of dissimilarity in understory species between our climate treatments, which makes it more difficult to interpret the relative contributions with respect to climate using this methodology.

The response of functional diversity to climate and herbivory

We found significant effects of both climate and herbivore assemblage on FDis and FDiv, and differences between climates and treatments appear to be driven by differences in functional group dominance (as observed by Orr et al., in press) and herbivore identity. Cattle appear to be driving FDis patterns at Arid, whereas wild herbivores appear to be driving patterns at Intermediate. FDis values were higher overall at Mesic climate than both Intermediate and Arid, meaning that species' traits are less centered around the community trait mean, which indicates that species' trait values, as well as species abundances are more even at Intermediate and Arid.

The difference in FDiv values between herbivore treatments at Intermediate indicates that when all herbivores were removed, there was a higher abundance of species with trait values that diverged from one another. This divergence may be due to the high abundance of both annual grasses and native shrubs at the intermediate climate, as studies on the effects of herbivores on grasses and shrubs often have opposite results (Papanikolaou et al., 2011).

We found that FEve did not differ significantly due to herbivore treatment, which is in line with some research (Niu, He, & Lechowicz, 2016b; Török et al., 2018). Similarly, we found no effect of herbivore treatment on FRic, which appears to be contradictory to other studies (Niu, He, Zhang, & Lechowicz, 2016). Surprisingly, there was also no effect of climate on FEve and FRic, even though we see a significant difference in climate conditions, high community dissimilarity between climates, and a change in dominant species. In particular, FEve includes species' abundances in its calculation, so one might expect it to be more sensitive to changes in plant community composition. However, studies have found that functional diversity metrics respond differently than species diversity to environmental stress

and change (Niu et al., 2014). While functional diversity metrics may not align with predictions based on species diversity (Lamanna et al., 2014), they can be better indicators of community assembly than species richness (Mouchet, Villéger, Mason, & Mouillot, 2010). While both climate and herbivore assemblage were found to significantly alter plant species diversity at this site (Orr et al., in press), our findings show that this does not reduce functional richness or evenness, indicating that some aspects of ecosystem function may be conserved even with large changes in species between treatments.

Conclusions

In this study, we used a multi-factor large herbivore enclosure experiment to simulate the three most common herbivore change scenarios globally and explored the interaction between aridity and herbivore community composition functional trait composition of herbaceous plant communities in an oak savanna ecosystem. We found that even over a relatively large climate gradient for this landscape, the effects of herbivores on community-level traits can be very large, sometimes even exceeding that of climate change alone. Therefore, we may be able to utilize grazing to maintain community-level traits important to ecosystem function, potentially mitigating the effects of climate change to some degree.

Our findings demonstrate interacting effects between changes in large herbivore grazing and climate on community-level functional traits, with climate context sometimes inverting the community-level response to grazing. We determined this change was due to shifts from herbivore tolerance to avoidance traits. This change illustrates the importance of considering the role of climate context and herbivore assemblage together when predicting functional trait changes.

Our study additionally demonstrates that cattle and large wild herbivores can differ in the magnitude and direction of effects on functional traits and diversity. Further, those responses can be reversed or halted via interactions with climate, with climate only affecting trait responses due to the additional removal of wild herbivores but not cattle-only removal.

As humans continue to alter ecosystems, it is becoming increasingly important to understand the resulting effects on functional traits and diversity as they are inextricably tied with ecosystem functioning. This is particularly true for California Mediterranean ecosystems and oak savannas which are under threat from climate change (McCullough et al., 2016) and are extensively grazed by livestock. Through this study, we highlight the challenges of generalizing the effects of either herbivore communities or climate on complex responses such as functional trait and diversity responses. By understanding the interaction between climate and herbivore assemblages, we are better able to predict how critical functional traits will be altered in the future.

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Supplement 1: Climate Treatments

We used PRISM climate data downscaled to 30 meters (McCullough et al., 2016) to determine if our climate treatments differed significantly in total annual precipitation (ppt), mean daily maximum temperature (tmin), mean daily minimum temperature (tmax), climate water deficit (cwd) and potential evapotranspiration (pet). We averaged the data for the years of 1983 – 2013 and calculated each climate metric for our 27 plots.

Due to non-normality and/or unequal variances, we performed PERMANOVAS using on each variable as a function of our climate treatments with herbivore treatment replicates as a blocking factor (Table S1-1). We then performed Tukey’s HSD to determined significance between climate treatments.

All climate treatment significantly differed in ppt, tmax, and tmn (Table S1-2). Mesic and Intermediate did not significantly differ in cwd or pet (Table S1-2).

Table S1-1: ANOVA results for climate variables

Climate Variable	Source of Variation	df	SS	MS	Iter	p
Climate Water Deficit	Climate	2	90539.420	45269.709	5000	<.0001
	Block	6	42122.630	7020.439	5000	<.0001
	Residuals	18	16265.640	903.647		
Potential Evapotranspiration	Climate	2	75829.430	37914.717	5000	<.0001
	Block	6	47301.130	7883.522	5000	0.001
	Residuals	18	20191.600	1121.756		
Precipitation	Climate	2	3123.313	1561.657	5000	<.0001
	Block	6	15.834	2.639	732	0.232
	Residuals	18	33.776	1.876		
Mean Daily Maximum Temperature	Climate	2	12.425	6.213	5000	<.0001
	Block	6	0.189	0.032	5000	<.0001
	Residuals	18	0.029	0.002		
Mean Daily Minimum Temperature	Climate	2	7.671	3.835	5000	<.0001
	Block	6	0.018	0.003	5000	0.015
	Residuals	18	0.012	0.001		

Table S1-2: Tukey HSD Pairwise comparisons for each climate variable.

