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Divergent drought responses in two cold desert shrublands

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Abstract

The frequency and intensity of extreme droughts are projected to increase in the future, yet current research indicates that ecosystem sensitivity to extremes will vary. Despite hundreds of observational and experimental drought studies across ecosystems, the underlying mechanism explaining the inconsistent responses to drought remains poorly understood. Differences in the magnitude or duration of drought, land use history, existing plant communities, or unique site conditions might all influence the drought response of a site. Due to unresolved questions related to ecosystem sensitivity to drought, additional studies are needed to improve our predictions about the drought responses across ecosystems. Here, we minimized differences in drought intensity, climatic variation, and land use history by conducting a rainfall manipulation study in two adjacent (~60 m apart) plant communities with distinct dominant species (*Artemisia arbuscula* and *Artemisia cana*) in eastern Oregon, USA. We used rainfall shelters to create a 1-in-100-year drought at each site to understand how chronic (4-year) drought will impact common, but understudied sagebrush steppe plant communities. We found that above- and belowground net primary production at both sites was remarkably resistant to four years of drought. Interestingly, litter increased over time in drought plots at the more productive site, and we hypothesize that hydraulic lift and litter interacted to increase shallow soil water content under drought at that site. The site with harsher edaphic features and a soil duripan experienced fewer changes in plant community composition than the more productive site, potentially due to the presence of specialized plant species at the harsher site. Non-native plant cover increased (primarily from *Ventenata dubia*) and native forb cover and density decreased across our four sampling years. This suggests that management may be needed to conserve native forb diversity and limit species invasion, especially as the climate and historic fire regimes change.

Kerry M. Byrne and Justin C. Luong contributed equally to the work reported here.

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KEYWORDS
aboveground net primary production (ANPP), *Artemisia arbuscula*, *Artemisia cana*, belowground net primary production (BNPP), international drought experiment (IDE), phylogenetic diversity, sagebrush steppe, *Ventenata dubia*

INTRODUCTION

The frequency and intensity of extreme droughts are projected to continue increasing over the next century, yet a growing body of research indicates that drought sensitivity will vary across ecosystems (Byrne et al., 2013; Knapp, Hoover, et al., 2015; Smith et al., 2024; Wilcox et al., 2017; Wu et al., 2011). Both observational and experimental studies have reported that drought reduces ecosystem functions (e.g., net primary production, Hoover et al., 2014; Manea et al., 2016; Warter et al., 2021), changes plant community composition (Batbaatar et al., 2022; Byrne et al., 2017; Copeland et al., 2016; Hoover et al., 2014), and decreases phylogenetic diversity (Li et al., 2019; Luong et al., 2021). Generally, drought experiments have found that arid ecosystems are more sensitive to drought than mesic ecosystems (the resource limitation hypothesis; Huxman et al., 2004), yet many studies have also found that ecosystem functions (Batbaatar et al., 2022; Frank, 2007; Grime et al., 2000; Haugum et al., 2021; Tielbörger et al., 2014), plant community composition (Evans et al., 2011; Haugum et al., 2021; Jentsch et al., 2011; Tielbörger et al., 2014), and phylogenetic diversity (Aguirre-Gutiérrez et al., 2020; Copeland et al., 2016; Rurangwa et al., 2021) are remarkably stable under extreme drought. The underlying mechanisms explaining inconsistent responses to drought across and within ecosystems remain poorly understood.

There are several possible explanations for divergent drought responses across studies. First, differences in the magnitude or duration of drought might cause variation in ecological response (Kooyers, 2015). For example, many drought studies are observational and have occurred opportunistically with differing durations, magnitudes, and even differing definitions of drought (Slette et al., 2019). The use of drought shelters and consistent methodologies across sites helps reduce some of the inconsistencies associated with observational studies (Hoover et al., 2018; Knapp et al., 2017; Smith et al., 2024). Yet most published drought experiment studies are relatively short-term: many last less than one year, and most are 1–4 years in duration (Hoover et al., 2018; Matos et al., 2020). Moreover, even when consistent methodologies are employed across sites, precipitation varies spatially and temporally (Knapp et al., 2017). At a given site, larger absolute differences in precipitation between control and drought plots are observed in wetter years compared with drier years (Hoover et al., 2018; Kreyling et al., 2017). This is exacerbated in multi-site studies, where temporal differences among years are also confounded by spatial differences in precipitation (e.g., interannual precipitation variability) patterns and environmental conditions among sites (Kreyling et al., 2017; Matos et al., 2020). Combined, these shortcomings of drought shelters still limit the inference about differences in short-term drought sensitivity among sites.

Community-level responses can buffer or exacerbate drought response due to portfolio effects related to species turnover and reordering of dominant species (Griffin-Nolan et al., 2019; Naeem, 2016; Smith et al., 2009; Yachi & Loreau, 1999). A lack of apparent drought response may indicate portfolio effects within a plant community related to the simultaneous decrease of one species and the increase of another with similar traits (Adler et al., 2013; Robroek et al., 2017; van Staalduinen & Anten, 2005; Yachi & Loreau, 1999). For example, Robroek et al. (2017) found that drought led to species turnover, but turnover favored equivalent functional groupings across peat bog plant communities in Europe. Phylogenetically related species often share similar traits (Gilbert & Parker, 2016; Verdu et al., 2012), and plant communities with many related taxa could support portfolio effects in response to drought regardless of species turnover (Losos, 2008). Environmentally harsh site factors can further result in closely related species developing similar traits through phylogenetic niche conservatism (Drenovsky et al., 2012; Liu et al., 2015; Losos, 2008).

Distinctive site conditions, such as finer-scale environmental features (e.g., soil chemical and physical properties, rooting depth) or land use legacies, may influence the drought response of an ecosystem. For example, plant-available water strongly depends on soil texture and rooting depth, meaning that two sites with varying soil textures or other soil characteristics that affect rooting depth will experience different drought severity despite similar reductions in rainfall (Ploughe et al., 2019; Vicca et al., 2012). Land use legacies (e.g., livestock grazing, nitrogen deposition, species invasion, changes in fire return intervals) are site-specific abiotic and biotic properties due to the land use history (Foster et al., 2003). The ways in which land use legacies affect contemporary

patterns and processes in ecology are well documented, yet few studies have investigated how land use legacies interact with drought or other global change factors to affect future ecosystem trajectories (Perring et al., 2016; Verheyen, 2022). Of the few published studies, there is evidence that differing land use histories affect ecosystem sensitivity to drought, although responses may be context-dependent (Marqués et al., 2022; Mausolf et al., 2018).

The Great Basin ecoregion is the largest interconnected habitat type across continental North America (Miller et al., 2011; West & Young, 2000). It spans across much of western North America, although land use legacies (non-native species invasions, differing grazing histories, and habitat fragmentation) and intensified drought threaten its persistence (Nagy et al., 2021; Smith et al., 2022; Snyder et al., 2019). Almost all research to date has focused on the dominant plant alliance of *Artemisia tridentata*, due to its ubiquitous distribution. However, it is a heterogeneous and diverse system, and other sagebrush species dominate in areas with differing abiotic conditions. Within the greater Great Basin landscape, adjacent plant communities often have different dominant sagebrush species, structures, and functions (Miller et al., 2011).

Climate change predictions for the Great Basin include less predictable rainfall with fewer, but larger rain pulses, and a smaller snowpack, which will impact species that rely on late-season moisture (Bradley, 2010; Loik et al., 2004). Species distribution models for *A. tridentata* communities indicate that climate change will decrease the suitable habitat area for sagebrush (Bradley, 2010; Still & Richardson, 2015). Yet, several field studies present contradictory results. Studies at warmer, lower elevation sites found that drought reduced sagebrush growth (Apodaca et al., 2017; Poore et al., 2009). However, at high elevation, *A. tridentata* cover increased with artificial warming (Harte et al., 2015) and after drought (Debinski et al., 2010). Holdrege et al. (2021) found that fewer, larger precipitation events increased the growth of sagebrush, while Karban and Pezzola (2017) observed little mortality during a naturally occurring severe drought. Inconsistent results across site-level studies demonstrate that it may be hard to predict the response of other key sagebrush species based on studies focusing solely on *A. tridentata*.

Due to the unresolved questions related to ecosystem sensitivity to drought and existing research focusing primarily on *A. tridentata*, additional studies are needed that minimize differences in drought magnitude, interannual variation in precipitation, climatic history, and land use legacies to improve our predictions about plant community drought responses. As such, we sought to minimize differences in drought intensity, climatic variation, and land use history in our experiment to compare plant functional group and community drought responses in two adjacent (~60 m apart) sagebrush communities with understudied dominant sagebrush species. Our design allowed us to focus on the influence of local-scale environmental variation and plant community characteristics that influence drought response. We characterized and contrasted the effects of drought on plant community composition, mean phylogenetic distances, and net primary production across four years. We predicted that drought would differently affect the composition of adjacent plant communities dominated by distinct sagebrush species, but overall, drought would increase grass while decreasing shrub cover and reduce above-and belowground productivity and native seedling density. We hypothesized there would be lower species richness and reduced abundance of annual forbs during drought, which would narrow phylogenetic diversity.

METHODS

Study site

We conducted our study at two sites approximately 60 m apart within a grazing exclosure established in 1993 in Klamath County, Oregon, USA (42.301111, −121.018056). The research area last burned in 1985 and is located near the westernmost extent of the sagebrush steppe ecosystem within the Great Basin. The two study sites have unique edaphic features that lead to differences in the ecological structure and function of the plant communities. One site is dominated by *Artemisia arbuscula* Nutt. (low sagebrush) while the other site is dominated by *Artemisia cana* Pursh (silver sagebrush). These species often form unique plant communities in areas absent of *A. tridentata* (Miller et al., 2011). *A. arbuscula* is a low-growing sagebrush species that occupies more than 11 million hectares across western North America in areas with xeric, shallow soils with a heavy clay layer or duripan. Soils at our *A. arbuscula*-dominated site (AA site) are classified as clay loam, with relatively high clay (32%) and sand (35%) content and an impermeable duripan at approximately 12 cm depth (Nunes & Byrne, 2022). Although the herbaceous vegetation in *A. arbuscula* communities often overlaps with *A. tridentata* communities, productivity is lower and bare ground is more prevalent (Francis, 2004; Miller et al., 2011). In contrast, *A. cana* is often found in transitional wet-to-dry areas with higher soil moisture. *A. cana* is the second most abundant sagebrush species in North America, distributed across 14 million hectares. There is higher

productivity, more persistent litter, and very little exposed bare ground in *A. cana* communities compared with *A. arbuscula*-dominated sites (Miller et al., 2011). Soils at our *A. cana*-dominated site (AC site) are classified as silty clay, with greater clay (42%) and silt (43%) content than the AA site (Nunes & Byrne, 2022).

Subdominant vegetation within each site is distinct. The most common perennial grasses (Poaceae) at the AA site are *Festuca idahoensis* Elmer (Idaho fescue) and *Elymus elymoides* (Raf.) Swezey (squirreltail). *Poa secunda* J. Presl. (Sandberg bluegrass) is more abundant at the AC site. An invasive annual grass, *Ventenata dubia* (Leers) Durieu (ventenata grass), is increasingly common at both sites, but more prominent at the AA site. At the AC site, both *V. dubia* and annual *Bromus* species (*B. japonicus* Thunb. (Japanese brome) and *B. tectorum* L. (cheatgrass)) are dominant invaders. Common forbs at the AA site include *Eriogonum sphaerocephalum* Douglas Ex. Benth (rock buckwheat) and *Erigeron bloomeri* A. Gray (scabland fleabane), while common forbs at the AC site include *Perideridia oregana* (S. Watson) Mathias (Oregon yampah) and *Achillea millefolium* L. (common yarrow). There are no co-dominant shrub species present at either site.