Climate Variable	Comparison	Diff	Lwr	Upr	p
Climate Water Deficit	Intermediate-Arid	108.588	72.422	144.755	<.0001
	Mesic-Arid	133.328	97.162	169.494	<.0001
	Mesic-Intermediate	24.739	-11.427	60.905	0.216
Potential Evapotranspiration	Intermediate-Arid	124.247	83.952	164.542	<.0001
	Mesic-Arid	94.684	54.389	134.979	<.0001
	Mesic-Intermediate	-29.563	-69.858	10.732	0.175
Precipitation	Intermediate-Arid	-7.432	-9.080	-5.784	<.0001
	Mesic-Arid	-25.605	-27.253	-23.957	<.0001
	Mesic-Intermediate	-18.173	-19.821	-16.525	<.0001
Mean Daily Maximum Temperature	Intermediate-Arid	0.358	0.310	0.407	<.0001
	Mesic-Arid	1.584	1.536	1.633	<.0001
	Mesic-Intermediate	1.226	1.178	1.274	<.0001
Mean Daily Minimum Temperature	Intermediate-Arid	0.261	0.229	0.292	<.0001
	Mesic-Arid	1.238	1.207	1.269	<.0001
	Mesic-Intermediate	0.978	0.946	1.009	<.0001

Supplement 2: Species Lists, abundances, and trait data sources

Table S2-1: 2017 Species list and abundances

Leaf area (LA), specific leaf area (SLA), and leaf dry matter content (LDMC) were all calculated from samples taken from the field sites unless noted in Table S-2 (Arid Block B for Arid plots; Intermediate Block E for Intermediate plots, and Mesic Block H for Mesic plots).

climate	treatment	Block	species_name	Abundance
Arid	Open	A	<i>Bromus hordeaceus</i>	27.46%
Arid	Open	A	<i>Erodium</i> sp.	25.73%
Arid	Open	A	<i>Medicago polymorpha</i>	8.15%
Arid	Open	A	<i>Bromus diandrus</i>	6.37%
Arid	Open	A	<i>Acmispon wrangelianus</i>	5.02%
Arid	Open	A	<i>Trifolium</i> sp.	4.81%
Arid	Open	A	<i>Triteleia ixioides</i>	2.84%
Arid	Open	A	<i>Gilia tricolor</i>	2.76%
Arid	Open	A	<i>Plagiobothrys nothofulvus</i>	2.47%
Arid	Open	A	<i>Hordeum murinum</i>	1.93%
Arid	Open	A	<i>Cerastium glomeratum</i>	1.77%
Arid	Open	A	<i>Leptosiphon</i> sp.	1.46%
Arid	Partial	A	<i>Bromus diandrus</i>	32.98%
Arid	Partial	A	<i>Bromus hordeaceus</i>	13.39%
Arid	Partial	A	<i>Trifolium</i> sp.	5.89%
Arid	Partial	A	<i>Bromus tectorum</i>	4.63%
Arid	Partial	A	<i>Erodium</i> sp.	4.46%
Arid	Partial	A	<i>Hordeum murinum</i>	4.38%
Arid	Partial	A	<i>Triteleia ixioides</i>	4.37%
Arid	Partial	A	<i>Phacelia</i> sp.	3.18%
Arid	Partial	A	<i>Gilia tricolor</i>	2.68%
Arid	Partial	A	<i>Acmispon wrangelianus</i>	2.43%
Arid	Partial	A	<i>Festuca myuros</i>	2.37%
Arid	Partial	A	<i>Medicago polymorpha</i>	2.11%
Arid	Partial	A	<i>Bromus rubens</i>	1.77%
Arid	Partial	A	<i>Medicago polymorpha</i>	1.64%
Arid	Partial	A	<i>Avena fatua</i>	1.46%
Arid	Partial	A	<i>Claytonia perfoliata</i>	1.44%
Arid	Partial	A	<i>Cerastium glomeratum</i>	1.18%
Arid	Total	A	<i>Bromus hordeaceus</i>	39.87%
Arid	Total	A	<i>Bromus diandrus</i>	33.73%
Arid	Total	A	<i>Hordeum murinum</i>	5.57%
Arid	Total	A	<i>Trifolium</i> sp.	5.39%
Arid	Total	A	<i>Festuca myuros</i>	2.97%
Arid	Total	A	<i>Erodium</i> sp.	2.42%
Arid	Total	A	<i>Bromus tectorum</i>	1.85%
Arid	Open	B	<i>Bromus hordeaceus</i>	25.15%
Arid	Open	B	<i>Erodium</i> sp.	15.59%
Arid	Open	B	<i>Bromus tectorum</i>	9.39%
Arid	Open	B	<i>Medicago polymorpha</i>	7.98%
Arid	Open	B	<i>Bromus diandrus</i>	7.29%
Arid	Open	B	<i>Acmispon wrangelianus</i>	5.36%
Arid	Open	B	<i>Plagiobothrys nothofulvus</i>	5.30%
Arid	Open	B	<i>Trifolium</i> sp.	4.22%

Arid	Open	B	<i>Phacelia</i> sp.	2.84%
Arid	Open	B	<i>Hordeum murinum</i>	2.60%
Arid	Open	B	<i>Calandrinia menziesii</i>	1.87%
Arid	Open	B	<i>Stellaria</i> sp.	1.87%
Arid	Open	B	<i>Leptosiphon</i> sp.	1.79%
Arid	Partial	B	<i>Bromus diandrus</i>	32.99%
Arid	Partial	B	<i>Bromus hordeaceus</i>	20.39%
Arid	Partial	B	<i>Trifolium</i> sp.	11.00%
Arid	Partial	B	<i>Triteleia ixioides</i>	6.02%
Arid	Partial	B	<i>Bromus tectorum</i>	4.49%
Arid	Partial	B	<i>Acmispon wrangelianus</i>	3.10%
Arid	Partial	B	<i>Hordeum murinum</i>	2.84%
Arid	Partial	B	<i>Erodium</i> sp.	2.37%
Arid	Partial	B	<i>Gilia tricolor</i>	2.34%
Arid	Partial	B	<i>Phacelia</i> sp.	1.57%
Arid	Partial	B	<i>Medicago polymorpha</i>	1.35%
Arid	Partial	B	<i>Dichelostemma capitatum</i>	1.29%
Arid	Partial	B	<i>Claytonia perfoliata</i>	1.18%
Arid	Total	B	<i>Bromus diandrus</i>	42.30%
Arid	Total	B	<i>Bromus hordeaceus</i>	34.91%
Arid	Total	B	<i>Trifolium</i> sp.	4.49%
Arid	Total	B	<i>Triteleia ixioides</i>	3.81%
Arid	Total	B	<i>Hordeum murinum</i>	3.53%
Arid	Total	B	<i>Festuca myuros</i>	1.89%
Arid	Open	C	<i>Bromus hordeaceus</i>	29.79%
Arid	Open	C	<i>Erodium</i> sp.	27.90%
Arid	Open	C	<i>Medicago polymorpha</i>	8.84%
Arid	Open	C	<i>Bromus diandrus</i>	6.91%
Arid	Open	C	<i>Trifolium</i> sp.	5.21%
Arid	Open	C	<i>Acmispon wrangelianus</i>	3.61%
Arid	Open	C	<i>Triteleia ixioides</i>	3.08%
Arid	Open	C	<i>Hordeum murinum</i>	2.10%
Arid	Open	C	<i>Stellaria</i> sp.	1.71%
Arid	Open	C	<i>Gilia tricolor</i>	1.53%
Arid	Partial	C	<i>Bromus diandrus</i>	30.64%
Arid	Partial	C	<i>Bromus hordeaceus</i>	21.31%
Arid	Partial	C	<i>Trifolium</i> sp.	11.07%
Arid	Partial	C	<i>Triteleia ixioides</i>	4.93%
Arid	Partial	C	<i>Bromus tectorum</i>	4.85%
Arid	Partial	C	<i>Hordeum murinum</i>	4.78%
Arid	Partial	C	<i>Erodium</i> sp.	2.89%
Arid	Partial	C	<i>Avena fatua</i>	2.79%
Arid	Partial	C	<i>Gilia tricolor</i>	1.70%
Arid	Partial	C	<i>Stipa pulchra</i>	1.58%
Arid	Partial	C	<i>Medicago polymorpha</i>	1.32%
Arid	Partial	C	<i>Acmispon wrangelianus</i>	1.27%
Arid	Partial	C	<i>Medicago polymorpha</i>	1.08%
Arid	Total	C	<i>Bromus hordeaceus</i>	43.41%
Arid	Total	C	<i>Bromus diandrus</i>	26.53%
Arid	Total	C	<i>Hordeum murinum</i>	6.54%
Arid	Total	C	<i>Trifolium</i> sp.	5.55%
Arid	Total	C	<i>Festuca myuros</i>	2.94%
Arid	Total	C	<i>Erodium</i> sp.	2.31%

Arid	Total	C	<i>Bromus tectorum</i>	1.84%
Arid	Total	C	<i>Triteleia ixioides</i>	1.46%
Intermediate	Open	D	<i>Bromus diandrus</i>	34.84%
Intermediate	Open	D	<i>Ericameria nauseosa</i>	14.64%
Intermediate	Open	D	<i>Bromus hordeaceus</i>	11.59%
Intermediate	Open	D	<i>Erodium</i> sp.	9.23%
Intermediate	Open	D	<i>Bromus tectorum</i>	6.12%
Intermediate	Open	D	<i>Plagiobothrys nothofulvus</i>	4.61%
Intermediate	Open	D	<i>Acmispon wrangelianus</i>	4.14%
Intermediate	Open	D	<i>Bromus rubens</i>	3.90%
Intermediate	Open	D	<i>Medicago polymorpha</i>	2.07%
Intermediate	Partial	D	<i>Bromus diandrus</i>	41.73%
Intermediate	Partial	D	<i>Bromus hordeaceus</i>	9.99%
Intermediate	Partial	D	<i>Ericameria nauseosa</i>	9.97%
Intermediate	Partial	D	<i>Ribes californicum</i> var. <i>hesperium</i>	5.68%
Intermediate	Partial	D	<i>Nemophila menziesii</i>	5.55%
Intermediate	Partial	D	<i>Bromus tectorum</i>	4.95%
Intermediate	Partial	D	<i>Erodium</i> sp.	2.98%
Intermediate	Partial	D	<i>Bromus rubens</i>	2.83%
Intermediate	Partial	D	Asteraceae sp.	2.27%
Intermediate	Partial	D	<i>Phacelia</i> sp.	1.95%
Intermediate	Partial	D	<i>Gayophytum diffusum</i> ssp. <i>parviflorum</i>	1.84%
Intermediate	Partial	D	<i>Festuca myuros</i>	1.63%
Intermediate	Total	D	<i>Bromus diandrus</i>	41.05%
Intermediate	Total	D	<i>Ericameria nauseosa</i>	16.98%
Intermediate	Total	D	<i>Bromus rubens</i>	9.81%
Intermediate	Total	D	<i>Bromus tectorum</i>	8.38%
Intermediate	Total	D	<i>Erodium</i> sp.	6.92%
Intermediate	Total	D	<i>Bromus hordeaceus</i>	5.38%
Intermediate	Total	D	<i>Gayophytum diffusum</i> ssp. <i>parviflorum</i>	2.20%
Intermediate	Open	E	<i>Ericameria nauseosa</i>	27.07%
Intermediate	Open	E	<i>Bromus hordeaceus</i>	16.72%
Intermediate	Open	E	<i>Bromus tectorum</i>	13.21%
Intermediate	Open	E	<i>Bromus diandrus</i>	12.06%
Intermediate	Open	E	<i>Bromus rubens</i>	5.63%
Intermediate	Open	E	<i>Erodium</i> sp.	4.60%
Intermediate	Open	E	<i>Festuca myuros</i>	3.27%
Intermediate	Open	E	<i>Gayophytum diffusum</i> ssp. <i>parviflorum</i>	2.68%
Intermediate	Open	E	<i>Acmispon wrangelianus</i>	2.60%
Intermediate	Open	E	<i>Urtica dioica</i>	1.74%
Intermediate	Open	E	<i>Medicago polymorpha</i>	1.42%
Intermediate	Partial	E	<i>Bromus diandrus</i>	61.14%
Intermediate	Partial	E	<i>Bromus hordeaceus</i>	9.92%
Intermediate	Partial	E	<i>Bromus tectorum</i>	5.88%
Intermediate	Partial	E	<i>Erodium</i> sp.	5.18%
Intermediate	Partial	E	<i>Urtica dioica</i>	3.19%
Intermediate	Partial	E	<i>Ericameria nauseosa</i>	2.78%
Intermediate	Partial	E	<i>Bromus rubens</i>	2.17%
Intermediate	Total	E	<i>Bromus diandrus</i>	42.98%
Intermediate	Total	E	<i>Ericameria nauseosa</i>	15.32%
Intermediate	Total	E	<i>Erodium</i> sp.	6.68%
Intermediate	Total	E	<i>Bromus hordeaceus</i>	6.63%
Intermediate	Total	E	<i>Festuca myuros</i>	5.77%