Mean hydrologic year (October–September) precipitation (1990–2020) for this area is 314 mm (Appendix S1: Figure S1), and mean minimum and maximum temperatures are 0.89 and 15.8°C. Most precipitation arrives as rain or snow during the winter months, and the growing season is March–September. Meteorological data were measured ~10 km from the study sites at the Oregon Gerber Reservoir Climate station (42.205556, −121.138889; 1500 m above sea level) managed by the Western Regional Climate Center.

Experimental design

We selected areas with similar species composition within each sagebrush community in July 2016 and established 10 2 × 2 m plots at each site with at least one established *A. arbuscula* or *A. cana* individual rooted near the plot center (for AA and AC respectively). Plots were randomly assigned to drought or control treatments ($n = 5$ at each site). We constructed 3 × 3 m rain-out (drought) shelters (Yahdjian & Sala, 2002) following a standard protocol from the International Drought Experiment (Knapp, Carroll, et al., 2015) to passively exclude 41% of ambient precipitation to simulate a 1-in-100-year drought, based on local 100-year precipitation records. Drought plots had a 0.5-m buffer around plot edges to reduce the horizontal flow of precipitation from outside the plots. Shelters were built with wooden frames and 15-cm wide strips of corrugated polycarbonate (Dynaglas brand), which transmits greater than 90% of photosynthetically active radiation (Loik et al., 2019). Corrugated polycarbonate channeled precipitation into a gutter that directed water away from the plots. Shelters were about 1.2 m on the shorter end and 2.0 m on the taller end, creating shelters that were at least 0.75 m above maximum vegetation height (Appendix S1: Figure S2).

We monitored volumetric soil water content ("soil water") at shallow depths in each treatment (0–10 cm at AA site, $n = 3$; 5–15 cm at AC site, $n = 2$) every 4 h to evaluate the effectiveness of the drought treatment. We monitored deeper (20–30 cm) soil water in one plot for each treatment at the AC site, but not the AA site, due to the duripan. Probes (Decagon EC-5 VWC, Pullman, Washington, USA) were installed perpendicular to the soil surface for the duration of the experiment. Some probes had to be re-installed after soil saturation during the winter months due to freeze–thaw cycles that occasionally shifted the probe location.

Data collection

We measured plant species composition and aboveground net primary production (ANPP) at the sites each year from 2016 to 2020 near peak biomass (early July). We visually estimated the canopy cover of each species in a 1.0 m^2 subplot of each 4.0 m^2 plot, lumping *B. japonicus* and *B. tectorum* together. We recorded species richness by surveying the entire 4.0 m^2 plot. We quantified the density of nine common forb species and *Artemisia* seedling density within the 1.0 m^2 subplots (Appendix S1: Table S1).

We nondestructively estimated ANPP and litter in a permanently marked 0.5 m^2 point-frame within each 4.0 m^2 plot. Using a 62 × 80 cm (0.5 m^2) quadrat with 50 equidistant points, we estimated litter and cover by plant lifeform (shrubs, forbs, and grasses—including graminoids), and then measured average vegetation height to estimate plot-level ANPP. We selected 15 calibration plots annually (outside of treatment plots) where we used the point-frame to nondestructively measure plant cover and average vegetation height, then destructively sampled ANPP of the calibration plots by clipping current year vegetative growth. We clipped biomass at the soil surface, separated by plant lifeform, and then weighed samples after drying them at 55°C for ≥48 h. We then fit a regression relating the nondestructive plant cover measurements to ANPP within the calibration plots. Finally, we estimated ANPP in our experimental plots using the multiple regression developed by our

calibration plots to convert our nondestructive ANPP measurements to grams per square meter (see Byrne et al., 2011 for details).

We used root ingrowth cores to estimate belowground net primary production (BNPP). Each October, we excavated one or two 5-cm-diameter cores per plot to a depth of 20 cm at the AC site and ~10 cm at the AA site (due to the duripan). We focused on the upper soil layer because globally grasses were found to position 44% of their total root biomass in the top 10 cm (Jackson et al., 1996), while others found an exponential decline in root biomass with increasing depth (Frank et al., 2010). All cores were excavated near the bunchgrass canopy edge to limit sampling heterogeneity. We placed a mesh cylinder with 1.0 mm^2 openings within each excavated core and filled it with sieved root-free soil from the site. Each following October, we removed the ingrowth cores by drilling an 8-cm-diameter hole saw into the soil surrounding the ingrowth core. After excavation, we brushed away roots and soil from the outside of the ingrowth core. We air-dried ingrowth cores to minimize decomposition before processing, then used a series of sieves and buckets with water and air to gently separate the roots from the soil and clean the roots. We dried roots at 55°C for ≥48 h before weighing and then combusted samples at 500°C for 5 h to determine ash content. We converted our BNPP estimates to grams per square meter and report on an ash-free basis (see Byrne, 2021 for details).

Phylogenetic relationships

We created a phylogeny (Appendix S1: Figure S3) containing the 47 species from both sites with PHYLOCOM (Webb et al., 2008). We used ages from the R2G2_20140601 super tree that was amended by Parker et al. (2015) to include additional taxa from the Western USA at the species and genus levels. Phylogenetic diversity metrics were calculated at the zeroth quantile for nearest taxon distance (NTD) and the 10th quantile (PD_{10}) for assessing relationships at small evolutionary scales (e.g., species or genus level) and the 50th quantile for mean pairwise distance (MPD) for coarser evolutionary scales (Parker et al., 2015). PD_{10} was developed by Gilbert and Parker (2022) to further assess biotic interactions because it limits the swamping effect in communities with many distantly related phylogenetic pairs. We abundance-weighted metrics by multiplying a (plot × species cover) and (species × phylogenetic metric) matrix (Griffin-Nolan et al., 2019).

Analysis

We collected pretreatment data in 2016 to ensure there were no plot effects prior to implementing treatments. We grouped species cover based on native status and separately by life form. We used ANOVA to confirm there were no pretreatment effects ($p_{all} > 0.05$) on response metrics (we did not collect pretreatment BNPP). We used data from 2017 to 2020 to compare treatment effects on ANPP, BNPP, litter, plant abundance (native cover, non-native cover, grass cover, forb cover, shrub cover, forb species density, shrub seedling density) and diversity metrics (native richness, non-native richness, Shannon diversity, NTD, PD_{10}, MPD) using generalized linear models (GLMs). We included drought, site, and time (sampling year) as the fixed effects and drought × site and drought × time as the interaction terms (there were no three-way interaction effects for any of the response variables, so we removed it to retain statistical power; Goodhue et al., 2007). Data were confirmed for parametric assumptions prior to using GLMs.

We used permutational analysis of variances (PERMANOVA) to compare drought, site, and time effects with Bray–Curtis dissimilarity indices. Then we tested whether functional groups were significant predictors and their potential contribution to community change using a canonical correspondence analysis (CCA). CCA allows for the determination of how increases in different functional groups were associated with directional shifts in community composition across years and study sites. We used similarity analyses (SIMPER) to determine which species were driving within-site differences from drought. Differences in plant community composition were represented using a nonmetric multidimensional space plot (NMDS).

All analyses were completed with R statistical software V 4.0.4 (R Core Team, 2020) using COWPLOT, GGPLOT2, LUBRIDATE, PLYR, RESHAPE2, TIDYVERSE, and VEGAN packages (Oksanen et al., 2018; Wickham, 2020; Wickham et al., 2018; Wilke, 2020).

RESULTS

Efficacy of rain-out shelters

During the first three years of the study period (2017–2019) precipitation was 20%–30% above average, while it was about 30% lower than the long-term average in the fourth year (2020; Appendix S1: Figure S1). At the AA site, shallow soil water was lower under

drought in three of the four experimental years, but in 2019, soil water was higher under drought (Appendix S1: Figure S4, Table S2). Deeper soil water (20–30 cm) at the AC site was consistently lower under drought, while shallow soil water was slightly lower under drought during the first study year; but thereafter (Fall 2017) soil water was consistently higher under drought until the probes malfunctioned during late Fall 2019 (Appendix S1: Figure S4, Table S2).

Net primary production and litter

ANPP ($t = 6.647$, $p < 0.001$) and BNPP ($t = 4.767$, $p < 0.001$) were both consistently higher at the AC site across years, although there was large interannual variation in NPP at both sites (Figure 1). Notably, BNPP was nearly three times greater than ANPP over the course of the study. Neither ANPP nor BNPP was affected by drought. ANPP ($t = -2.283$, $p = 0.023$) decreased over time, while BNPP did not change over time. Examined separately, BNPP declined over time at the AA ($p < 0.001$, $R^2 = 0.55$) but not at the AC site. The AC site had higher litter cover than the AA site ($t = 3.327$, $p = 0.001$) and litter cover increased over time ($t = 2.618$, $p = 0.011$; Figure 2). An interaction effect indicated that litter was higher during drought at the AC site ($t = 2.946$, $p = 0.004$) but not at the AA site.

Community composition and diversity

Both native ($t = 3.437$, $p < 0.001$) and non-native plant cover ($t = 2.580$, $p = 0.012$) were higher at the AC site but were unaffected by drought. Non-native plant cover ($t = 2.000$, $p = 0.049$) increased over time (Figure 2), while native cover did not vary over time. Grass ($t = 3.672$, $p < 0.001$) and shrub cover ($t = 4.263$, $p < 0.001$) were both higher at the AC site, but forb cover was similar at the sites. Drought ($t = -4.093$, $p < 0.001$) reduced forb cover at both sites, but an interaction effect with site resulted in a larger reduction in forb cover at the AA site ($t = 2.208$, $p = 0.030$). Forb cover decreased over the sampling period ($t = -2.501$, $p = 0.014$; Figure 2), but grass and shrub cover did not change over time.

Plant community composition differed between the AA and AC sites ($F = 65.4$, $p < 0.001$; Figure 3) and varied through time ($F = 3.39$, $p = 0.010$). Drought shifted plant community composition ($F = 4.582$, $p = 0.007$), but an interaction effect indicated that drought more strongly affected the AC site ($F = 6.02$, $p < 0.001$). CCA showed that functional groups explained 28.5% of the variation between communities (Table 1). Similarity analyses indicated that species driving differences between drought and control treatments at the AA site were *V. dubia* (14%), *Packera cana* (10%) and *Danthonia californica* (8%) and solely annual *Bromus* species (22%) at the AC site.