Intermediate	Total	E	<i>Bromus tectorum</i>	4.37%
Intermediate	Total	E	<i>Bromus rubens</i>	3.44%
Intermediate	Total	E	<i>Acmispon wrangelianus</i>	2.04%
Intermediate	Total	E	<i>Viola purpurea</i>	2.04%
Intermediate	Total	E	<i>Gayophytum diffusum ssp. parviflorum</i>	1.78%
Intermediate	Open	F	<i>Ericameria nauseosa</i>	38.24%
Intermediate	Open	F	<i>Bromus diandrus</i>	12.48%
Intermediate	Open	F	<i>Bromus tectorum</i>	11.92%
Intermediate	Open	F	<i>Bromus hordeaceus</i>	10.74%
Intermediate	Open	F	<i>Erodium sp.</i>	9.34%
Intermediate	Open	F	<i>Bromus rubens</i>	7.16%
Intermediate	Open	F	<i>Hordeum murinum</i>	1.48%
Intermediate	Partial	F	<i>Bromus diandrus</i>	40.54%
Intermediate	Partial	F	<i>Ericameria nauseosa</i>	20.30%
Intermediate	Partial	F	<i>Bromus tectorum</i>	10.71%
Intermediate	Partial	F	<i>Bromus hordeaceus</i>	6.47%
Intermediate	Partial	F	<i>Erodium sp.</i>	5.40%
Intermediate	Partial	F	<i>Festuca myuros</i>	3.37%
Intermediate	Partial	F	<i>Bromus rubens</i>	3.19%
Intermediate	Partial	F	<i>Gayophytum diffusum ssp. parviflorum</i>	3.19%
Intermediate	Total	F	<i>Bromus diandrus</i>	46.13%
Intermediate	Total	F	<i>Ericameria nauseosa</i>	26.39%
Intermediate	Total	F	<i>Bromus hordeaceus</i>	8.49%
Intermediate	Total	F	<i>Bromus tectorum</i>	5.89%
Intermediate	Total	F	<i>Erodium sp.</i>	4.34%
Mesic	Open	G	<i>Ribes californicum var. hesperium</i>	30.67%
Mesic	Open	G	<i>Ranunculus californicus</i>	13.24%
Mesic	Open	G	<i>Bromus tectorum</i>	10.25%
Mesic	Open	G	<i>Collinsia parviflora</i>	10.25%
Mesic	Open	G	<i>Melica californica</i>	6.36%
Mesic	Open	G	<i>Gayophytum diffusum ssp. parviflorum</i>	5.73%
Mesic	Open	G	<i>Acmispon wrangelianus</i>	5.00%
Mesic	Open	G	<i>Galium aparine</i>	4.83%
Mesic	Open	G	<i>Symphoricarpos mollis</i>	3.30%
Mesic	Open	G	<i>Mimulus subsecundus</i>	2.85%
Mesic	Partial	G	<i>Ribes californicum var. hesperium</i>	29.07%
Mesic	Partial	G	<i>Galium aparine</i>	17.05%
Mesic	Partial	G	<i>Bromus tectorum</i>	8.25%
Mesic	Partial	G	<i>Melica californica</i>	6.00%
Mesic	Partial	G	<i>Symphoricarpos mollis</i>	5.78%
Mesic	Partial	G	<i>Hosackia crassifolia var. crassifolia</i>	4.12%
Mesic	Partial	G	<i>Phacelia sp.</i>	3.75%
Mesic	Partial	G	<i>Gayophytum diffusum ssp. parviflorum</i>	3.14%
Mesic	Partial	G	<i>Mimulus subsecundus</i>	2.72%
Mesic	Partial	G	<i>Plagiobothrys nothofulvus</i>	2.69%
Mesic	Partial	G	<i>Collinsia childii</i>	2.65%
Mesic	Partial	G	<i>Pholistoma auritum</i>	2.49%
Mesic	Partial	G	<i>Acmispon wrangelianus</i>	2.35%
Mesic	Total	G	<i>Ribes californicum var. hesperium</i>	35.94%
Mesic	Total	G	<i>Galium aparine</i>	14.19%
Mesic	Total	G	<i>Symphoricarpos mollis</i>	8.36%
Mesic	Total	G	<i>Collinsia childii</i>	7.36%
Mesic	Total	G	<i>Melica californica</i>	5.33%

Mesic	Total	G	<i>Bromus tectorum</i>	5.31%
Mesic	Total	G	<i>Hosackia crassifolia</i> var. <i>crassifolia</i>	4.48%
Mesic	Total	G	<i>Claytonia perfoliata</i>	3.12%
Mesic	Total	G	<i>Mimulus subsecundus</i>	2.30%
Mesic	Total	G	<i>Acmispon wrangelianus</i>	2.09%
Mesic	Total	G	<i>Plagiobothrys nothofulvus</i>	2.01%
Mesic	Open	H	<i>Ribes californicum</i> var. <i>hesperium</i>	37.87%
Mesic	Open	H	<i>Ranunculus californicus</i>	17.10%
Mesic	Open	H	<i>Bromus tectorum</i>	8.65%
Mesic	Open	H	<i>Collinsia parviflora</i>	7.46%
Mesic	Open	H	<i>Melica californica</i>	6.85%
Mesic	Open	H	<i>Gayophytum diffusum</i> ssp. <i>parviflorum</i>	5.43%
Mesic	Open	H	<i>Acmispon wrangelianus</i>	3.33%
Mesic	Open	H	<i>Plagiobothrys nothofulvus</i>	2.87%
Mesic	Open	H	<i>Mimulus subsecundus</i>	2.41%
Mesic	Partial	H	<i>Ribes californicum</i> var. <i>hesperium</i>	30.82%
Mesic	Partial	H	<i>Galium aparine</i>	17.60%
Mesic	Partial	H	<i>Symphoricarpos mollis</i>	15.54%
Mesic	Partial	H	<i>Bromus tectorum</i>	3.99%
Mesic	Partial	H	<i>Melica californica</i>	3.20%
Mesic	Partial	H	<i>Pholistoma auritum</i>	3.20%
Mesic	Partial	H	<i>Phacelia</i> sp.	2.98%
Mesic	Partial	H	<i>Plagiobothrys nothofulvus</i>	2.94%
Mesic	Partial	H	<i>Collinsia childii</i>	2.75%
Mesic	Partial	H	<i>Gayophytum diffusum</i> ssp. <i>parviflorum</i>	2.08%
Mesic	Partial	H	<i>Claytonia perfoliata</i>	2.02%
Mesic	Partial	H	<i>Acmispon wrangelianus</i>	1.59%
Mesic	Partial	H	<i>Hosackia crassifolia</i> var. <i>crassifolia</i>	1.52%
Mesic	Total	H	<i>Ribes californicum</i> var. <i>hesperium</i>	29.92%
Mesic	Total	H	<i>Galium aparine</i>	18.78%
Mesic	Total	H	<i>Symphoricarpos mollis</i>	10.85%
Mesic	Total	H	<i>Collinsia childii</i>	9.62%
Mesic	Total	H	<i>Bromus tectorum</i>	5.47%
Mesic	Total	H	<i>Melica californica</i>	4.38%
Mesic	Total	H	<i>Plagiobothrys nothofulvus</i>	2.55%
Mesic	Total	H	<i>Acmispon wrangelianus</i>	2.40%
Mesic	Total	H	<i>Penstemon laetus</i>	1.75%
Mesic	Total	H	<i>Claytonia perfoliata</i>	1.69%
Mesic	Total	H	<i>Dichelostemma capitatum</i>	1.56%
Mesic	Total	H	<i>Clarkia unguiculata</i>	1.15%
Mesic	Open	I	<i>Ribes californicum</i> var. <i>hesperium</i>	29.05%
Mesic	Open	I	<i>Ranunculus californicus</i>	12.85%
Mesic	Open	I	<i>Acmispon wrangelianus</i>	9.03%
Mesic	Open	I	<i>Gayophytum diffusum</i> ssp. <i>parviflorum</i>	6.53%
Mesic	Open	I	<i>Collinsia parviflora</i>	6.16%
Mesic	Open	I	<i>Bromus tectorum</i>	5.61%
Mesic	Open	I	<i>Symphoricarpos mollis</i>	5.49%
Mesic	Open	I	<i>Galium aparine</i>	5.13%
Mesic	Open	I	<i>Prunus virginiana</i>	3.66%
Mesic	Open	I	<i>Mimulus subsecundus</i>	2.04%
Mesic	Open	I	<i>Festuca myuros</i>	2.01%
Mesic	Open	I	<i>Plagiobothrys nothofulvus</i>	1.95%
Mesic	Open	I	<i>Melica californica</i>	1.62%

Mesic	Partial	I	<i>Ribes californicum var. hesperium</i>	24.15%
Mesic	Partial	I	<i>Galium aparine</i>	18.74%
Mesic	Partial	I	<i>Penstemon sp.</i>	5.74%
Mesic	Partial	I	<i>Prunus virginiana</i>	5.27%
Mesic	Partial	I	<i>Acmispon wrangelianus</i>	4.81%
Mesic	Partial	I	<i>Mimulus subsecundus</i>	4.74%
Mesic	Partial	I	<i>Symphoricarpos mollis</i>	4.39%
Mesic	Partial	I	<i>Gayophytum diffusum ssp. parviflorum</i>	3.54%
Mesic	Partial	I	<i>Hosackia crassifolia var. crassifolia</i>	2.71%
Mesic	Partial	I	<i>Melica californica</i>	2.58%
Mesic	Partial	I	<i>Phacelia sp.</i>	2.18%
Mesic	Partial	I	<i>Stipa pulchra</i>	2.16%
Mesic	Partial	I	<i>Pholistoma auritum</i>	2.11%
Mesic	Partial	I	<i>Claytonia perfoliata</i>	1.94%
Mesic	Partial	I	<i>Festuca myuros</i>	1.91%
Mesic	Partial	I	<i>Leptosiphon sp.</i>	1.78%
Mesic	Partial	I	<i>Bromus tectorum</i>	1.63%
Mesic	Total	I	<i>Ribes californicum var. hesperium</i>	23.96%
Mesic	Total	I	<i>Galium aparine</i>	20.15%
Mesic	Total	I	<i>Penstemon sp.</i>	8.73%
Mesic	Total	I	<i>Bromus tectorum</i>	4.60%
Mesic	Total	I	<i>Plagiobothrys nothofulvus</i>	4.60%
Mesic	Total	I	<i>Prunus virginiana</i>	3.65%
Mesic	Total	I	<i>Melica californica</i>	3.63%
Mesic	Total	I	<i>Mimulus subsecundus</i>	3.47%
Mesic	Total	I	<i>Acmispon wrangelianus</i>	3.09%
Mesic	Total	I	<i>Symphoricarpos mollis</i>	3.03%
Mesic	Total	I	<i>Clarkia unguiculata</i>	2.83%
Mesic	Total	I	<i>Stipa pulchra</i>	2.69%
Mesic	Total	I	<i>Pholistoma auritum</i>	2.62%
Mesic	Total	I	<i>Claytonia perfoliata</i>	1.93%
Mesic	Total	I	<i>Gayophytum diffusum ssp. parviflorum</i>	1.67%

Table S2-2: 2017 Data sources.

Species were not collected if they were too rare or not evenly dispersed enough throughout the plot to warrant collection. Seed mass and Leaf Nitrogen Content (LNC) values were obtained from Try Plant Trait Database (TRY DB) for the same species unless otherwise noted, and all records were averaged from available public sources. Table notes where substitutions were made when specific plant species had no data records. When choosing species for substitution, we prioritized using data collected in 2019 or from another replicate of the same climate and herbivore treatment. If not available, we then performed searches for data for species of the same genus that grew in the region, or chose members of the same genus outside the region or from the family-level.