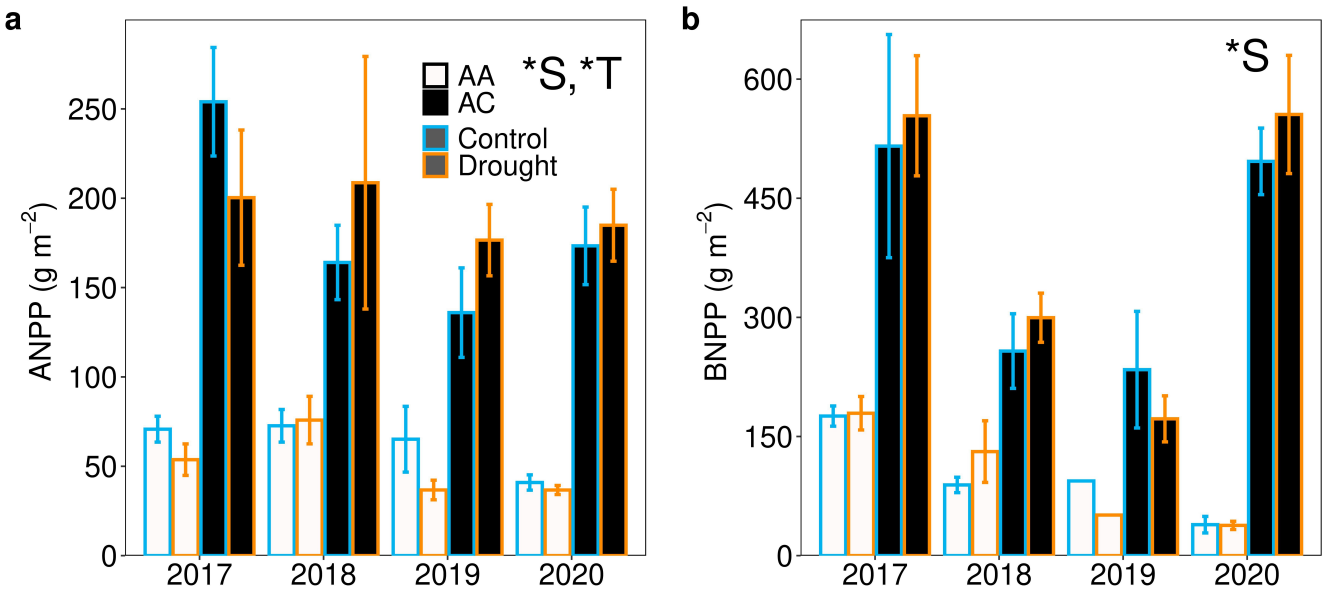
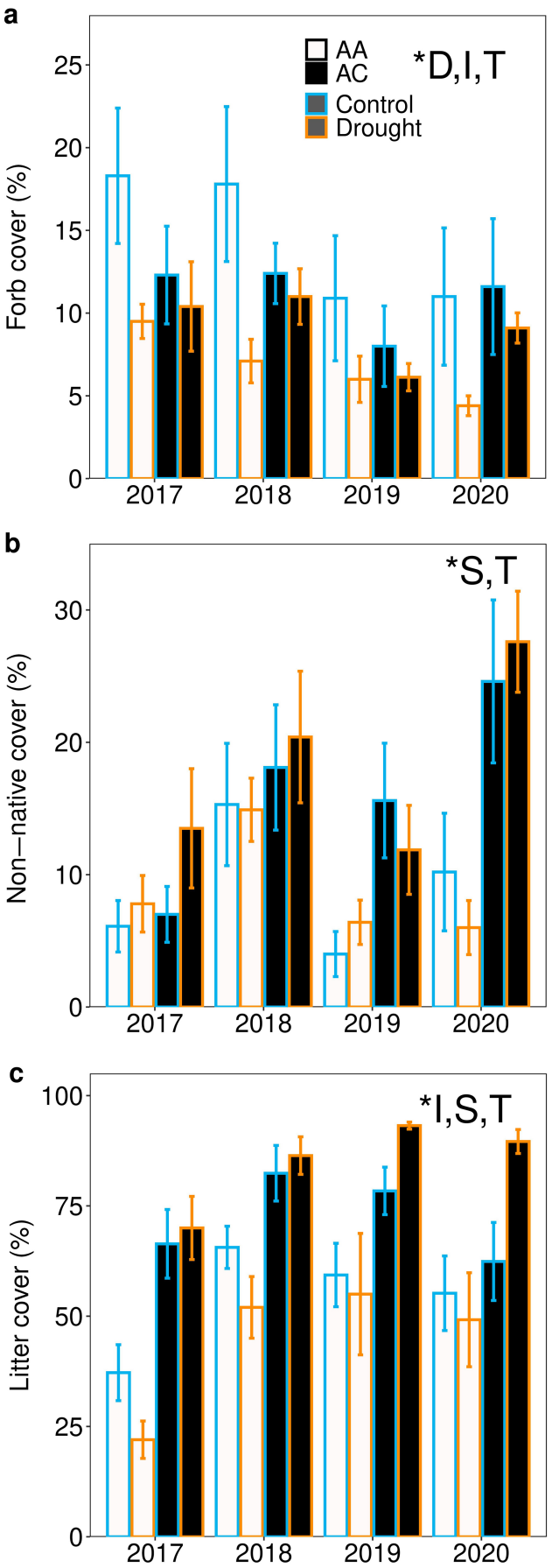


FIGURE 1 (a) Aboveground (ANPP) and (b) belowground (BNPP) net primary production in control and drought treatments from 2017 to 2020 (mean ± SE). In 2019, BNPP samples at the AA site were damaged, so there was only one replicate. *D, drought effect; *S, site effect; *T, time effect; *I, D × S interaction. The *y*-axis scales and ranges vary per plot. AA, sites dominated by *Artemisia arbuscula*; AC, sites dominated by *Artemisia cana*.



Mean *Artemisia* seedling recruitment was low (0.25 ± 0.11 individuals m^{-2} at the AA site and 0.20 ± 0.07 individuals m^{-2} at the AC site) and did not vary between sites nor over time. Interestingly, *Artemisia* recruitment was higher under drought ($t = 2.230$, $p = 0.029$). Total native annual forb density was not affected by drought nor site, but decreased over time ($t = -6.126$, $p = 0.026$). Individual forb species had mixed responses to drought (Appendix S1: Table S1). *Ac. millefolium* was the only forb that was negatively affected by drought ($t = -2.471$, $p = 0.018$).

Native species richness was higher at the AA site ($t = -2.471$, $p = 0.016$; Figure 4a), while non-native richness was higher at the AC site ($t = 4.090$, $p < 0.001$; Figure 4b). Both native and non-native species were unaffected by drought. Shannon diversity decreased over time ($t = -3.494$, $p < 0.001$) and an interaction effect resulted in lower diversity during drought for the AC site, but not the AA site ($t = -2.876$, $p = 0.005$; Figure 4c). NTD did not vary by site nor with drought. PD_{10} and MPD were higher at the AC site (PD_{10}: $t = 5.269$, $p < 0.001$; MPD: $t = 8.265$, $p = 0.027$) and increased due to drought (PD_{10}: $t = 2.236$, $p = 0.028$; MPD: $t = 2.262$, $p = 0.027$; Appendix S1: Figure S6). NTD, MPD, and PD_{10} did not vary over time.

DISCUSSION

Despite removing differences in land use legacies, drought magnitudes, interannual variation in precipitation, and climate history, our study found divergent responses to drought at adjacent sites with differing dominant species. The more productive site with much deeper soils (dominated by *A. cana*) was more drought sensitive and exhibited greater shifts in species composition compared with the less productive site with greater bare ground and shallower soils with a duripan (dominated by *A. arbuscula*). Differences in drought response can be attributed to edaphic factors (e.g., differences in soil texture, chemistry, and rooting depth), plant species attributes, and the unexpected litter accumulation within the drought treatment at the more productive site. We did not find strong evidence that drought reduced species richness as originally hypothesized, but drought increased community-weighted phylogenetic distances

FIGURE 2 (a) Forb, (b) non-native plant cover, and (c) litter cover in control and drought treatments from 2017 to 2020 (mean ± SE). *D, drought effect; *S, site effect; *T, time effect; *I, D × S interaction. The *y*-axis scales and ranges vary per plot.

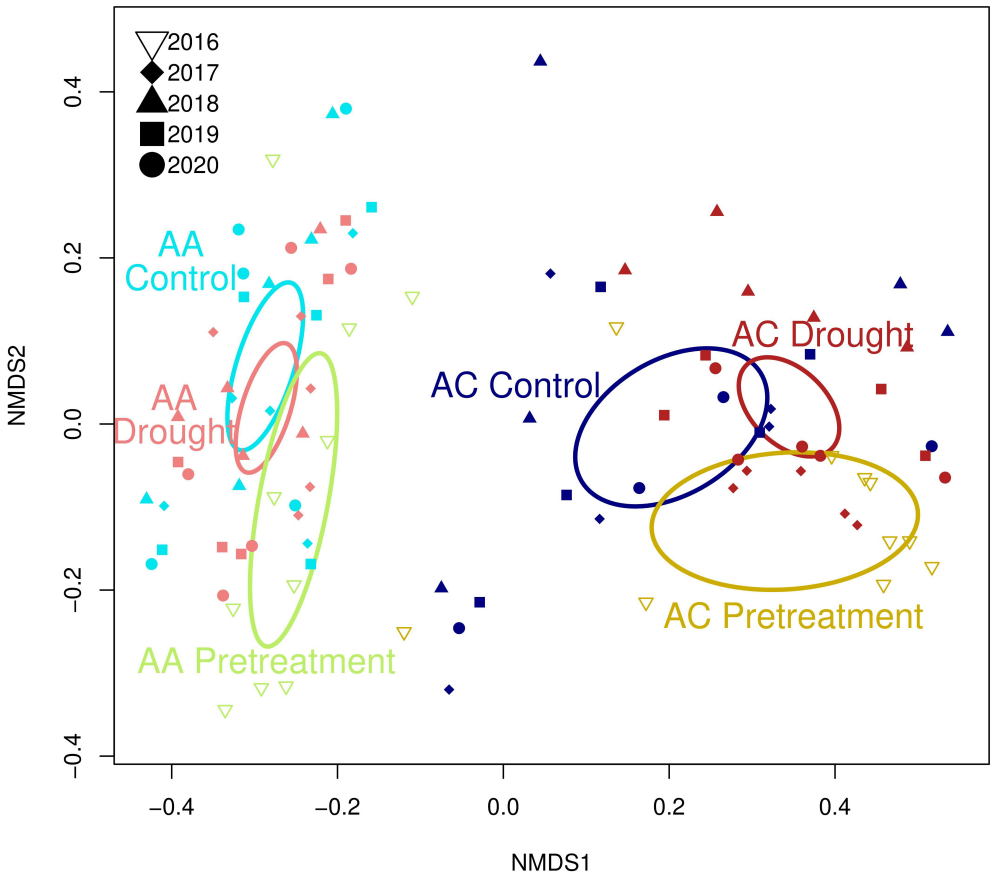


FIGURE 3 Nonmetric multidimensional scaling (NMDS) ordination ($k = 2$, stress = 0.153) of plant community composition. Points represent the community composition of a plot monitored during any given year from 2016 to 2020. The AC site has darker shades while the AA site has lighter shades. The distance between points represents the relative similarity of plant communities between plots. AA, sites dominated by *Artemisia arbuscula*; AC, sites dominated by *Artemisia cana*.

TABLE 1 Plant functional groups that are correlated with community composition change between the sites dominated by *Artemisia arbuscula* and *Artemisia cana* and control and drought treatments using canonical correspondence analysis (CCA).