climate	treatment	Block	species_name	LA, SLA, and LDMC data sources
Arid	Open	B	<i>Bromus tectorum</i>	2019 trait collection
Arid	Partial	A	<i>Claytonia perfoliata</i>	LA and SLA from TRY DB
Arid	Partial	B	<i>Claytonia perfoliata</i>	LA and SLA from TRY DB
Arid	Partial	B	<i>Dichelostemma capitatum</i>	TRY DB
Arid	Partial	A	<i>Gilia tricolor</i>	SLA from Arid-Open Blocks A and C
Arid	Partial	B	<i>Gilia tricolor</i>	SLA from Arid-Open Blocks A and C
Arid	Partial	C	<i>Gilia tricolor</i>	SLA from Arid-Open Blocks A and C
Arid	Partial	A	<i>Hordeum murinum</i>	LA from 2019 trait collection
Arid	Partial	B	<i>Hordeum murinum</i>	LA from 2019 trait collection
Arid	Partial	C	<i>Hordeum murinum</i>	LA from 2019 trait collection
Arid	Open	A	<i>Leptosiphon</i> sp.	LA estimate from Lambrecht (2013) field measurements of <i>L. bicolor</i> ; SLA from TRY DB records for <i>L. bicolor</i> .
Arid	Open	B	<i>Leptosiphon</i> sp.	LA estimate from Lambrecht (2013) field measurements of <i>L. bicolor</i> ; SLA from TRY DB records for <i>L. bicolor</i> .
Arid	Partial	A	<i>Medicago polymorpha</i>	LDMC from Arid-Open
Arid	Partial	B	<i>Medicago polymorpha</i>	LDMC from Arid-Open
Arid	Partial	C	<i>Medicago polymorpha</i>	LDMC from Arid-Open
Arid	Partial	A	<i>Phacelia</i> sp.	TRY DB <i>Phacelia tanacetifolia</i>
Arid	Open	B	<i>Phacelia</i> sp.	TRY DB <i>Phacelia tanacetifolia</i>
Arid	Partial	B	<i>Phacelia</i> sp.	TRY DB <i>Phacelia tanacetifolia</i>
Arid	Open	B	<i>Stellaria</i> sp.	TRY DB <i>Stellaria media</i>
Arid	Open	C	<i>Stellaria</i> sp.	TRY Plant Trait Database <i>Stellaria media</i> records
Arid	Partial	C	<i>Stipa pulchra</i>	TRY Plant Trait Database <i>Stellaria media</i> records
Intermediate	Open	D	<i>Acmispon wrangelianus</i>	SLA and LDMC from TRY DB; LA from average of arid and mesic
Intermediate	Open	E	<i>Acmispon wrangelianus</i>	SLA and LDMC from TRY DB; LA from average of arid and mesic
Intermediate	Total	E	<i>Acmispon wrangelianus</i>	SLA and LDMC from TRY DB; LA from average of arid and mesic
Intermediate	Partial	D	Asteraceae sp.	TRY DB
Intermediate	Partial	D	<i>Bromus diandrus</i>	LA and SLA take from Intermediate Partial blocks F and E
Intermediate	Partial	E	<i>Bromus diandrus</i>	LA and SLA take from Intermediate Partial blocks F and E
Intermediate	Partial	F	<i>Bromus diandrus</i>	LA and SLA take from Intermediate Partial blocks F and E

Intermediate	Open	D	<i>Bromus rubens</i>	LA and LDMC from Arid blocks; SLA from TRY DB
Intermediate	Partial	D	<i>Bromus rubens</i>	LA and LDMC from Arid blocks; SLA from TRY DB
Intermediate	Total	D	<i>Bromus rubens</i>	LA and LDMC from Arid blocks; SLA from TRY DB
Intermediate	Open	E	<i>Bromus rubens</i>	LA and LDMC from Arid blocks; SLA from TRY DB
Intermediate	Partial	E	<i>Bromus rubens</i>	LA and LDMC from Arid blocks; SLA from TRY DB
Intermediate	Total	E	<i>Bromus rubens</i>	LA and LDMC from Arid blocks; SLA from TRY DB
Intermediate	Open	F	<i>Bromus rubens</i>	LA and LDMC from Arid blocks; SLA from TRY DB
Intermediate	Partial	F	<i>Bromus rubens</i>	LA and LDMC from Arid blocks; SLA from TRY DB
Intermediate	Open	D	<i>Bromus tectorum</i>	2019 trait collection
Intermediate	Partial	D	<i>Bromus tectorum</i>	2019 trait collection
Intermediate	Total	D	<i>Bromus tectorum</i>	2019 trait collection
Intermediate	Open	E	<i>Bromus tectorum</i>	2019 trait collection
Intermediate	Partial	E	<i>Bromus tectorum</i>	2019 trait collection
Intermediate	Total	E	<i>Bromus tectorum</i>	2019 trait collection
Intermediate	Open	F	<i>Bromus tectorum</i>	2019 trait collection
Intermediate	Partial	F	<i>Bromus tectorum</i>	2019 trait collection
Intermediate	Total	F	<i>Bromus tectorum</i>	2019 trait collection
Intermediate	Partial	D	<i>Phacelia</i> sp.	TRY Plant Trait Database records for <i>Phacelia tanacetifolia</i>
Intermediate	Open	D	<i>Plagiobothrys nothofulvus</i>	Int-Open blocks D and E
Intermediate	Partial	D	<i>Ribes californicum</i> var. <i>hesperium</i>	Int-Open blocks D and E
Intermediate	Open	E	<i>Urtica dioica</i>	LA and SLA from TRY DB
Intermediate	Partial	E	<i>Urtica dioica</i>	LA and SLA from TRY DB
Intermediate	Total	E	<i>Viola purpurea</i>	TRY DB <i>Viola adunca</i>
Mesic	Open	G	<i>Bromus tectorum</i>	2019 trait collection
Mesic	Partial	G	<i>Bromus tectorum</i>	TRY DB
Mesic	Total	G	<i>Bromus tectorum</i>	2019 trait collection
Mesic	Open	H	<i>Bromus tectorum</i>	2019 trait collection
Mesic	Partial	H	<i>Bromus tectorum</i>	TRY DB
Mesic	Total	H	<i>Bromus tectorum</i>	2019 trait collection
Mesic	Open	I	<i>Bromus tectorum</i>	2019 trait collection
Mesic	Partial	I	<i>Bromus tectorum</i>	TRY DB
Mesic	Total	I	<i>Bromus tectorum</i>	2019 trait collection
Mesic	Total	H	<i>Clarkia unguiculata</i>	SLA and LDMC from <i>Clarkia purpurea</i> from TRY DB; LA estimate from Jonas & Geber (1999)
Mesic	Total	I	<i>Clarkia unguiculata</i>	SLA and LDMC from <i>Clarkia purpurea</i> from TRY DB; LA estimate from Jonas & Geber (1999)
Mesic	Total	G	<i>Claytonia perfoliata</i>	LA and SLA from TRY DB
Mesic	Partial	H	<i>Claytonia perfoliata</i>	LA and SLA from TRY DB
Mesic	Total	H	<i>Claytonia perfoliata</i>	LA and SLA from TRY DB
Mesic	Partial	I	<i>Claytonia perfoliata</i>	LA and SLA from TRY DB

Mesic	Total	I	<i>Claytonia perfoliata</i>	LA and SLA from TRY DB
Mesic	Partial	G	<i>Collinsia childii</i>	Intermediate Partial
Mesic	Total	G	<i>Collinsia childii</i>	Intermediate Partial
Mesic	Partial	H	<i>Collinsia childii</i>	Intermediate Partial
Mesic	Total	H	<i>Collinsia childii</i>	Intermediate Partial
Mesic	Open	G	<i>Collinsia parviflora</i>	Intermediate Partial
Mesic	Open	H	<i>Collinsia parviflora</i>	Intermediate Partial
Mesic	Open	I	<i>Collinsia parviflora</i>	Intermediate Partial
Mesic	Total	H	<i>Dichelostemma capitatum</i>	TRY DB
Mesic	Open	I	<i>Festuca myuros</i>	2019 trait collection
Mesic	Partial	I	<i>Festuca myuros</i>	2019 trait collection
Mesic	Total	G	<i>Hosackia crassifolia</i> var. <i>crassifolia</i>	Mesic Partial
Mesic	Partial	I	<i>Leptosiphon</i> sp.	LA estimate from Lambrecht (2013) field measurements of <i>L. bicolor</i> ; SLA from TRY DB <i>Leptosiphon bicolor</i> .
Mesic	Open	G	<i>Mimulus subsecundus</i>	SLA from TRY DB <i>Mimulus douglasii</i>
Mesic	Partial	G	<i>Mimulus subsecundus</i>	SLA from TRY DB <i>Mimulus douglasii</i>
Mesic	Total	G	<i>Mimulus subsecundus</i>	SLA from TRY DB <i>Mimulus douglasii</i>
Mesic	Open	H	<i>Mimulus subsecundus</i>	SLA from TRY DB <i>Mimulus douglasii</i>
Mesic	Open	I	<i>Mimulus subsecundus</i>	SLA from TRY DB <i>Mimulus douglasii</i>
Mesic	Partial	I	<i>Mimulus subsecundus</i>	SLA from TRY DB <i>Mimulus douglasii</i>
Mesic	Total	I	<i>Mimulus subsecundus</i>	SLA from TRY DB <i>Mimulus douglasii</i>
Mesic	Total	H	<i>Penstemon laetus</i>	LA and SLA values from TRY DB records for all N. American <i>Penstemon</i> species
Mesic	Partial	I	<i>Penstemon</i> sp.	LA and SLA values from TRY DB records for all N. American <i>Penstemon</i> species
Mesic	Total	I	<i>Penstemon</i> sp.	LA and SLA values from TRY DB records for all N. American <i>Penstemon</i> species
Mesic	Partial	G	<i>Phacelia</i> sp.	TRY DB <i>Phacelia tanacetifolia</i>
Mesic	Partial	H	<i>Phacelia</i> sp.	TRY DB <i>Phacelia tanacetifolia</i>
Mesic	Partial	I	<i>Phacelia</i> sp.	TRY DB <i>Phacelia tanacetifolia</i>
Mesic	Open	I	<i>Prunus virginiana</i>	LA and SLA from TRY DB <i>Prunus virginiana</i> ; LDMC TRY DB <i>Prunus fasciculata</i>
Mesic	Partial	I	<i>Prunus virginiana</i>	LA and SLA from TRY DB <i>Prunus virginiana</i> ; LDMC TRY DB <i>Prunus fasciculata</i>
Mesic	Total	I	<i>Prunus virginiana</i>	LA and SLA from TRY DB <i>Prunus virginiana</i> ; LDMC TRY DB <i>Prunus fasciculata</i>
Mesic	Partial	I	<i>Stipa pulchra</i>	TRY DB <i>Stipa</i> genus records
Mesic	Total	I	<i>Stipa pulchra</i>	TRY DB <i>Stipa</i> genus records

Supplement 3: Models, AIC Tables, and Summaries

Table S3-1: Community-weighted means (CWM) Linear Mixed Effects Models (LMMs) and their degrees of freedom (df) and AICc Values. Final best-fit models are in bold.

Leaf Area _{CWM} (LA _{CWM})			Specific Leaf Area _{CWM} (SLA _{CWM})		
Model	df	AICc	Model	df	AICc
LA_{CWM} ~ climate * treatment + (1 Block)	11	25.58	SLA ~ climate * treatment + (1 Block)	11	60.65
LA _{CWM} ~ climate + treatment + (1 Block)	7	53.28	SLA _{CWM} ~ climate + treatment + (1 Block)	7	68.07
LA _{CWM} ~ climate + (1 Block)	5	48.77	SLA _{CWM} ~ climate + (1 Block)	5	71.66
LA _{CWM} ~ treatment + (1 Block)	5	52.22	SLA _{CWM} ~ treatment + (1 Block)	5	76.30
LA _{CWM} ~ 1 + (1 Block)	3	48.45	SLA _{CWM} ~ 1 + (1 Block)	3	78.10
Leaf Dry Matter Content _{CWM} (LDMC _{CWM})			Seed Mass _{CWM}		
Model	df	AICc	Model	df	AICc
LDMC _{CWM} ~ climate * treatment + (1 Block)	11	215.19	Seed mass _{CWM} ~ climate * treatment + (1 Block)	11	40.37
LDMC _{CWM} ~ climate + treatment + (1 Block)	7	208.87	Seed mass_{CWM} ~ climate + treatment + (1 Block)	7	31.31
LDMC _{CWM} ~ climate + (1 Block)	5	214.22	Seed mass _{CWM} ~ climate + (1 Block)	5	43.80
LDMC_{CWM} ~ treatment + (1 Block)	5	209.84	Seed mass _{CWM} ~ treatment + (1 Block)	5	38.35
LDMC _{CWM} ~ 1 + (1 Block)	3	215.61	Seed mass _{CWM} ~ 1 + (1 Block)	3	47.91
Leaf Nitrogen Content _{CWM} (LNC _{CWM})					
Model	df	AICc			
LNC _{CWM} ~ climate * treatment + (1 Block)	11	63.64			
LNC_{CWM} ~ climate + treatment + (1 Block)	7	52.52			
LNC _{CWM} ~ climate + (1 Block)	5	60.76			
LNC _{CWM} ~ treatment + (1 Block)	5	57.12			
LNC _{CWM} ~ 1 + (1 Block)	3	61.72			

Table S3-2. Final Linear Mixed Effects Models (LMMs) for each Community-weighted mean and their Marginal R2 and Conditional R2 calculated using the r.squaredGLMM function from the MuMIn R Package.