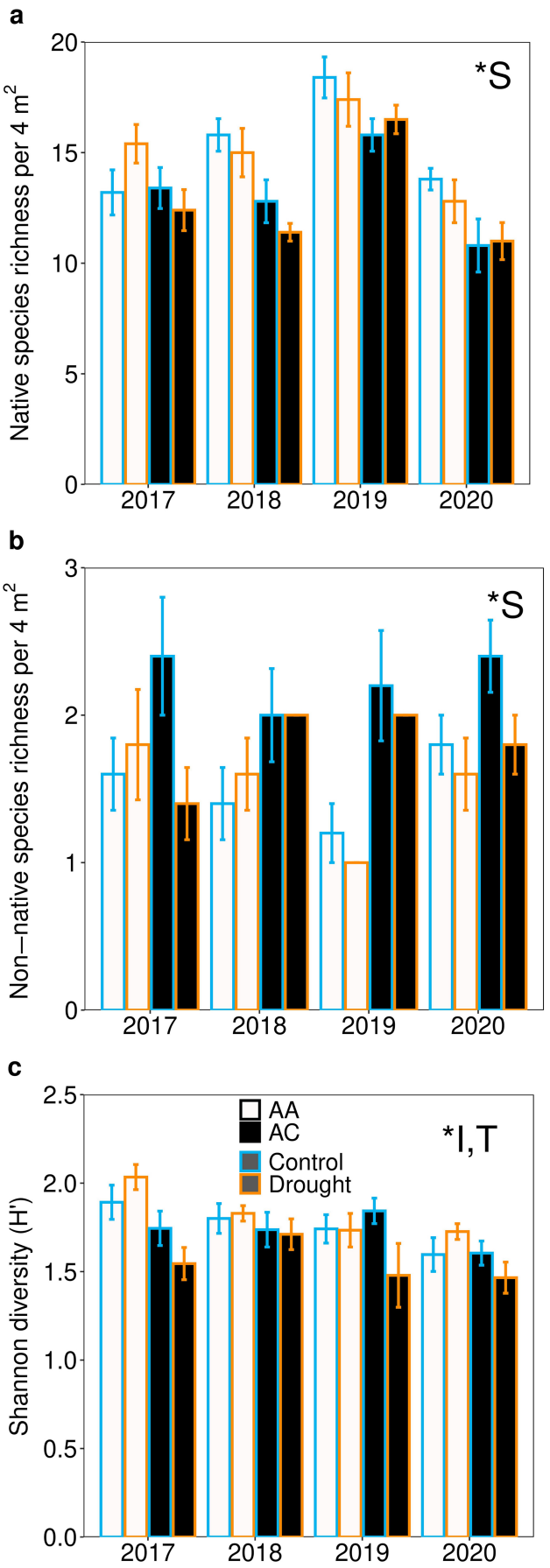
Plant functional group	*F*	R^2	*p*
Native shrubs	23.7	0.155	0.001*
Non-native annual grasses	17.5	0.115	0.001*
Native grasses	8.35	0.055	0.001*
Non-native perennial grasses	7.12	0.047	0.001*
Native forbs	2.36	0.020	0.020*
Residuals		0.609	

Note: Residuals are unexplained variances.
*$p < 0.05$.

that resulted in plant communities with taxa that were more distantly related. Surprisingly, both sites were resistant to drought-induced changes in NPP, although interannual variation in both ANPP and BNPP was strong.

Soil water

Drought consistently reduced shallow soil water at the AA site in most years and reduced deep soil water at the AC site in all years. In contrast, while drought initially reduced shallow soil water at the AC site, after the first growing season (Fall 2017) soil water was consistently higher under drought shelters for the remainder of the experiment (Appendix S1: Figure S3). Although we were surprised by this unexpected response in an experiment designed to reduce precipitation, we do not believe it was due to measurement error or shortcomings in the rain-out shelters for several reasons. First, the rain-out shelters used in the experiment are used in grasslands and shrublands globally (Smith et al., 2024) and are widely accepted as effective (Yahdjian & Sala, 2002 has over 300 citations). Furthermore, drought shelters at a similar cold desert in Idaho, USA, were found to effectively reduce soil water (Tredennick et al., 2018). Second, our soil water data indicate the shelters effectively reduced shallow soil water at the AA site. Due to our



unique experimental design (two sites within close proximity using the same rain-out shelters), we can assume that the shelters caused identical reductions in precipitation at both sites (but nonidentical reductions in soil water). Finally, the rain-out shelters caused a strong and consistent (50%–89%) reduction in deeper soil water ($n = 1$) at the AC site, providing yet another line of evidence that our rain-out shelters reduced soil water, at least at depth. If this is the case, then why was shallow soil water higher under drought at the AC site?

We speculate that both hydraulic redistribution of soil water and increased litter in the drought treatment explain the higher shallow soil water in the drought treatment at the AC site. Hydraulic redistribution or lift of water from deeper soils to shallow drier soils has been widely documented in regions with pronounced dry seasons (Caldwell et al., 1998; Neumann & Cardon, 2012) and was first demonstrated in *A. tridentata* var. *vaseyana* in the Great Basin (Richards & Caldwell, 1987). In our study, a duripan that precludes deep tap roots is present at approximately 12 cm below the soil surface at the site dominated by *A. arbuscula*; therefore, we would not expect plant-induced hydraulic lift. Indeed, we found the expected pattern (e.g., drought reduced shallow soil water) at the AA site. In contrast, the site dominated by *A. cana* has deeper soils and lacks a duripan. Although we can find no specific studies documenting hydraulic lift in *A. cana*, it has similar morphology to *A. tridentata* (e.g., roots extending 2 or more meters into the soil; Letts et al., 2010) and grows in a semiarid environment with relatively little summer precipitation; closely related species developing with the same abiotic filters suggest the potential for phylogenetic niche conservatism (Losos, 2008) between taxa and the capacity for hydraulic redistribution of soil water (Caldwell et al., 1998).

Hydraulic lift alone does not explain the increased soil water under drought conditions, but we also found that litter increased over time and was higher in the drought treatment at the AC site (Figure 3c). We hypothesize that the increased litter decreased bare soil evaporation in the drought treatment (Magliano et al., 2017), providing a mechanism to conserve shallow soil water compared with the control plots. Indeed, plant litter is known to regulate soil moisture and there is often a

FIGURE 4 (a) Native and (b) non-native plant species richness and (c) Shannon diversity index for control and drought treatments from 2017 to 2020 (mean ± SE). *D, drought effect; *S, site effect; *T, time effect; *I, D × S interaction. The *y*-axis scales and ranges vary per plot. AA, sites dominated by *Artemisia arbuscula*; AC, sites dominated by *Artemisia cana*.

positive relationship between litter and soil moisture across ecosystems (Boeken & Orenstein, 2001; Deutsch et al., 2010; Facelli & Pickett, 1991; Loydi et al., 2013). Although we did not identify the species that contributed to litter in this study, it is likely that the increased litter was mostly from annual grasses (K. M. Byrne, personal observation). Annual grasses are known to increase litter in western North America (Balch et al., 2013; Davies & Nafus, 2013) and Wolkovich et al. (2009) also found that non-native annual grasses contributed to higher shallow soil moisture by 20% through litter accumulation. This surprising result could have large implications for overall ecosystem function during future extreme droughts in shrublands and woodlands where hydraulic lift interacts with litter to increase shallow soil water. Over time, increases in shallow soil water could increase nutrient cycling (Cardon et al., 2013) and alter species composition, favoring ruderal and shallow-rooted species such as grasses and annual forbs that are typically non-native (Kulmatiski et al., 2017). This could create a positive feedback loop (D'Antonio & Vitousek, 1992), leading to additional litter accumulation and a more continuous fine fuel layer, potentially decreasing fire return intervals (Balch et al., 2013; Davies & Nafus, 2013; Tortorelli et al., 2020).

Net primary production

As expected, the AC site had higher net primary production than the AA site, likely due to inherent differences in soil type and moisture (Fernandez-Going et al., 2012; Reynolds et al., 1997; Van Auken, 2009). However, we found that ANPP within both plant communities was remarkably resistant to the drought treatment but decreased over time, paralleling patterns in ambient precipitation. These findings contradict the resource limitation hypothesis (Huxman et al., 2004), which predicts that arid and semi-arid ecosystems like the sagebrush steppe would be more sensitive to changes in precipitation than mesic ecosystems. Instead, our findings are congruent with other experiments and meta-analyses that have found that shrublands are more resistant to experimental drought than grasslands globally (Báez et al., 2013; Gao et al., 2019; Haugum et al., 2021; Smith et al., 2024) and other drought manipulation and observational studies in the Great Basin focused on *A. tridentata* (Harte et al., 2015; Holdrege et al., 2021; Karban & Pezzola, 2017) and *Artemisia tripartita* (Tredennick et al., 2018).

BNPP was also resistant to drought, but unlike ANPP, did not decrease over time. Allocation to maintain BNPP may be adaptive in arid, nutrient-limited habitats, as optimal partitioning theory suggests plants allocate growth to organs that help acquire limiting resources (Bloom et al., 1985; Luong & Loik, 2022). Although there are fewer studies reporting the effects of drought on BNPP, published results are inconsistent, with some studies reporting a decrease in BNPP due to drought (Frank, 2007; Holguin et al., 2022; Slette et al., 2022) and others reporting stable BNPP under drought (Alon & Sternberg, 2019; Batbaatar et al., 2022; Byrne et al., 2013; Holguin et al., 2022). Alternatively, our finding could be due to a portfolio effect (Naeem, 2016; Yachi & Loreau, 1999) during species turnover favoring fewer species that can tolerate drought in the root zone (Harrison et al., 2015; Smith et al., 2009), yet we cannot confirm this as our root measurements were not species-specific. However, we found increased phylogenetic distances across large (MPD) and small (PD_{10}) evolutionary scales in response to drought, likely indicating truncation of plant communities and species turnover (Monnet et al., 2014; Verdu et al., 2012).

Increased phylogenetic distances could indicate that plant communities exposed to drought supported taxa that were less closely related across small and large evolutionary scales, suggesting that drought resistance was potentially restricted to certain, but distantly related plant lineages in the region (García-Camacho et al., 2017). Alternatively, increased community-weighted mean phylogenetic distance (PD_{50}) within the community could be related to invasions of less distant taxa, such as annual grasses (Appendix S1: Figure S3). Indeed, we saw increases in invasive annual grasses in our study, which demonstrates that increased diversity may not always be positive for ecological communities (Bennett et al., 2014). Similarly, an increase in PD_{10} (phylogenetic distance at the 10th quantile; generally associated with within-family differences; Gilbert & Parker, 2022) was likely associated with increased cover of non-native species more distantly related to species within observed the plant families.

When examined separately, we found that BNPP declined over time at the AA site, while it first declined then rebounded in the final year at the AC site (Figure 2). Perhaps these site-level differences in BNPP responses are due to the hydraulic lift of water to shallower soils at the AC site, or increases in nutrient availability as the litter decomposed, or the combination of the two factors (Aanderud & Richards, 2009; Armas et al., 2012; Cardon et al., 2013). Regardless, additional studies focused on root interactions are needed to improve our understanding of plant community responses in the face of chronic drought.

Species composition

The more productive AC site exhibited greater drought-induced changes in plant community composition and cover compared with the AA site. Interestingly, the opposite was true belowground: three years of drought caused greater shifts in the seed bank at the AA site (Nunes & Byrne, 2022). Despite having lower cover of almost all plant cover types, the less productive AA site consistently had higher native richness. Similar to serpentine grasslands, which have unique edaphic factors due to high levels of heavy metals (Going et al., 2009; Reynolds et al., 1997), areas dominated by *A. arbuscula* may have higher native richness and greater drought resistance due to harsh soil properties that exclude invaders that have not adapted to the unique physical and chemical soil factors (Going et al., 2009; Huenneke et al., 1990). Interestingly, species composition in the drought plots was much less variable over time than in the control plots (Figure 2). This contraction in the plant communities could be due to abiotic filtering at both sites favoring plants with key traits or growth patterns (Luong et al., 2021), although these were outside of the scope of our study and warrant further research.

Plant cover (native, non-native, grass and shrub cover), composition, and recruitment of native species in *A. arbuscula* and *A. cana* plant communities showed high resistance to extreme drought, consistent with past work done on conspecifics: *A. tridentata* (Debinski et al., 2010; Karban & Pezzola, 2017), *A. tripartita* (Tredennick et al., 2018), and *Artemisia californica* (Puritty et al., 2019). *A. arbuscula* and *A. cana* communities occur in a semi-arid region and likely have adaptations to persist in drought (Carroll et al., 2021; Kolb & Sperry, 1999; Schwinning & Ehleringer, 2001). Alternatively, drought-induced responses may only be evident across longer timespans, especially in ecosystems dominated by long-lived species (Sala et al., 2012). For example, Evans et al. (2011) did not find strong drought responses in a semiarid grassland until the seventh study year. Anderson and Inouye (2001) suggest that there might be 2-to 4-year lags between precipitation and changes in species composition and functional groups in *Artemisia* shrublands.

Forb cover and density of some native forbs decreased over time, whereas non-native plant cover increased only at the more productive AC site. Increases in non-native plant cover in AC plots were driven by non-native annual grasses: *V. dubia, B. japonicus*, and *B. tectorum*. Non-native annual grasses have been expanding across the Great Basin for decades, linked with disturbance and changes in climate (Boyte et al., 2019; Smith et al., 2022). Drought negatively affects both native and non-native species (Garbowski et al., 2021; Puritty et al., 2019) but certain invasive forbs (Mojzes et al., 2020) and annual grasses (Garbowski et al., 2021; Ross, 2022) may benefit during and after drought (Puritty et al., 2019) by taking advantage of early-season soil moisture and potentially outcompeting other species (Garbowski et al., 2021). Indeed, in our study, the interaction of drought and non-native annual grasses could have limited germination and increased the mortality of native species (LaForgia et al., 2020), resulting in lower native forb cover and density over time. In turn, this may have further contributed to invasion by decreasing biotic resistance and freeing space needed for invasion (Pearson et al., 2016). Anderson and Inouye (2001) note in their 45-year study of compositional changes in *A. tridentata* communities that increased cover of native species was associated with lower density, richness, and non-native species cover.

Increased invasion by *V. dubia* is concerning as non-native annual grasses significantly alter fire regimes in the Great Basin region (Balch et al., 2013; Davies & Nafus, 2013; Tortorelli et al., 2023; Whisenant, 1990). Notably, *V. dubia* has successfully invaded forest scabland sites (*Artemisia ridgida* and *A. arbuscula* dominated) previously resistant to non-native annual grass invasion by *B. tectorum* and *Elymus caput-medusae* (medusahead) in western North America (Tortorelli et al., 2020). Additionally, non-native annual grass species have relatively low and variable forage quality (Bovey et al., 1961; Brummer et al., 2023), suggesting active management may be necessary to help limit *V. dubia* positive feedback cycles that accelerate wildfire risk (Fernández-Guisuraga et al., 2023) and reduce rangeland forage (DiTomaso, 2000).

CONCLUSIONS

We found that plant composition and productivity in two cold desert shrubland communities dominated by understudied sagebrush species were resistant to four years of experimental drought. We were surprised to discover that drought increased shallow but decreased deeper soil water at our more productive shrubland site, which was likely linked with hydraulic lift and amplified litter cover of non-native species under drought conditions. Our study provides insight into the complicated nature of interacting global change factors that can result in unanticipated drought effects. Common biotic mechanisms such as the invasion of non-native annual grasses simultaneously during our drought treatments demonstrate the challenges of predicting the impacts of multiple interacting global change factors.

AUTHOR CONTRIBUTIONS

Kerry M. Byrne conceptualized the study, acquired funding, developed the methodology, conducted the investigation, managed the project, curated the data, and contributed to writing, review, and editing. Justin C. Luong performed the formal analysis, curated the data, created visualizations, and contributed to writing the original draft as well as review and editing. Kristen M. Kaczynski secured funding and contributed to writing, review, and editing.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

Data (Byrne et al., 2025) are available from Dryad: https://doi.org/10.5061/dryad.0zpc8677v.

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REFERENCES

Aanderud, Z. T., and J. H. Richards. 2009. "Hydraulic Redistribution May Stimulate Decomposition." *Biogeochemistry* 95(2): 323–333. https://doi.org/10.1007/s10533-009-9339-3.

Adler, P. B., A. Fajardo, A. R. Kleinhesselink, and N. J. B. Kraft. 2013. "Trait-Based Tests of Coexistence Mechanisms." *Ecology Letters* 16(10): 1294–1306. https://doi.org/10.1111/ele.12157.

Aguirre-Gutiérrez, J., Y. Malhi, S. L. Lewis, S. Fauset, S. Adu-Bredu, K. Affum-Baffoe, T. R. Baker, et al. 2020. "Long-Term Droughts May Drive Drier Tropical Forests towards Increased Functional, Taxonomic and Phylogenetic Homogeneity." *Nature Communications* 11(1): 1–10. https://doi.org/10.1038/s41467-020-16973-4.

Alon, M., and M. Sternberg. 2019. "Effects of Extreme Drought on Primary Production, Species Composition and Species Diversity of a Mediterranean Annual Plant Community." *Journal of Vegetation Science* 30(6): 1045–61. https://doi.org/10.1111/jvs.12807.

Anderson, J. E., and R. S. Inouye. 2001. "Landscape-Scale Changes in Plant Species Abundance and Biodiversity of a Sagebrush Steppe over 45 Years." *Ecological Monographs* 71(4): 531–556. https://doi.org/10.1890/0012-9615(2001)071[0531:LSCIPS]2.0.CO;2.

Apodaca, L. F., D. A. Devitt, and L. F. Fenstermaker. 2017. "Assessing Growth Response to Climate in a Great Basin Big Sagebrush (*Artemisia tridentata*) Plant Community." *Dendrochronologia* 45: 52–61. https://doi.org/10.1016/j.dendro.2017.06.007.

Armas, C., J. H. Kim, T. M. Bleby, and R. B. Jackson. 2012. "The Effect of Hydraulic Lift on Organic Matter Decomposition, Soil Nitrogen Cycling, and Nitrogen Acquisition by a Grass Species." *Oecologia* 168(1): 11–22. https://doi.org/10.1007/s00442-011-2065-2.

Báez, S., S. L. Collins, W. T. Pockman, J. E. Johnson, and E. E. Small. 2013. "Effects of Experimental Rainfall Manipulations on Chihuahuan Desert Grassland and Shrubland Plant Communities." *Oecologia* 172(4): 1117–27. https://doi.org/10.1007/s00442-012-2552-0.

Balch, J. K., B. A. Bradley, C. M. D'Antonio, and J. Gómez-Dans. 2013. "Introduced Annual Grass Increases Regional Fire Activity across the Arid Western USA (1980–2009)." *Global Change Biology* 19(1): 173–183. https://doi.org/10.1111/gcb.12046.

Batbaatar, A., C. N. Carlyle, E. W. Bork, S. X. Chang, and J. F. Cahill, Jr. 2022. "Multi-Year Drought Alters Plant Species Composition More than Productivity across Northern Temperate Grasslands." *Journal of Ecology* 110(1): 197–209. https://doi.org/10.1111/1365-2745.13796.

Bennett, J. R., G. Elliott, B. Mellish, L. N. Joseph, A. I. T. Tulloch, W. J. M. Probert, M. M. I. Di Fonzo, J. M. Monks, H. P. Possingham, and R. Maloney. 2014. "Balancing Phylogenetic Diversity and Species Numbers in Conservation Prioritization, Using a Case Study of Threatened Species in New Zealand." *Biological Conservation* 174: 47–54. https://doi.org/10.1016/j.biocon.2014.03.013.

Bloom, A. J., F. S. Chapin, III, and H. A. Mooney. 1985. "Resource Limitation in Plants – An Economic Analogy." *Annual Review of Ecology and Systematics* 16: 363–392. https://doi.org/10.1146/annurev.es.16.110185.002051.

Boeken, B., and D. Orenstein. 2001. "The Effect of Plant Litter on Ecosystem Properties in a Mediterranean Semi-Arid Shrubland." *Journal of Vegetation Science* 12(6): 825–832. https://doi.org/10.2307/3236870.

Bovey, R. W., D. Le Tourneau, and L. C. Erickson. 1961. "The Chemical Composition of Medusahead and Downy Brome." *Weeds* 9(2): 307–311. https://doi.org/10.2307/4040420.

Boyte, S. P., B. K. Wylie, and D. J. Major. 2019. "Validating a Time Series of Annual Grass Percent Cover in the Sagebrush Ecosystem." *Rangeland Ecology and Management* 72(2): 347–359. https://doi.org/10.1016/j.rama.2018.09.004.

Bradley, B. A. 2010. "Assessing Ecosystem Threats from Global and Regional Change: Hierarchical Modeling of Risk to Sagebrush Ecosystems from Climate Change, Land Use and Invasive Species in Nevada, USA." *Ecography* 33(1): 198–208. https://doi.org/10.1111/j.1600-0587.2009.05684.x.

Brummer, F., L. R. Morris, and A. Laarman. 2023. "Forage Quality of *Ventenata dubia* in a Southeastern Oregon Meadow System." *Rangeland Ecology and Management* 91(1): 87–94. https://doi.org/10.1016/j.rama.2023.08.006.

Byrne, K. M. 2021. "Technical Note: A Rapid Method to Estimate Root Production in Grasslands, Shrublands, and Forests." *Rangeland Ecology & Management* 76: 74–77. https://doi.org/10.1016/j.rama.2021.02.004.

Byrne, K. M., P. B. Adler, and W. K. Lauenroth. 2017. "Contrasting Effects of Precipitation Manipulations in Two Great Plains Plant Communities." *Journal of Vegetation Science* 28(2): 238–249. https://doi.org/10.1111/jvs.12486.

Byrne, K. M., W. K. Lauenroth, and P. B. Adler. 2013. "Contrasting Effects of Precipitation Manipulations on Production in Two Sites within the Central Grassland Region, USA." *Ecosystems* 16(6): 1039–51. https://doi.org/10.1007/s10021-013-9666-z.

Byrne, K. M., W. K. Lauenroth, P. B. Adler, and C. M. Byrne. 2011. "Estimating Aboveground Net Primary Production in Grasslands: A Comparison of Nondestructive Methods." *Rangeland Ecology & Management* 64(5): 498–505. https://doi.org/10.2111/REM-D-10-00145.1.

Byrne, K. M., J. C. Luong, and K. K. Kacyzynski. 2025. "Sagebrush Vegetation Response to Experimental Drought." Dataset. Dryad. https://doi.org/10.5061/dryad.0zpc8677v.