Final Model	Marginal R2	Conditional R2
LA _{CWM}	0.876	0.876
SLA _{CWM}	0.850	0.850
LDMC _{CWM}	0.285	0.544
Seed Mass _{CWM}	0.674	0.674
LNC _{CWM}	0.506	0.506

Table S3-4. Linear Mixed Effects Models (LMMs) for each functional diversity metric and their degrees of freedom (df) and AICc Values. Final, best-fit models are in bold.

Functional Richness (FRic)			Functional Evenness (FEve)		
Model	df	AICc	Model	df	AICc
FRic ~ climate * treatment + (1 Block)	11	150.60	FEve ~ climate * treatment + (1 Block)	11	-14.30
FRic ~ climate + treatment + (1 Block)	7	136.68	FEve ~ climate + treatment + (1 Block)	7	-28.17
FRic ~ climate + (1 Block)	5	130.59	FEve ~ climate + (1 Block)	5	-29.60
FRic ~ treatment + (1 Block)	5	133.42	FEve ~ treatment + (1 Block)	5	-34.67
FRic ~ 1 + (1 Block)	3	128.56	FEve ~ 1 + (1 Block)	3	-34.98
Functional Diversity (FDiv)			Functional Dispersion (FDis)		
Model	df	AICc	Model	df	AICc
FDiv ~ climate * treatment + (1 Block)	11	-51.37	FDis ~ climate * treatment + (1 Block)	11	-8.57
FDiv ~ climate + treatment + (1 Block)	7	-41.69	FDis ~ climate + treatment + (1 Block)	7	19.70
FDiv ~ climate + (1 Block)	5	-33.22	FDis ~ climate + (1 Block)	5	20.81
FDiv ~ treatment + (1 Block)	5	-45.20	FDis ~ treatment + (1 Block)	5	17.47
FDiv ~ 1 + (1 Block)	3	-37.00	FDis ~ 1 + (1 Block)	3	18.63

Table S3-5: Final Linear Mixed Effects Models (LMMs) for each functional diversity and their Marginal R2 and Conditional R2 calculated using the r.squaredGLMM function from the MuMIn R Package.

Final Model	Marginal R2	Conditional R2
FRic ~ 1 + (1 Block)	0	0.335
FEve ~ 1 + (1 Block)	0	5.291e-10
FDiv ~ climate * treatment + (1 Block)	0.798	0.885
FDis ~ climate * treatment + (1 Block)	0.894	0.894

Table S3-6: ANOVA and PERMANOVA Table for A. Specific averages, B. Fixed averages and C. ITV. Tables include degrees freedom (df), Sum of Squares (SS), Mean Sum of Squares (MS), F-values, and p-values. Leaf Area CWM was calculated with a PERMANOVA, all other traits were done with ANOVAs.

A. Specific Averages

Trait	Source of Variation	df	SS	MS	F	p
Leaf Area _{CWM}	climate	2	1769.9	884.97	10.737	0.000853
	treatment	2	971.6	485.8	5.894	0.010743
	climate:treatment	4	4781.5	1195.38	14.503	1.84e-05
	Residuals	18	1483.7	82.43		
Specific Leaf Area _{CWM}	climate	2	8.2533	4.1267	21.5465	1.67E-05
	treatment	2	4.5392	2.2696	11.8501	0.0005202
	climate:treatment	4	5.9698	1.4924	7.7925	0.0007917
	Residuals	18	3.4474	0.1915		
Leaf Dry Matter Content _{CWM}	climate	2	889.71	444.85	6.9647	0.005751
	treatment	2	1006.03	503.02	7.8753	0.003491
	climate:treatment	4	584.8	146.2	2.2889	0.099653
	Residuals	22	1149.71	63.87		

B. Fixed Averages

Trait	Source of Variation	df	SS	MS	F	p
Leaf Area _{CWM}	climate	2	550.58	275.29	3.7	0.04508
	treatment	2	337	168.5	2.265	0.13266
	climate:treatment	4	1650.65	412.66	5.546	0.00433
	Residuals	18	1339.29	74.4		
Specific Leaf Area _{CWM}	climate	2	7.3471	3.6735	21.0642	1.93E-05
	treatment	2	3.5235	1.7618	10.102	0.001144
	climate:treatment	4	3.6179	0.9045	5.1863	0.005866
	Residuals	18	3.1391	0.1744		
Leaf Dry Matter Content _{CWM}	climate	2	617.64	308.818	5.6673	0.01233
	treatment	2	584.63	292.313	5.3644	0.01488
	climate:treatment	4	589.25	147.314	2.7034	0.06343
	Residuals	22	980.84	54.491		

C. ITV Averages

Trait	Source of Variation	df	SS	MS	F	p
Leaf Area _{CWM}	climate	2	1647.46	823.73	55.508	2.00e-08
	treatment	2	176.28	88.14	5.939	0.0105
	climate:treatment	4	1403.23	350.81	23.640	5.86e-07
	Residuals	18	267.12	14.84		

Supplement 4: Analysis of Similarities

To understand the composition of each site's community, we calculated a Jaccard dissimilarity index using the community abundance data for the species constituting 90% cover in each plot (package). To calculate significant differences between plots and climates, we performed three, analysis of similarities (ANOSIM), one investigating the effect of climate on plant community, and one for each climate treatment to compare the effect of herbivore treatment within each climate. The analysis returns an R statistic between where a value of 1 indicates complete dissimilarity.

We found that between climate treatments, there was a very high level of dissimilarity ($R = 0.9646$, $p = 0.001$). Within climates, Arid had high amount of dissimilarity ($R = 0.8436$, $p = 0.008$), followed by Mesic (0.7284 , $p = 0.016$), and finally Intermediate ($R = 0.3086$, $p = 0.029$).