Caldwell, M. M., T. E. Dawson, and J. H. Richards. 1998. "Hydraulic Lift: Consequences of Water Efflux from the Roots of Plants." *Oecologia* 113(2): 151–161. https://doi.org/10.1007/s004420050363.

Cardon, Z. G., J. M. Stark, P. M. Herron, and J. A. Rasmussen. 2013. "Sagebrush Carrying out Hydraulic Lift Enhances Surface Soil Nitrogen Cycling and Nitrogen Uptake into Inflorescences." *Proceedings of the National Academy of Sciences of the United States of America* 110(47): 18988–93. https://doi.org/10.1073/pnas.1311314110.

Carroll, C. J. W., I. J. Slette, R. J. Griffin-Nolan, L. E. Baur, A. M. Hoffman, E. M. Denton, J. E. Gray, et al. 2021. "Is a Drought a Drought in Grasslands? Productivity Responses to Different Types of Drought." *Oecologia* 197(4): 1017–26. https://doi.org/10.1007/s00442-020-04793-8.

Copeland, S. M., S. P. Harrison, A. M. Latimer, E. I. Damschen, A. M. Eskelinen, B. Fernandez-Going, M. J. Spasojevic, B. L. Anacker, and J. H. Thorne. 2016. "Ecological Effects of Extreme Drought on Californian Herbaceous Plant Communities." *Ecological Monographs* 86(3): 295–311. https://doi.org/10.1002/ecm.1218.

D'Antonio, C. M., and P. M. Vitousek. 1992. "Biological Invasions by Exotic Grasses, the Grass/Fire Cycle, and Global Change." *Annual Review of Ecology and Systematics* 23(June): 63–87. http://www.jstor.org/stable/2097282.

Davies, K. W., and A. M. Nafus. 2013. "Exotic Annual Grass Invasion Alters Fuel Amounts, Continuity and Moisture Content." *International Journal of Wildland Fire* 22(3): 353–58. https://doi.org/10.1071/WF11161.

Debinski, D. M., H. Wickham, K. Kindscher, J. C. Caruthers, and M. Germino. 2010. "Montane Meadow Change during Drought Varies with Background Hydrologic Regime and Plant Functional Group." *Ecology* 91(6): 1672–81. https://doi.org/10.1890/09-0567.1.

Deutsch, E. S., E. W. Bork, and W. D. Willms. 2010. "Separation of Grassland Litter and Ecosite Influences on Seasonal Soil Moisture and Plant Growth Dynamics." *Plant Ecology* 209(1): 135–145. https://doi.org/10.1007/s11258-010-9729-6.

DiTomaso, J. M. 2000. "Invasive Weeds in Rangelands: Species, Impacts, and Management." *Weed Science* 48(2): 255–265. https://doi.org/10.1614/0043-1745(2000)048[0255:IWIRSI]2.0.CO;2.

Drenovsky, R. E., A. Khasanova, and J. J. James. 2012. "Trait Convergence and Plasticity among Native and Invasive Species in Resource-Poor Environments." *American Journal of Botany* 99(4): 629–639. https://doi.org/10.3732/ajb.1100417.

Evans, S. E., K. M. Byrne, W. K. Lauenroth, and I. C. Burke. 2011. "Defining the Limit to Resistance in a Drought-Tolerant Grassland: Long-Term Severe Drought Significantly Reduces the Dominant Species and Increases Ruderals." *Journal of Ecology* 99(6): 1500–1507. https://doi.org/10.1111/j.1365-2745.2011.01864.x.

Facelli, J. M., and S. T. A. Pickett. 1991. "Plant Litter: Its Dynamics and Effects on Plant Community Structure." *Botanical Review* 57(1): 1–32. https://doi.org/10.1007/BF02858763.

Fernandez-Going, B. M., B. L. Anacker, and S. P. Harrison. 2012. "Temporal Variability in California Grasslands: Soil Type and Species Functional Traits Mediate Response to Precipitation." *Ecology* 93(9): 2104–14. https://doi.org/10.1890/11-2003.1.

Fernández-Guisuraga, J. M., L. Calvo, P. M. Fernandes, A. Hulet, B. Perryman, B. Schultz, K. S. Jensen, et al. 2023. "Estimates of Fine Fuel Litter Biomass in the Northern Great Basin Reveal Increases during Short Fire-Free Intervals Associated with Invasive Annual Grasses." *Science of the Total Environment* 860: 160634. https://doi.org/10.1016/j.scitotenv.2022.160634.

Foster, D., F. Swanson, J. Aber, I. Burke, N. Brokaw, D. Tilman, and A. Knapp. 2003. "The Importance of Land-Use Legacies to Ecology and Conservation." *BioScience* 53(1): 77–88. https://doi.org/10.1641/0006-3568(2003)053[0077:TIOLUL]2.0.CO;2.

Francis, J. K. 2004. *Wildland Shrubs of the United States and its Territories: Thamnic Descriptions*, Vol. 1. San Juan: Fort Collins, CO. https://doi.org/10.2737/IITF-GTR-26.

Frank, D. A. 2007. "Drought Effects on Above- and Belowground Production of a Grazed Temperate Grassland Ecosystem." *Oecologia* 152(1): 131–39. https://doi.org/10.1007/s00442-006-0632-8.

Frank, D. A., A. W. Pontes, E. M. Maine, J. Caruana, R. Raina, S. Raina, and J. D. Fridley. 2010. "Grassland Root Communities: Species Distributions and How They Are Linked to Aboveground Abundance." *Ecology* 91(11): 3201–9. https://doi.org/10.1890/09-1831.1.

Gao, J., L. Zhang, Z. Tang, and S. Wu. 2019. "A Synthesis of Ecosystem Aboveground Productivity and its Process Variables under Simulated Drought Stress." *Journal of Ecology* 107(6): 2519–31. https://doi.org/10.1111/1365-2745.13218.

Garbowski, M., D. B. Johnston, D. V. Baker, and C. S. Brown. 2021. "Invasive Annual Grass Interacts with Drought to Influence Plant Communities and Soil Moisture in Dryland Restoration." *Ecosphere* 12(3): e03417. https://doi.org/10.1002/ecs2.3417.

García-Camacho, R., J. A. J. Metz, M. C. Bilton, and K. Tielbörger. 2017. "Phylogenetic Structure of Annual Plant Communities along an Aridity Gradient. Interacting Effects of Habitat Filtering and Shifting Plant-Plant Interactions." *Israel Journal of Plant Sciences* 64: 122–134. https://doi.org/10.1080/07929978.2017.1288477.

Gilbert, G. S., and I. M. Parker. 2016. "The Evolutionary Ecology of Plant Disease: A Phylogenetic Perspective." *Annual Review of Phytopathology* 54(1): 549–578. https://doi.org/10.1146/annurev-phyto-102313-045959.

Gilbert, G. S., and I. M. Parker. 2022. "Phylogenetic Distance Metrics for Studies of Focal Species in Communities: Quantiles and Cumulative Curves." *Diversity* 14(521): 1–15. https://doi.org/10.3390/d14070521.

Going, B. M., J. Hillerislambers, and J. M. Levine. 2009. "Abiotic and Biotic Resistance to Grass Invasion in Serpentine Annual Plant Communities." *Oecologia* 159(4): 839–847. https://doi.org/10.1007/s00442-008-1264-y.

Goodhue, D., W. Lewis, and R. Thompson. 2007. "Research Note—Statistical Power in Analyzing Interaction Effects: Questioning the Advantage of PLS with Product Indicators." *Information Systems Research* 18(2): 211–227. https://doi.org/10.1287/isre.1070.0123.

Griffin-Nolan, R. J., D. M. Blumenthal, S. L. Collins, T. E. Farkas, A. M. Hoffman, K. E. Mueller, T. W. Ocheltree, M. D. Smith, K. D. Whitney, and A. K. Knapp. 2019. "Shifts in Plant Functional Composition Following Long-Term Drought in Grasslands." *Journal of Ecology* 107(5): 2133–48. https://doi.org/10.1111/1365-2745.13252.

Grime, J. P., V. K. Brown, K. Thompson, G. J. Masters, S. H. Hillier, I. P. Clarke, A. P. Askew, D. Corker, and J. P. Kielty. 2000. "The Response of Two Contrasting Limestone Grasslands to Simulated Climate Change." *Science* 289(5480): 762–65. https://doi.org/10.1126/science.289.5480.762.

Harrison, S. P., E. S. Gornish, and S. Copeland. 2015. "Climate-Driven Diversity Loss in a Grassland Community." *Proceedings of the National Academy of Sciences of the United States of America* 112(28): 8672–77. https://doi.org/10.1073/pnas.1502074112.

Harte, J., S. R. Saleska, and C. Levy. 2015. "Convergent Ecosystem Responses to 23-Year Ambient and Manipulated Warming Link Advancing Snowmelt and Shrub Encroachment to Transient and Long-Term Climate–Soil Carbon Feedback." *Global Change Biology* 21(6): 2349–56. https://doi.org/10.1111/gcb.12831.

Haugum, S. V., P. Thorvaldsen, V. Vandvik, and L. G. Velle. 2021. "Coastal Heathland Vegetation Is Surprisingly Resistant to Experimental Drought across Successional Stages and Latitude." *Oikos* 130(11): 2015–27. https://doi.org/10.1111/oik.08098.

Holdrege, M. C., K. H. Beard, and A. Kulmatiski. 2021. "Woody Plant Growth Increases with Precipitation Intensity in a Cold Semiarid System." *Ecology* 102(1): e03212. https://doi.org/10.1002/ecy.3212.

Holguin, J., S. L. Collins, and J. R. McLaren. 2022. "Belowground Responses to Altered Precipitation Regimes in Two Semi-Arid Grasslands." *Soil Biology and Biochemistry* 171: 108725. https://doi.org/10.1016/j.soilbio.2022.108725.

Hoover, D. L., A. K. Knapp, and M. D. Smith. 2014. "Resistance and Resilience of a Grassland Ecosystem to Climate Extremes." *Ecology* 95(9): 2646–56. http://www.jstor.org/stable/43494493.

Hoover, D. L., K. R. Wilcox, and K. E. Young. 2018. "Experimental Droughts with Rainout Shelters: A Methodological Review." *Ecosphere* 9(1): e02088. https://doi.org/10.1002/ecs2.2088.

Huenneke, L. F., S. P. Hamburg, R. Koide, H. A. Mooney, and P. M. Vitousek. 1990. "Effects of Soil Resources on Plant Invasion and Community Structure in Californian Serpentine Grassland." *Ecology* 71(2): 478–491. https://doi.org/10.2307/1940302.

Huxman, T. E., M. D. Smith, P. A. Fay, A. K. Knapp, M. R. Shaw, M. E. Loik, S. D. Smith, et al. 2004. "Convergence across Biomes to a Common Rain-Use Efficiency." *Nature* 429(6992): 651–54. https://doi.org/10.1038/nature02561.

Jackson, R. B., J. Canadell, J. R. Ehleringer, H. A. Mooney, O. E. Sala, and E. D. Schulze. 1996. "A Global Analysis of Root Distributions for Terrestrial Biomes." *Oecologia* 108(3): 389–411. https://doi.org/10.1007/BF00333714.

Jentsch, A., J. Kreyling, M. Elmer, E. Gellesch, B. Glaser, K. Grant, R. Hein, et al. 2011. "Climate Extremes Initiate Ecosystem-Regulating Functions while Maintaining Productivity." *Journal of Ecology* 99(3): 689–702. https://doi.org/10.1111/j.1365-2745.2011.01817.x.

Karban, R., and E. Pezzola. 2017. "Effects of a Multi-Year Drought on a Drought-Adapted Shrub, *Artemisia tridentata*." *Plant Ecology* 218(5): 547–554. https://doi.org/10.1007/s11258-017-0710-5.

Knapp, A. K., M. L. Avolio, C. Beier, C. J. W. Carroll, S. L. Collins, J. S. Dukes, L. H. Fraser, et al. 2017. "Pushing Precipitation to the Extremes in Distributed Experiments: Recommendations for Simulating Wet and Dry Years." *Global Change Biology* 23(5): 1774–82. https://doi.org/10.1111/gcb.13504.

Knapp, A. K., C. J. W. Carroll, E. M. Denton, K. J. La Pierre, S. L. Collins, and M. D. Smith. 2015. "Differential Sensitivity to Regional-Scale Drought in Six Central US Grasslands." *Oecologia* 177(4): 949–957. https://doi.org/10.1007/s00442-015-3233-6.

Knapp, A. K., D. L. Hoover, K. R. Wilcox, M. L. Avolio, S. E. Koerner, K. J. La Pierre, M. E. Loik, Y. Luo, O. E. Sala, and M. D. Smith. 2015. "Characterizing Differences in Precipitation Regimes of Extreme Wet and Dry Years: Implications for Climate Change Experiments." *Global Change Biology* 21(7): 2624–33. https://doi.org/10.1111/gcb.12888.

Kolb, K. J., and J. S. Sperry. 1999. "Differences in Drought Adaptation between Sub-Species of Sagebrush (*Artemesia tridentata*)." *Ecology* 80(7): 2373–84. https://doi.org/10.1890/0012-9658(1999)080[2373:DIDABS]2.0.CO;2.

Kooyers, N. J. 2015. "The Evolution of Drought Escape and Avoidance in Natural Herbaceous Populations." *Plant Science* 234: 155–162. https://doi.org/10.1016/j.plantsci.2015.02.012.

Kreyling, J., M. A. S. A. Khan, F. Sultana, W. Babel, C. Beierkuhnlein, T. Foken, J. Walter, and A. Jentsch. 2017. "Drought Effects in Climate Change Manipulation Experiments: Quantifying the Influence of Ambient Weather Conditions and Rain-out Shelter Artifacts." *Ecosystems* 20(2): 301–315. https://doi.org/10.1007/s10021-016-0025-8.

Kulmatiski, A., P. B. Adler, J. M. Stark, and A. T. Tredennick. 2017. "Water and Nitrogen Uptake Are Better Associated with Resource Availability than Root Biomass." *Ecosphere* 8(3): e01738. https://doi.org/10.1002/ecs2.1738.

LaForgia, M. L., S. P. Harrison, and A. M. Latimer. 2020. "Invasive Species Interact with Climatic Variability to Reduce Success of Natives." *Ecology* 101(6): e03022. https://doi.org/10.1002/ecy.3022.

Letts, M. G., D. R. E. Johnson, and C. A. Coburn. 2010. "Drought Stress Ecophysiology of Shrub and Grass Functional Groups on Opposing Slope Aspects of a Temperate Grassland Valley." *Botany* 88(9): 850–866. http://10.0.4.115/B10-054.

Li, D., J. E. D. Miller, and S. Harrison. 2019. "Climate Drives Loss of Phylogenetic Diversity in a Grassland Community." *Proceedings of the National Academy of Sciences of the United States of America* 116(40): 19989–94. https://doi.org/10.1073/pnas.1912247116.

Liu, H., Q. Xu, P. He, L. S. Santiago, K. Yang, and Q. Ye. 2015. "Strong Phylogenetic Signals and Phylogenetic Niche Conservatism in Ecophysiological Traits across Divergent Lineages of Magnoliaceae." *Scientific Reports* 5: 1–12. https://doi.org/10.1038/srep12246.

Loik, M. E., D. D. Breshears, W. K. Lauenroth, and J. Belnap. 2004. "A Multi-Scale Perspective of Water Pulses in Dryland Ecosystems: Climatology and Ecohydrology of the Western USA." *Oecologia* 141(2): 269–281. https://doi.org/10.1007/s00442-004-1570-y.

Loik, M. E., J. C. Lesage, T. M. Brown, and D. O. Hastings. 2019. "Drought-Net Rainfall Shelters Did Not Cause Nondrought Effects on Photosynthesis for California Central Coast Plants." *Ecohydrology* 12(7): e2138. https://doi.org/10.1002/eco.2138.

Losos, J. B. 2008. "Phylogenetic Niche Conservatism, Phylogenetic Signal and the Relationship between Phylogenetic Relatedness and Ecological Similarity among Species." *Ecology Letters* 11(10): 995–1003. https://doi.org/10.1111/j.1461-0248.2008.01229.x.

Loydi, A., R. L. Eckstein, A. Otte, and T. W. Donath. 2013. "Effects of Litter on Seedling Establishment in Natural and Semi-Natural Grasslands: A Meta-Analysis." *Journal of Ecology* 101(2): 454–464. https://doi.org/10.1111/1365-2745.12033.

Luong, J. C., K. D. Holl, and M. E. Loik. 2021. "Leaf Traits and Phylogeny Explain Plant Survival and Community Dynamics in Response to Extreme Drought in a Restored Coastal Grassland." *Journal of Applied Ecology* 58(8): 1670–80. https://doi.org/10.1111/1365-2664.13909.

Luong, J. C., and M. E. Loik. 2022. "Adjustments in Physiological and Morphological Traits Suggest Drought-Induced Competitive Release of Some California Plants." *Ecology and Evolution* 12(4): e8773. https://doi.org/10.1002/ece3.8773.

Magliano, P. N., R. Giménez, J. Houspanossian, R. A. Páez, M. D. Nosetto, R. J. Fernández, and E. G. Jobbágy. 2017. "Litter Is More Effective than Forest Canopy Reducing Soil Evaporation in Dry Chaco Rangelands." *Ecohydrology* 10(7): e1879. https://doi.org/10.1002/eco.1879.

Manea, A., D. R. Sloane, and M. R. Leishman. 2016. "Reductions in Native Grass Biomass Associated with Drought Facilitates the Invasion of an Exotic Grass into a Model Grassland System." *Oecologia* 181(1): 175–183. https://doi.org/10.1007/s00442-016-3553-1.

Marqués, L., D. M. P. Peltier, J. J. Camarero, M. A. Zavala, J. Madrigal-González, G. Sangüesa-Barreda, and K. Ogle. 2022. "Disentangling the Legacies of Climate and Management on Tree Growth." *Ecosystems* 25(1): 215–235. https://doi.org/10.1007/s10021-021-00650-8.

Matos, I. S., I. O. Menor, S. W. Rifai, and B. H. Pimentel Rosado. 2020. "Deciphering the Stability of Grassland Productivity in Response to Rainfall Manipulation Experiments." *Global Ecology and Biogeography* 29(3): 558–572. https://doi.org/10.1111/geb.13039.

Mausolf, K., W. Härdtle, K. Jansen, B. M. Delory, D. Hertel, C. Leuschner, V. M. Temperton, G. von Oheimb, and A. Fichtner. 2018. "Legacy Effects of Land-Use Modulate Tree Growth Responses to Climate Extremes." *Oecologia* 187(3): 825–837. https://www.jstor.org/stable/48719069.

Miller, R. F., S. T. Knick, D. A. Pyke, C. W. Meinke, S. E. Hanser, M. J. Wisdom, and A. L. Hild. 2011. "*Characteristics of Sagebrush Habitats and Limitations to Long-Term Conservation*." Greater Sage-Grouse. Berkeley, CA: University of California Press. https://doi.org/10.1525/california/9780520267114.003.0011.

Mojzes, A., G. Ónodi, B. Lhotsky, T. Kalapos, and G. Kröel-Dulay. 2020. "Experimental Drought Indirectly Enhances the Individual Performance and the Abundance of an Invasive Annual Weed." *Oecologia* 193(3): 571–581. https://doi.org/10.1007/s00442-020-04711-y.

Monnet, A. C., F. Jiguet, C. N. Meynard, D. Mouillot, N. Mouquet, W. Thuiller, and V. Devictor. 2014. "Asynchrony of Taxonomic, Functional and Phylogenetic Diversity in Birds." *Global Ecology and Biogeography* 23(7): 780–88. https://doi.org/10.1111/geb.12179.

Naeem, S. 2016. "Biodiversity as a Goal and Driver of Restoration 5789." In *Foundations of Restoration Ecology*, 2nd ed., edited by M. A. Palmer, J. B. Zedler, and D. A. Falk. Covelo, CA: Island Press.

Nagy, R. C., E. J. Fusco, J. K. Balch, J. T. Finn, A. Mahood, J. M. Allen, and B. A. Bradley. 2021. "A Synthesis of the Effects of Cheatgrass Invasion on US Great Basin Carbon Storage." *Journal of Applied Ecology* 58(2): 327–337. https://doi.org/10.1111/1365-2664.13770.

Neumann, R. B., and Z. G. Cardon. 2012. "The Magnitude of Hydraulic Redistribution by Plant Roots: A Review and Synthesis of Empirical and Modeling Studies." *New Phytologist* 194(2): 337–352. https://doi.org/10.1111/j.1469-8137.2012.04088.x.

Nunes, A. M., and K. M. Byrne. 2022. "Drought and Shrub Cover Differentially Affect Seed Bank Composition within Two Sagebrush Steppe Communities." *Journal of Arid Environments* 202: 104752. https://doi.org/10.1016/j.jaridenv.2022.104752.

Oksanen, A. J., F. G. Blanchet, M. Friendly, R. Kindt, P. Legendre, D. Mcglinn, and P. R. Minchin. 2018. "Vegan: Community Ecology Package."

Parker, I. M., M. Saunders, M. Bontrager, A. P. Weitz, R. Hendricks, R. Magarey, K. Suiter, and G. S. Gilbert. 2015. "Phylogenetic Structure and Host Abundance Drive Disease Pressure in Communities." *Nature* 520: 542–44. https://doi.org/10.1038/nature14372.

Pearson, D. E., Y. K. Ortega, J. B. Runyon, and J. L. Butler. 2016. "Secondary Invasion: The Bane of Weed Management." *Biological Conservation* 197: 8–17. https://doi.org/10.1016/j.biocon.2016.02.029.

Perring, M. P., P. De Frenne, L. Baeten, S. L. Maes, L. Depauw, H. Blondeel, M. M. Carón, and K. Verheyen. 2016. "Global Environmental Change Effects on Ecosystems: The Importance of Land-Use Legacies." *Global Change Biology* 22(4): 1361–71. https://doi.org/10.1111/gcb.13146.

Ploughe, L. W., E. M. Jacobs, G. S. Frank, S. M. Greenler, M. D. Smith, and J. S. Dukes. 2019. "Community Response to Extreme Drought (CRED): A Framework for Drought-Induced Shifts in Plant–Plant Interactions." *New Phytologist* 222(1): 52–69. https://doi.org/10.1111/nph.15595.

Poore, R. E., C. A. Lamanna, J. J. Ebersole, and B. J. Enquist. 2009. "Controls on Radial Growth of Mountain Big Sagebrush and Implications for Climate Change." *Western North American Naturalist* 69(4): 556–562. https://doi.org/10.3398/064.069.0416.

Puritty, C. E., E. H. Esch, S. P. Castro, E. M. Ryan, D. A. Lipson, and E. E. Cleland. 2019. "Drought in Southern California Coastal Sage Scrub Reduces Herbaceous Biomass of Exotic Species More than Native Species, but Exotic Growth Recovers Quickly When Drought Ends." *Plant Ecology* 220(2): 151–169. https://doi.org/10.1007/s11258-019-00912-5.

R Core Team. 2020. *R: A Language and Environment for Statistical Computing*. Vienna: R Foundation for Statistical Computing.

Reynolds, H. L., B. A. Hungate, F. S. Chapin, and C. M. D'Antonio. 1997. "Soil Heterogeneity and Plant Competition in an Annual Grassland." *Ecology* 78(7): 2076–90. https://doi.org/10.2307/2265946.

Richards, J. H., and M. M. Caldwell. 1987. "Hydraulic Lift: Substantial Nocturnal Water Transport between Soil Layers by *Artemisia tridentata* Roots." *Oecologia* 73(4): 486–89. http://www.jstor.org/stable/4218396.

Robroek, B. J. M., V. E. J. Jassey, R. J. Payne, M. Martí, L. Bragazza, A. Bleeker, A. Buttler, et al. 2017. "Taxonomic and Functional Turnover Are Decoupled in European Peat Bogs." *Nature Communications* 8(1): 1161. https://doi.org/10.1038/s41467-017-01350-5.

Ross, M. 2022. "Response and Recovery of Grassland Plant Communities Exposed To Multiyear Drought Differs Across a Precipitation Gradient." Master's thesis, Colorado State University, Fall 2022. https://hdl.handle.net/10217/235989.

Rurangwa, M. L., J. Aguirre-Gutiérrez, T. J. Matthews, P. Niyigaba, J. P. Wayman, J. A. Tobias, and R. J. Whittaker. 2021. "Effects of Land-Use Change on Avian Taxonomic, Functional and Phylogenetic Diversity in a Tropical Montane Rainforest." *Diversity and Distributions* 27(9): 1732–46. https://doi.org/10.1111/ddi.13364.

Sala, O. E., L. A. Gherardi, L. Reichmann, E. Jobbágy, and D. Peters. 2012. "Legacies of Precipitation Fluctuations on Primary Production: Theory and Data Synthesis." *Philosophical Transactions of the Royal Society B: Biological Sciences* 367(1606): 3135–44. https://doi.org/10.1098/rstb.2011.0347.

Schwinning, S., and J. R. Ehleringer. 2001. "Water Use Trade-Offs and Optimal Adaptations to Pulse-Driven Arid Ecosystems." *Journal of Ecology* 89(3): 464–480. https://doi.org/10.1046/j.1365-2745.2001.00576.x.

Slette, I. J., D. L. Hoover, M. D. Smith, and A. K. Knapp. 2022. "Repeated Extreme Droughts Decrease Root Production, but Not the Potential for Post-Drought Recovery of Root Production, in a Mesic Grassland." *Oikos* 2023(1): e08899. https://doi.org/10.1111/oik.08899.

Slette, I. J., A. K. Post, M. Awad, T. Even, A. Punzalan, S. Williams, M. D. Smith, and A. K. Knapp. 2019. "How Ecologists Define Drought, and Why We Should Do Better." *Global Change Biology* 25(10): 3193–3200. https://doi.org/10.1111/gcb.14747.

Smith, J. T., B. W. Allred, C. S. Boyd, K. W. Davies, M. O. Jones, A. R. Kleinhesselink, J. D. Maestas, S. L. Morford, and D. E. Naugle. 2022. "The Elevational Ascent and Spread of Exotic Annual Grass Dominance in the Great Basin, USA." *Diversity and Distributions* 28(1): 83–96. https://doi.org/10.1111/ddi.13440.

Smith, M. D., A. K. Knapp, and S. L. Collins. 2009. "A Framework for Assessing Ecosystem Dynamics in Responseto Chronic Resource Alterations Induced by Global Change." *Ecology* 90(12): 3279–89. https://doi.org/10.1890/08-1815.1.

Smith, M. D., K. D. Wilkins, M. C. Holdrege, P. Wilfahrt, S. L. Collins, A. K. Knapp, O. E. Sala, et al. 2024. "Extreme Drought Impacts Have Been Underestimated in Grasslands and Shrublands Globally." *Proceedings of the National Academy of Sciences of the United States of America* 121(4): e2309881120. https://doi.org/10.1073/pnas.2309881120.

Snyder, K. A., L. Evers, J. C. Chambers, J. Dunham, J. B. Bradford, and M. E. Loik. 2019. "Effects of Changing Climate on the Hydrological Cycle in Cold Desert Ecosystems of the Great Basin and Columbia Plateau." *Rangeland Ecology & Management* 72(1): 1–12. https://doi.org/10.1016/j.rama.2018.07.007.

Still, S. M., and B. A. Richardson. 2015. "Projections of Contemporary and Future Climate Niche for Wyoming Big Sagebrush (*Artemisia tridentata* subsp. *wyomingensis*): A Guide for Restoration." *Natural Areas Journal* 35(1): 30–43. https://doi.org/10.3375/043.035.0106.

Tielbörger, K., M. C. Bilton, J. Metz, J. Kigel, C. Holzapfel, E. Lebrija-Trejos, I. Konsens, H. A. Parag, and M. Sternberg. 2014. "Middle-Eastern Plant Communities Tolerate 9 Years of Drought in a Multi-Site Climate Manipulation Experiment." *Nature Communications* 5(1): 5102. https://doi.org/10.1038/ncomms6102.

Tortorelli, C. M., J. B. Kim, N. M. Vaillant, K. Riley, A. Dye, T. C. Nietupski, K. C. Vogler, et al. 2023. "Feeding the Fire: Annual Grass Invasion Facilitates Modeled Fire Spread across Inland Northwest Forest-Mosaic Landscapes." *Ecosphere* 14(2): e4413. https://doi.org/10.1002/ecs2.4413.

Tortorelli, C. M., M. A. Krawchuk, and B. K. Kerns. 2020. "Expanding the Invasion Footprint: *Ventenata dubia* and Relationships to Wildfire, Environment, and Plant Communities in the Blue Mountains of the Inland Northwest, USA." *Applied Vegetation Science* 23(4): 562–574. https://doi.org/10.1111/avsc.12511.

Tredennick, A. T., A. R. Kleinhesselink, J. B. Taylor, and P. B. Adler. 2018. "Ecosystem Functional Response across Precipitation Extremes in a Sagebrush Steppe." *PeerJ* 6: e4485. https://doi.org/10.7717/peerj.4485.

Van Auken, O. W. 2009. "Causes and Consequences of Woody Plant Encroachment into Western North American Grasslands." *Journal of Environmental Management* 90(10): 2931–42. https://doi.org/10.1016/j.jenvman.2009.04.023.

van Staalduinen, M. A., and N. P. R. Anten. 2005. "Differences in the Compensatory Growth of Two Co-Occurring Grass Species in Relation to Water Availability." *Oecologia* 146(2): 190–99. https://doi.org/10.1007/s00442-005-0225-y.

Verdu, M., L. Gomez-Aparicio, and A. Valiente-Banuet. 2012. "Phylogenetic Relatedness as a Tool in Restoration Ecology: A Meta-Analysis." *Proceedings of the Royal Society B: Biological Sciences* 279(1734): 1761–67. https://doi.org/10.1098/rspb.2011.2268.

Verheyen, K. 2022. "Land-Use Legacies Predispose the Response of Trees to Drought in Restored Forests." *Global Change Biology* 28(4): 1204–11. https://doi.org/10.1111/gcb.15983.

Vicca, S., A. K. Gilgen, M. Camino Serrano, F. E. Dreesen, J. S. Dukes, M. Estiarte, S. B. Gray, et al. 2012. "Urgent Need for a Common Metric to Make Precipitation Manipulation Experiments Comparable." *New Phytologist* 195(3): 518–522. https://doi.org/10.1111/j.1469-8137.2012.04224.x.

Warter, M. M., M. B. Singer, M. O. Cuthbert, D. Roberts, K. K. Caylor, R. Sabathier, and J. Stella. 2021. "Drought Onset and Propagation into Soil Moisture and Grassland Vegetation Responses during the 2012-2019 Major Drought in Southern California." *Hydrology and Earth System Sciences* 25(6): 3713–29. https://doi.org/10.5194/hess-25-3713-2021.

Webb, C. O., D. D. Ackerly, and S. W. Kembel. 2008. "Phylocom: Software for the Analysis of Phylogenetic Community Structure and Trait Evolution." *Bioinformatics* 24(18): 2098–2100. https://doi.org/10.1093/bioinformatics/btn358.

West, N. E., and J. A. Young. 2000. In *North American Terrestrial Vegetation*, edited by M. G. Barbour and W. D. Billings. New York, NY: Cambridge University Press.

Whisenant, S. G. 1990. "Postfire Population Dynamics of *Bromus japonicus*." *The American Midland Naturalist* 123(2): 301–8. https://doi.org/10.2307/2426558.

Wickham, H. 2020. "Package 'Plyr'. Tools for Splitting, Applying and Combining Data."

Wickham, H., W. Chang, L. Henry, T. L. Pedersen, K. Takahashi, C. Wilke, K. Woo, and RStudio. 2018. "Create Elegant Data Visualisations Using the Grammar of Graphics Description."

Wilcox, K. R., Z. Shi, L. A. Gherardi, N. P. Lemoine, S. E. Koerner, D. L. Hoover, E. Bork, et al. 2017. "Asymmetric Responses of Primary Productivity to Precipitation Extremes: A Synthesis of Grassland Precipitation Manipulation Experiments." *Global Change Biology* 23(10): 4376–85. https://doi.org/10.1111/gcb.13706.

Wilke, C. O. 2020. "Cowplot: Streamlined Plot Theme and Plot Annotations for 'Ggplot2'."

Wolkovich, E. M., D. T. Bolger, and K. L. Cottingham. 2009. "Invasive Grass Litter Facilitates Native Shrubs through Abiotic Effects." *Journal of Vegetation Science* 20(6): 1121–32. https://doi.org/10.1111/j.1654-1103.2009.01110.x.

Wu, Z., P. Dijkstra, G. W. Koch, J. Peñuelas, and B. A. Hungate. 2011. "Responses of Terrestrial Ecosystems to Temperature and Precipitation Change: A Meta-Analysis of Experimental Manipulation." *Global Change Biology* 17(2): 927–942. https://doi.org/10.1111/j.1365-2486.2010.02302.x.

Yachi, S., and M. Loreau. 1999. "Biodiversity and Ecosystem Productivity in a Fluctuating Environment: The Insurance Hypothesis." *Proceedings of the National Academy of Sciences of the United States of America* 96: 1463–68. https://doi.org/10.1073/pnas.96.4.1463.

Yahdjian, L., and O. E. Sala. 2002. "A Rainout Shelter Design for Intercepting Different Amounts of Rainfall." *Oecologia* 133(2): 95–101. https://doi.org/10.1007/s00442-002-1024-3.

SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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